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Evolving Hierarchical Visually Guided Neural Network Agents to Investigate Complex Interactions

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A thesis submitted for the degree of

Doctor of Philosophy

of the

University of London

The Institute of Ophthalmology
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2007

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Abstract

A complex system is a system with a large number of interacting components without any mechanism for central control that displays self organisation. Understanding how these interactions affect the overall behaviour of a system is of great interest to science. Indeed, researchers use a wide variety of models to investigate complex systems.

The problem with most models is that they disregard the hierarchical nature of complex systems: they ignore the fact that components of real world systems tend to be complex systems as well. This prevents researchers from investigating the interactions taking place between the lower and the higher levels of the model which may be crucial in order to gain a full understanding of the examined phenomena and of complex systems in general. Therefore, this thesis introduces Mosaic World, a multi-agent model for the purpose of investigating interactions (focusing on 'complex' multilevel interactions) within a hierarchical complex system, in addition to other computational and biological hypotheses. Mosaic World comprises a population of evolving neural network agents that inhabit a changing visual environment.

By analysing the interactions that occur within Mosaic World, this thesis demonstrates the importance of incorporating hierarchical complexity into a model, and contributes to our understanding of hierarchical complex systems by showing how selective pressures cause differentiation across levels. Additionally, the study of multilevel interactions is used to probe several hypotheses and provides the following contributions among others:

- Analysis of agent evolvability as affected by the usage of different types of structural mutations in the evolutionary process.
- Demonstration that agents controlled by modular neural networks are fitter than agents that are controlled by non-modular neural networks; the improvement in fitness occurs through specialisation of modules.
- Empirical support for a biological theory suggesting that colour vision evolved as a method of dealing with ambiguous stimuli.

Acknowledgements

First of all, I would like to thank my supervisors: Peter Bentley for his dedicated supervision over the past few years, for going beyond the 'call of duty' and reading countless thesis versions, and for helping me navigate the often impossible looking maze of thesis write-up: all this while providing constant encouragement and affirmation of my achievements. Beau Lotto, for taking me on as a student and giving me the freedom to pursue my interests, for all the help and support during the past few years, and of course, for coming up with the original idea of Mosaic World.

I am also grateful to Martina Wicklein, for numerous discussions of science, for comments on the first draft of the thesis, and for her continuous willingness to help in any possible way. Thanks to David Corney for his encouragement, useful comments and discussions on the first draft of the thesis. Thanks to Daniel Hulme, David Malkin and Erwan LeMartelot for stimulating and insightful conversations that greatly contributed to my studies, and for making much of the PhD a lot of fun. Thanks to Karen Bonstein for her assistance and encouragement when it was needed. Thanks to Elena Alvarez-Buylla for numerous conversations that helped me shape my PhD as I was starting. Thanks to Niels van den Brink and Adam Jeayes (and the rest of the Elder Council) for very quickly becoming my good friends after I moved to the UK, and for exciting discussions that kept me sane during a large portion of these four years.

I'd also like to thank the people at the lab (and outside) who made my time enjoyable at UCL: Jamie Theobald, Rich Clarke, Ilias Bergstrom, Nikolai Bogatyrev, Lefkothea Andreou, Hooman Shayani, David Basanta, Ma'ayan Semo, Annelie Maass, Jay Sangha, Nick Burt, Yanai Duran, David Coffin, Wei Yan, Katrin Jonas, Betina Ip, Liat Kolet, Merv Davies, Vy Luong and George Bradley.

Finally, I wish to thank my family: my mother, Rachel, for relentlessly encouraging me to aspire higher and supporting me unconditionally. My father, Joseph, for always encouraging me to pursue science and instilling within me the passion to delve into the nature of things. My brother, Avner, for always being willing to support and help in any possible way, and providing encouragement whenever it was needed. And my son Tom, for providing some interesting (and challenging) times during the write-up process, and for delaying his arrival to

this world as much as he could (I know he had the thesis in mind) – enough to enable me to write the hardest three chapters in peace and quiet.

My most heartfelt thanks go to my beloved wife Karni, whom I owe far more than I could ever express: for encouraging me when I needed cheering, advising me when I needed guidance, and loving me when I needed support. Karni was always there: her love and companionship were the only certainties during these occasionally challenging times. Without her I would not be writing these lines.

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Chapter 1

Introduction

Until the arrival of the field of complex systems to the scientific arena, diverse systems such as the stock market, the weather, an ant-hill and the internet were perceived to have little in common. Throughout the last decade and a half it became increasingly clearer that there are in fact many commonalities between all these types of systems.

Although even now there is still no universal definition of a complex system (see [14, 36, 148, 166] for various definitions), it is possible to state that a complex system is a system with a large number of interacting components without any mechanism for central control. There is no conceptual limit placed on the components: they can be identical – but they do not have to be; they can interact with neighbours or with distant components; they can be simple – or they can be complex systems in their own right. The result is a system that displays self organisation despite the lack of central control. The behaviour of this system is emergent and cannot be normally predicted by looking at the individual components alone.

Even though the list of attributes varies according to the exact definition used, it is commonly accepted that interaction between components is one of the major requirements for a system to be termed a complex system. In fact, interactions may even be the most fundamental aspect:

> “Complex systems cannot be understood by studying parts in isolation. The very essence of the system lies in the interaction between parts and the overall behavior that emerges from the interactions” [166].

These interactions are highly nonlinear; perturbing a single component can potentially affect the entire system.

Understanding how interactions affect the overall behaviour of a system is of great interest to science [15]. The ability to affect or predict the emergent behaviour of certain complex systems could be useful in countless situations ranging from stabilising a problematic economy to helping the immune system fight pathogens. This may be achievable by altering the system in some fashion, for example, by adjusting its interaction with the environment in such a way that affects its emergent behaviour [167].

The methods which researchers use to investigate complex systems can be divided to two main groups [149]. The first includes mathematical models such as nonlinear dynamics, differential equations, game theory and network theory. One weakness of these models is that they only enable deriving aggregate variables – the collective behaviour of many elements – but do not give any indication as to how this aggregate behaviour is linked to the individual behaviour of all the elements, and why [156, 169, 171].

The second group consists of simulations via agent-based models, where the goal is to create models that capture some aspects of the real world [74]. Examples of agent-based models include artificial life models, genetic algorithms, and cellular automata [149, 166]. Generally speaking, it is impossible to simulate every detail of real phenomena if only from a computational point of view; thus, every model designer needs to decide which elements are important and should be included, and which are better to be left out. Although many models are significantly simpler than their real world counterparts, this approach is feasible; using this method, much can be learned about the real world. Nevertheless, the design stage is particularly problematic when modelling complex systems, as one of the fundamental paradigms of this field is that reductionism is not the right approach for investigating complex systems [14, 66, 166] – that the system's overall behaviour emerges from highly nonlinear interactions between potentially all of its components – including ones that may not appear to be important, and so, are possibly likely to be left out.

Perhaps unsurprisingly, there is a fundamental and crucial difference between most current models of complex systems and their real world counterparts. Unlike many computer models, components of real world systems tend to be complex systems as well. In turn, these components may also consist of complex systems. Consequently, interactions going on at the lowest levels may affect the higher levels, and vice versa. More importantly, the emergent whole [83] of a lower level – potentially the result of highly nonlinear and unpredictable interactions – may serve as a component for an emergent whole of the next level.

An example to help illustrate this important point: an ant-hill is a component of its ecosystem, which is a hierarchical complex system. The ant-hill itself is also a hierarchical complex system, one which consists of ants. An individual ant consists of organs. Each of these organs consists of cells. These cells are controlled by the ant's genes. Although the hierarchical structure of complex systems is a well known fact [84, 181], in most computer simulations of an ecosystem, the ant-hill is modelled rather simply, as an elementary component – without modelling the individual ants within, and in most simulations of an ant-hill, the ant is modelled rather simply, without considering its organs. However, in reality both types of 'elementary' components are not elementary, but are complex systems. More importantly, the emergent behaviour of these lower level components (the behaviour of an ant, the collective behaviour of an ant-hill) is an important element of the higher levels – and as stated, these behaviours cannot be easily modelled because of their emergent nature.

Although nested hierarchies are an integral aspect of complex systems, most models neglect to incorporate this aspect into their design. This may be the result of the inherent programmatic difficulty of modelling multiple levels of a hierarchical complex system. Regardless, this flaw causes a reasonable chance of incorrect modelling, particularly of the higher levels of the system (as small inaccuracies in the behaviour of lower levels can accumulate and cause larger inaccuracies in the behaviour of higher levels). Moreover, this prevents researchers from investigating the interactions going on between the lower and the higher levels such as – using the previous example – the effects of different models of ant organs or the evolution of genes that define those organs on the overall behaviour of the ant-hill or even the entire ecosystem.

This flaw in modelling complex systems occurs not only in computational models, but also in conceptual models as well. In fact, the field of economics has been criticised for traditionally ignoring the hierarchical nature of the economy by not attempting to directly link microeconomics and macroeconomics, instead researching each discipline independently [169].

This work argues that incorporating hierarchical complexity may be essential in order to correctly model a system and gain a more comprehensive understanding of the target phenomena; more importantly, the fact that the nested hierarchies aspect of complex systems is mostly disregarded raises the possibility that novel insights about complex systems in general may be obtained by specifically investigating multileveled interactions within a hierarchical complex system model.

In recent years, some models of complex systems were in fact constructed with hierarchical complexity in mind. This is mainly true for models coming from the field of ecology [100, 125, 170, 244] (whose members are fully aware of the importance of maintaining the hierarchical nature of complex systems and of the need to explore the interactions between different levels of the model [100, 170, 244]), but also true for models coming from other fields, such as computer science [123, 203], chemical engineering [127] and economics [224]. Ironically, even though these models are the only ones that can be appropriate for examining multileveled interactions within complex systems, they were mostly created to pursue directions other than complex systems. Therefore, it is the aim of this work to create a model for the purpose of investigating interactions within a hierarchical complex system, with a focus on multileveled interactions. It is believed that this study will contribute to our understanding of complex systems in a new way and improve our ability to predict and affect complex systems in general. Furthermore, by specifically focusing on multilevel interactions in a particular model, it will be possible to gain interesting insights about the modelled phenomena which normally would not appear in most models, thus, demonstrate the importance of incorporating hierarchical complexity into model design.

1.1 Aims and objectives

The main hypothesis of this research can be defined as follows:

It is useful to evolve hierarchical visually guided neural network agents for the purpose of investigating complex interactions.

Where:
The model can be referred to as 'useful' when it enables the demonstration and investigation of behaviours that normally do not appear in simpler, non-hierarchical or less hierarchical models and consequently, provides new insights into complex systems in general.

Hierarchical visually guided neural network agents are artificial agents used in a multi-agent system that are controlled by internal neural networks receiving visual stimuli from a simulated environment.

Complex interactions are defined in this work to:

- *be an information exchange between two or more elements within a hierarchical complex system, at the same or different level, where the interaction causes a modification to one or more of the elements (similar to a concept introduced in [26]).*
- *be affected by small perturbations to the elements or their context, which may cause highly unpredictable or unintuitive effects to the overall behaviour of the system.*
- *take place within a hierarchical system whose emergent results (which can be behaviours or objects) of lower levels can serve as basic components for a higher level (e.g. evolved agents are components of collective aggregates) [83].*

In this thesis, complex interactions will be represented using the ***affecting→affected*** *notation, where* ***affecting*** *interacts with* ***affected.*** *This may indicate that a physical effect* *takes place in the system; in this case,* ***affecting*** *has an effect on* ***affected*** *(e.g. critter→environment means that the environment is changed as a result of the critter consuming a part of it). Alternatively, this notation may indicate that a flow of information takes place in the system; in this case information flows from* ***affecting*** *to* ***affected*** *(e.g. environment→receptor indicates that information from the environment is perceived by a receptor).*

In order to provide evidence towards the hypothesis, the following objectives are defined:

1. Explore biological systems and universal principles in nature that are suitable for investigation using a hierarchical complex system model.

2. Develop a computational multi-agent, hierarchical complex system model, Mosaic World.

3. Identify key interactions in the model, and create accordingly a set of challenges that will focus on each one. Each challenge will consist of a small perturbation to the system or its context; the resulting effect on the interactions will be systematically investigated.

4. Correlate and understand the behaviour of the perturbed aspects of the system (its elements or context) with the results of those interactions in the system as a whole.

5. Demonstrate that incorporating hierarchical complexity into the model can provide an improvement in the understanding of the modelled phenomena, by finding novel observations that could not be made in a non hierarchical or less hierarchical model.

6. Demonstrate that the model can be used to support or refute existing and novel computational and biological hypotheses that cover some or all levels of the model including:
   - The usage of different types of structural mutations will affect the evolvability of neural network agents.
   - Like biological visual systems, physical similarity or behavioural similarity of resources will affect the visual system of evolving virtual agents.
   - Like biological visual systems, increased physical similarity of resources will affect the visual system of evolving virtual agents.
   - The need to deal with ambiguous environments is a possible reason for the evolution of colour vision in nature.

- Evolving virtual agents in environments of various levels of difficulty will result in behaviours that are similar to those encountered in nature under equivalent conditions.
- Virtual agents that are controlled by modular neural networks (specifically, a mixture-of-experts architecture) will be fitter than agents that use non-modular neural networks.
- Predation is sufficient to cause the emergence of multicellularity.
- Accidental aggregation, without any explicit immediate advantages, is sufficient to cause the emergence of multicellularity.
- Significant environmental variation can affect the evolution of morphogenesis.

1.2 Thesis overview

Chapter 2 reviews several topics that are required in order to recognise the problem that is presented in this thesis and the methods used to address this problem. In addition, a useful methodology for creation of models of biological phenomena is provided (and its source cited), which will be used throughout the thesis to justify the design decisions that are made.

Chapter 3 presents Mosaic World, the model which is used for all work in this thesis; this includes a thorough description of the system's components and operation, and also includes a conceptual analysis of the complex interactions that take place within the model.

Chapter 4 begins the investigation of complex interactions by presenting the first challenge to Mosaic World: evolvability. This challenge explores the relationship between agent evolvability and various types of genes→genes interactions by using five different types of structural mutations in the process of evolution.

Chapter 5 presents the colour vision challenge to Mosaic World. This challenge examines the effect of different environments (specifically, environments with various visual characteristics) on the visual evolution of agents that inhabit them (environment→receptor interactions).

Chapter 6 presents the behaviour challenge to Mosaic World. This challenge examines the effect of different environments (specifically, environments of various levels of difficulty) on the evolved behaviours of agents that inhabit them (environment→critter).

Chapter 7 expands the hierarchical nature of Mosaic World by replacing the standard networks used to control agents with modular neural networks. The challenge in this chapter is modular specialisation: by examining in detail the interactions that take place within the new mechanism (control network→module interactions), the effect of utilisation of modularity on agents in terms of fitness and functionality is assessed.

Chapter 8 further expands the hierarchical nature of Mosaic World by creating mechanisms that allow agents to aggregate. In this chapter, the aggregation challenge is presented to Mosaic World: by examining in detail the conditions that are required in order for agents to successfully utilise this mechanism (in terms of the interactions between agents, critter→critter, and the interactions between aggregates and agents, critter→aggregate), insights about the conditions in primordial Earth that triggered the original emergence of multicellularity are gained. In the second part of the chapter, the aggregation challenge is extended by examining whether a new ability of aggregates to change their shape and grow protective shells is utilised when a new environment is added to Mosaic World that provides new benefits but incurs new costs.

Chapter 9 concludes the thesis by summarising the results and describing four observations that can be obtained using this work. In addition, the chapter provides an evaluation of the model and revisits the objectives that were set for the thesis. The chapter concludes by reviewing several possible ways to extend the work described in this thesis.

1.3 Publications

Some of the work in this thesis has been published in the following papers:

Schlessinger, E., Bentley, P. J., and Lotto, R. B. (2006) Investigating the Emergence of Multicellularity Using a Population of Neural Network Agents. *In Proc. of Parallel Problem Solving from Nature (PPSN IX)*, September 9-13, 2006, Reykjavik, Iceland

Schlessinger, E., Bentley, P. J., and Lotto, R. B. (2006) Modular Thinking: Evolving Modular Neural Networks for Visual Guidance of Agents. *In Proc. of Genetic and Evolutionary Computation Conference (GECCO 2006)*, July 8-12, 2006, Seattle, WA

Schlessinger, E., Bentley, P. J., and Lotto, R. B. (2005) Analysing the Evolvability of Neural Network Agents through Structural Mutations. *In Proc. of European Conference on Artificial Life (ECAL 2005)*, September 5-9, 2005, Canterbury, UK

Schlessinger, E., Bentley, P. J., and Lotto, R. B. (2005) Evolving Visually Guided Agents in an Ambiguous Virtual World. *In Proc. of Genetic and Evolutionary Computation Conference (GECCO 2005)*, June 25-29, 2005, Washington, DC.

The following papers are in preparation:

Schlessinger, E. and Lotto, R. B. Is Ambiguity One of the Reasons for the Evolution of Colour Vision?

Schlessinger, E. and Lotto, R. B. Examining the Effects of Increased Resource Similarity on the Visual Evolution of Virtual Agents.

Schlessinger, E. and Lotto, R. B. A Study of the Foraging Behaviour of Virtual Agents Under Several Different Levels of Difficulty and Hunger.

Schlessinger, E., Bentley, P. J., and Lotto, R. B. The evolution of morphology for aggregates of agents.

Chapter 2

Background

In order to investigate complex interactions, a computational multi-agent, hierarchical complex system model has been developed. This chapter provides the relevant background for this work.

In this chapter, the field of complex systems, which is the context for this work, is reviewed, and several examples of work that qualify as investigations of complex interactions are given. In addition, the field of artificial life is presented together with some useful guidelines for building biological models. Since the model described in this thesis focuses on the evolution of neural network agents, relevant background on artificial neural networks, evolutionary computation, and the evolution of artificial neural networks is provided as well.

2.1 Complex Systems

Complex systems can be found everywhere: biological systems (living organisms [14], brains [14], protein folding [14], ant colonies [71, 148], ecosystems [6, 14]), manmade systems (the economy [8], human civilisation [14], traffic jams [128, 187], the internet [6]), natural systems (weather patterns [14]).

Complex systems are systems with many interacting components that display self organisation without any central organiser [6, 29, 148, 149, 166, 167]. Adaptability and robustness are two characteristics that can be used to describe most complex systems: adaptability – some complex systems will continue functioning even if their environment changes [6, 166, 167], and robustness – they may operate even if partially damaged [6, 166].

Complex systems are difficult to understand because they often display emergent global behaviour [148, 167], and thus, are difficult to understand using a reductionist approach – by examining every part in isolation [148, 166, 170]. It has been claimed that the only way to understand a complex system is by examining it as a whole, since the global behaviour of the system is a result of all its components and their interactions [166].

The components of complex systems can have a range of diverse attributes. They may be identical or different; for example, individual cars in a traffic jams are (conceptually) identical, whereas the components of the global economy are diverse and varied. They may be simple building blocks or be complex systems as well; for example, individual air and water molecules in a tornado are simple systems, unlike individual animals in an ecosystem which are complex systems. They may interact with close components or only with distant components; for example, in the economy, two very distant companies – geographically and economically – may trade, whereas in neural networks there has to be a direct connection between neurons for them to interact. They may have a specific role in the system or be interchangeable with other components; if they do have a role, it may be static or dynamic [6]. For example, in a flock of migrating geese, any member of the flock may act as the 'leader', however, individual worker ants in an anthill can never replace their queen.

The interactions that occur within a complex system typically form a complex network [6]. There are numerous possible types of interactions between components in a complex system [149]. These interactions have the potential of being highly nonlinear: a small change to one component may affect the entire system [148, 191]. The connectivity between components is not static and may change: interactions can be added or removed from the system. A pair of interactions may be symmetric (for example, competition among agents on resources in an ecosystem) or asymmetric (such as the interactions that take place between predator and prey) [149]. An interaction may have a cost/limited capacity associated with it (for example, an airport must limit the number of departures/landings per hour for space and time constraints), or an 'age' which sets its removal time (for example, individuals cannot stay in an organisation forever). Finally, there is often a random element affecting the interactions: noise within the system [6].

The field of complex systems aims to discover rules that govern the behaviour of different emergent, self-organising complex systems [6, 148, 167]. So far, it has contributed to evolutionary theory by taking ideas and results from other complex systems in order to better explain evolution (e.g. the concept of "energy landscape" which builds on fitness landscapes) [149]. In addition, the study of complex networks is a prominent subfield of complex systems that has recently discovered certain fundamental laws and organising principles that appear in real world complex networks [15] (for example, the fact that several distinct types of networks, including small world networks and scale free networks, frequently describe the connectivity of real world complex systems; all of which share certain commonalities [6]).

2.1.1 Hierarchical complexity

Real world complex systems frequently exhibit hierarchical complexity: a basic component in one level is often a complex system – an emergent whole [83] – at a lower level. Complex systems may consist of numerous such levels [75, 83, 100, 170, 181]. These levels may have different temporal and spatial scales [181]; for example, behaviours at the higher levels, i.e.

the ecosystem level, take place over larger spatial areas and also happen over larger periods of time than behaviours at lower levels, i.e. the brain of an animal which is a component of the ecosystem. Fig. 2.1 demonstrates a hierarchical complex system within a greater hierarchical complex system; there are a total of four levels in the greater system.

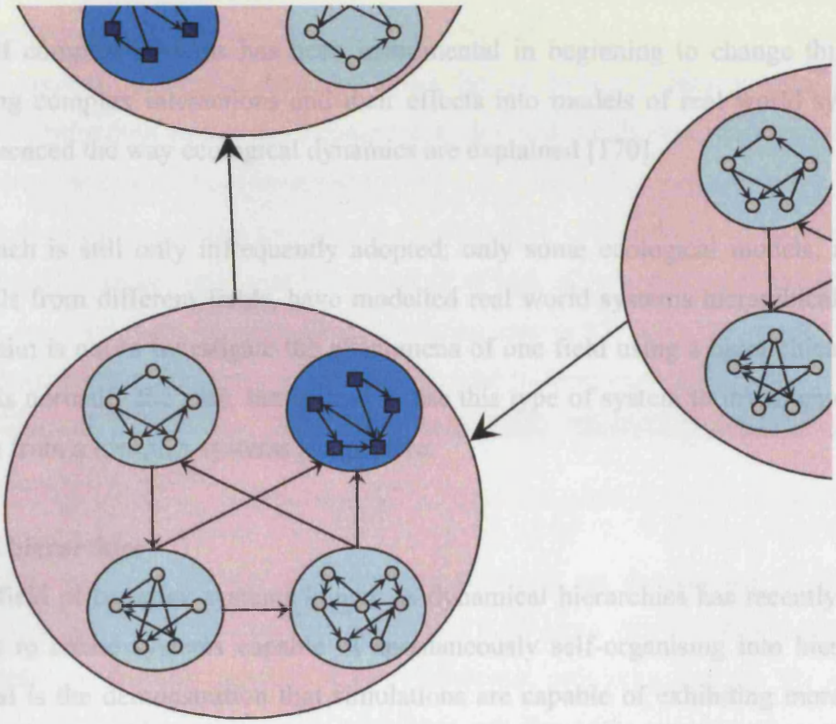


Fig. 2.1: A hierarchical complex system that is characterised by four distinct levels. The basic components of the greater hierarchical complex system (level 4: the entire figure) are the purple circles. Each of the purple circles is a hierarchical complex system in its own right (level 3) which comprises several smaller complex systems (level 2: blue and green circles), which are made up of basic elements (level 1: small circles and squares).

As briefly mentioned in the introduction chapter, a consistent limitation of the majority of investigations of real world complex systems is their focus on a limited range of levels of the model, mostly one, which are assumed to be separate from the other levels [100, 125, 127, 170]; this is obviously an unrealistic assumption, as it is clear that interactions that are initiated by a component at one level may affect the behaviour at other levels [100, 170] (presumably, this approach was taken in order to make the study more feasible [170]). In fact, it is increasingly demonstrated that the behaviour of a hierarchical complex system is a result of numerous nonlinear interactions that take place among components at different levels of the system [170]; this has already resulted in a large number of global ecological phenomena to be reinterpreted as events that are a result of interactions that take place between components at different levels – such as the colonisation within groups in a species [11] and the tendency of organisms within a population to be distributed in a log-normal manner over a terrain [222]. Those interactions that occur within a hierarchical complex system between components at different levels are included in the concept of 'complex interactions' which is introduced in this thesis (and also includes interactions that take place between components at the same level).

The field of complex systems has been instrumental in beginning to change this outlook. Incorporating complex interactions and their effects into models of real world systems has greatly influenced the way ecological dynamics are explained [170].

This approach is still only infrequently adopted; only some ecological models, and a few other models from different fields, have modelled real world systems hierarchically. In this thesis, the aim is not to investigate the phenomena of one field using a hierarchical complex system, as is normally the case, but instead to use this type of system to investigate complex interactions from a complex systems perspective.

Dynamical hierarchies

A new subfield of complex systems known as dynamical hierarchies has recently emerged, which aims to create systems capable of spontaneously self-organising into hierarchies; a specific goal is the demonstration that simulations are capable of exhibiting more than one hierarchical level of emergent structure [21, 75, 124]. However, to this date, models that exhibited more than a single level of emergent structure are rare [124].

According to researchers in this area, in order for a dynamic structure to be considered a new emergent level, it must be demonstrated that new functionalities emerge as a result of the interactions between simpler building blocks (which can be dynamical structures as well) [21, 75]. For example, Prokopenko et al [180] demonstrated a system where a collection of simple sensor cells can form multicellular structures – impact boundaries – which have two new properties: they can be closed and continuous, thus, can be considered to be second level emergent structures. Additionally, these structures can combine in order to enclose spaces, and so, effectively form impact networks which have a new property – a spanning tree topology – thus, can be considered third level emergent structures.

In contrast to the subfield of dynamical hierarchies, where the goal is the dynamical creation of multiple emergent hierarchies, this work focuses on the usage of a hierarchical complex system, which can be emergent, predefined or a mixture of both, in order to investigate complex interactions. Obviously, it is impractical to wait until a model that exhibits multiple dynamical hierarchies is created for the purpose of investigating complex interactions, as this may take quite some time. Therefore, the subfield of dynamical hierarchies is only of limited relevance to the work in this thesis.

2.1.2 Emergence

Emergence is a fundamental concept in complex systems and artificial life research. There are many different definitions of the term, and yet, there does not seem to be one that is universally accepted. A popular definition states that an emergent phenomenon is one that arises from the behaviour of low level components, but is difficult/impossible to predict or to reduce to the properties of those components [29, 148, 149, 157], or similarly, its behaviour cannot be derived by analysing a model of the system [31]. One criticism of these definitions is that the unpredictability may simply be a result of lack of information of the system, and so, it is not an appropriate criterion for determining emergence [29, 59]. Interestingly, this definition implies that an observer is required in order to form expectations about the result: if his expectations are correct, there is no emergence. However, if he is 'surprised', emergence occurs [30, 51, 191].

An alternative definition, which does not change based on the amount of information possessed or availability of an observer, states that emergence occurs when the interactions between many components generate a new behaviour providing that (i) the underlying components are not aware of this new behaviour, and (ii) a new vocabulary is required in order to describe the new behaviour but is not needed to describe the components [218].

Another alternative definition is weaker: emergence is defined as the collective behaviour of many elements that cannot be attributed to a single element [48].

To some extent, all the above definitions attempt to capture a notion that we grasp intuitively, thus, are precise only to a limited degree; consequently, some researchers have pursued more formal definitions of emergence that do not depend on any human descriptions. That said, there is no universal agreement on one formal definition as well.

One approach by Polani, which is based on information-theoretic criteria, attempts to characterise emergence in a way that naturally arises from the inherent structure of the dynamical system, thus, emergent descriptions are defined as a "complete decomposition of the system into independent subsystems which are individually predictable"; these subsystems are seen as "'emerging' from the global system dynamics." [177]. Another approach by Kubík is based on language-theoretic and grammar systems, and defines an emergent property as a one that is generated when a "multiagent system as a whole can generate a language (behaviour) that cannot be generated by the superimposition (summation) of individual agents' languages (behaviors)" [114]. Shalizi argues that emergence has nothing to do with external observers and is an intrinsic and objective quality; thus, he defines emergent processes as processes that have a greater predictive efficiency than the process they are derived from [205], that is, "each bit of macroscopic information delivers more predictive information at the higher levels than the lower ones" [206].

The lack of agreement for the definition of emergence makes any definition arguable. For this thesis, the popular definition is seen as most appropriate:

An emergent phenomenon is one that arises from the behaviour of low level components, but is difficult/impossible to predict or to reduce to the properties of those components [29, 148, 149, 157].

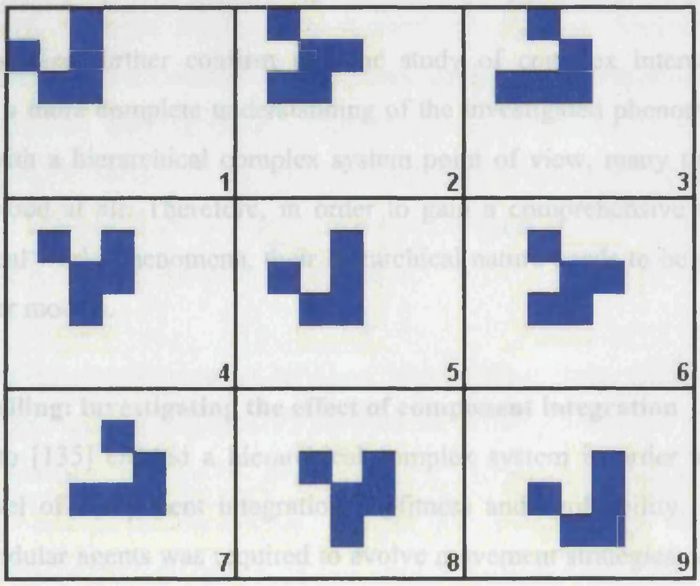


Fig. 2.2: An emergent Glider from Conway's game of life. Using a few simple rules, the object that appears in (1) 'glides' to the lower right in (5) and (9).

Examples of emergence include:

- The coordinated behaviour of a flock of birds emerges from the behaviour of individual birds [19].
- The ability of individual ants to find the shortest path to food sources is an emergent property of the interactions between searching ants [166].
- The fact there are many competing species and not just one is an emergent property of an ecosystem [149].
- The associative memory of the artificial neural network known as the Hopfield network is an emergent property [14].

- Conway's game of life [64] is a famous example of a cellular automata that exhibits emergent life-life behaviours (see fig. 2.2 for an illustration of the Glider object).

2.1.3 Complex interactions

Complex interactions are interactions that take place within a hierarchical complex system between elements at the same or different levels. In hierarchical complex systems, the emergent results of a lower level can serve as components for a higher level.

Since there are virtually no studies that explicitly focus on this area of research, in this section a review of related research that deals with complex interactions is given; unsurprisingly, most of the described work was not conducted within the context of complex systems. Interestingly, as the real world is characterised by an abundance of hierarchical complex systems, this type of research is very diverse and spans many scientific disciplines.

The following studies further confirm that the study of complex interactions is crucial towards gaining a more complete understanding of the investigated phenomena, and in fact, unless viewed with a hierarchical complex system point of view, many times it cannot be correctly understood at all. Therefore, in order to gain a comprehensive understanding of many types of real world phenomena, their hierarchical nature needs to be incorporated into relevant computer models.

Computer modelling: investigating the effect of component integration

Malkin and Lotto [135] created a hierarchical complex system in order to investigate the effect of the level of component integration on fitness and evolvability. In their study, a population of modular agents was required to evolve movement strategies, where the motion of each agent depends on the motion of its components, in order to reach energy sources; the fitter the agent, the more energy it collected. One of the evolvable traits every agent possessed controlled the level of component integration between the modular components, i.e., the degree to which each component affected the behaviour of the overall agent which was comprised by many components.

It was discovered that integrated agents are fitter but less evolvable, whereas unintegrated agents are less fit but more evolvable. This was the result of the interactions between the components of every agent given that the motion of each agent is an emergent behaviour resulting from the collective behaviours of its components. In an integrated agent, it is much easier for the components to evolve a coordinated collective behaviour which results in high fitness. In an unintegrated agent, it is virtually impossible to evolve a coordinate collective behaviour which results in low fitness. In turn, unintegrated agents are more evolvable as they enable smaller changes on the phenotype, whereas integrated agents are less evolvable as a result of the disruptive effect of changes. The results clearly show how interactions at low levels of a hierarchy affect the behaviour of a system at higher levels: the interactions of components making up agents affected the agents' behaviours, which in turn affected their fitnesses, which affected the evolution of populations of agents. In order to improve evolution, it was necessary to alter the interactions of the low-level components.

Computer modelling: a large scale traffic simulation

The Nagel group has created a traffic simulation tool for the purpose of analysing large scale traffic dynamics [13, 154, 155, 183]. This tool enables transportation planners, engineers and environmentalists to make better decisions regarding the effects of traffic. The system's capabilities were demonstrated by running a simulation of the transportation dynamics of Switzerland, which comprise a very large hierarchical complex system. The simulation divided Switzerland's street map to 3,066 distinct zones (local authorities). Using census information, 7.2 million inhabitants were simulated as agents, and a travel plan (3 trips per day) was assigned for each: leaving times, a destination and a route. Traffic flow was simulated using a realistic cellular-automata method, simulating details such as number of lanes, turn and merge lanes and traffic signal phases.

Using the aggregated interactions of millions of individual trips, detailed transportation dynamics were generated: the connectivity information of every simulated road as well as the congestion map and the location of grid-locks (and also the resulting air quality). Many interactions take place in this simulation; demand that is higher than the road's capacity causes congestion. Congestion affects travel time and causes grid-locks. In turn, these emergent behaviours may cause individual drivers to change their travel plans, and utilise less congested roads. Consequently, many of the possible routes for every destination are actually utilised, including some that would not normally be used. Interestingly, although utilisation of a traffic management system makes traffic more efficient by moving traffic from congested roads to less congested roads, it results in traffic predictions becoming less predictable, as the system is pushed closer to its maximum capacity, where even small fluctuations can have a large effect. Finally, the higher utilisation of the system also generates more air pollution.

Ecology: the roles of competition, predation and desiccation

Wilbur investigated the role that that competition, predation and desiccation (caused by ponds that dry at different rates) have in regulating the structure of a controlled ecology, specifically, the distribution and abundance of species [240]. He conducted a series of experiments using 36 small artificial ponds which were populated by 4 frog species and their predators, a species of newts.

The experiments demonstrated that species that live in high-density communities, which are characterised by limited food, are more resistant to competition than species that live in low-density communities. The same species are also more resistant to predation than species that live in low-density communities. However, species that live in high-density communities are more susceptible to desiccation than species that live in low-density communities. Based on these results, it was possible to conclude that predation only weakly affects the biomass of all frogs; however, it greatly affects the species composition since some species (low-density communities) are more sensitive to predators than others. Thus, predation reduces competition, consequently, survivors are able to grow rapidly enough to leave the ponds before they dried and so, avoided desiccation. When predation is not present, competition slows growth, and as a result, death by desiccation is more likely. This study concludes by stating that there is no one crucial force, such as predation or competition, that determines the structure of the ecology, but instead it is determined by the interaction of all forces.

These results show how interactions at one level of a hierarchy affect the behaviour of a system at higher levels, and vice versa: for example, by introducing or removing individual predators, the structure of the ecosystem – its biomass and species composition – changes, which in turn affects the survival and final body size of individual tadpoles. These changes are a result of the interactions between the different levels of this hierarchical complex system: organisms (tadpoles and newts), species and the ecosystem – together with the environment – which is what the original paper referred to as the forces of predation, competition and desiccation.

Metropolitan development

Innes and Booher [89] argue that the reason metropolitan development fails to achieve its goals, namely, economical development and environmental protection, is because it attempts to impose high level rules, through laws and regulations, on the system; although these may temporarily help, their consequences are unpredictable and generally are unable to solve the problem. They argue that once the social, political, and economic world are viewed as a complex system, and one understands the interactions between fiscal policy, governance structure, and infrastructure policy, it is possible to pursue both economical development and environmental goals, and not just one of the two. This can be achieved by treating metropolitan development like an adaptive self-organising system and allowing its components to interact and change in response to external conditions.

In order to achieve this goal: first, the components of the system must have full knowledge of its state and must be allowed to interact with each other – this will enable better coordination of activities. Currently, the system's components have only limited knowledge of its state and the environment, and so, cannot operate in its best interests and frequently only pursue their own limited goals. These components come from all levels of the system, including planners and policy makers as well as residents, businesses, community groups and public agencies. Of particular importance is that components are provided with feedback regarding the results of decisions made. Second, groups that include members from various agencies and jurisdictions should be created for the purpose of addressing problematic aspects of the system (e.g. air quality). Group members will come from all areas relevant to the problem, and will have the mandate to decide how to monitor the problem and how and when to act.

To summarise, in order for metropolitan development to succeed – enable both economical development and environmental protection – interactions between the system components must be increased, and new interactions between the system's components and the environment must be formed.

Design of distributed systems

Gribble designed a scalable, fault-tolerant storage system called a distributed data structure (DDS) [73]. A DDS is intended to be used as a virtual hash-table that is replicated across many storage units; it consists of many components that are located on different machines. Numerous software clients (such as web servers) can connect to the DDS and use it concurrently. A DDS relies on timeouts to detect failures of components (a component has failed if it does not respond within a given amount of time). Every component relies on a garbage collector (an automatic memory release mechanism) whose performance depends on the local machine's load.

A flaw in the DDS design caused a cascading reaction across all levels of the system: when many clients interact with the DDS it occasionally reaches near-maximum capacity; in this state, random fluctuations in the load placed on individual garbage collectors cause the component's throughput to decrease, thus, to 'fall back' on its load. In turn, this causes the DDS to reassign work to other components which results in further performance degradation. Once a component responds slower than the timeout period, the system assumes it has failed. Eventually, the entire system fails. Although the system was designed with robustness in mind, cascading interactions occasionally resulted in total failure.

One solution suggests that the system adapt its behaviour according to its dynamics: by monitoring the ongoing interactions, the system could determine it is in danger, and behave in a way that guarantees stable performance (e.g. reject some client requests). Interestingly, this conclusion is very similar to conclusions reached by the Nagel group regarding the usage of their traffic simulation tool to optimise traffic.

In addition to these diverse studies of complex interactions in various systems, there are many others in areas such as medicine and finance, as briefly summarised below:

Medicine

Seely and Christou [201] demonstrated that patients with the multiple organ dysfunction syndrome (MODS) can be better treated and monitored by evaluating the patient's response to trauma or shock as a hierarchical complex system ("a complex nonlinear system involving a great number of variables and systems of variables") that is characterised by numerous complex interactions between the metabolic, neural, endocrine, immune and inflammatory systems.

Financial Valuations

Limburg et al [130] argued that when performing valuations, the financial estimation of ecological processes ("ecosystem services") must take into account the possibility that the interactions between the financial processes and ecological processes may cause aspects of the ecology to irreversibly destabilise (for example, by over fishing, a species of fish may be driven to extinction), in order to be able to determine whether the result of a financial process is ecologically safe or not.

Whether in computer modelling, ecology, metropolitan development, distributed systems, medicine or finance, researchers have all shown that the overall behaviour of hierarchical complex systems is dependent on complex interactions between many levels of the components that make up those systems. Often seemingly inconsequential interactions at a low level of a hierarchy can have significant effects on resulting behaviours at higher levels. The work in this thesis is one of the first attempts to explicitly study such interactions and their effects in a complex Artificial Life system.

2.2 Artificial life

Artificial Life, or ALife, as it is commonly called, is a field that deals with investigating simulation models of living systems for the purpose of increasing our understanding of biological and other natural types of phenomena [157, 221]; ALife studies not only biological systems, but also social groups and economic populations [19]. Some view ALife as a branch of complex systems [19, 170]. ALife is thought to supplement traditional types of biological research by synthesising life-like behaviours within computers [120]. It is hoped that by studying various models of many different natural systems, fundamental principles that govern numerous classes of complex systems across fields can be discovered [19, 20, 158].

The field of ALife is still in its infancy, and even now, nearly two decades since the first workshop on the subject, there is still no agreement on major issues, such as whether ALife is a true discipline or merely a novel and useful collection of methods [158], as well as no established metrics for the main phenomena researched by its practitioners [158]. Indeed, even the main direction of the field is unresolved, such as whether it should only focus on investigating biological questions that are grounded in our reality, or also investigate theoretical questions that do not relate to life on earth as we know it (arguments supporting one view or another are in [41, 157, 237]).

Research in ALife is conducted by construction of easy to manipulate models that are powerful enough to capture much of the complexity of biological systems [221]. These types of models often involve some form of artificial evolution (using a type of evolutionary algorithm such as genetic algorithms [157]), but may not use evolution and still 'qualify' as ALife work. Evolution is fundamental to many ALife models because it can be used as a way to search a large space of possible solutions for a specific problem (see section 2.4); ideally, the discovered solution will mirror natural strategies that are utilised by biological organisms and gained through natural selection [157]. The overall aim is that by understanding how the models behave, and how this behaviour is affected by altering aspects of the model (parameters, initial conditions, etc), insight can be gained with regards the modelled phenomena [237].

ALife simulations are mostly agent-based, and normally take a bottom-up approach, where many simple elements (e.g. molecules, cells, organisms) are allowed to interact with the intention that global, life-like, patterns, which are normally the object of study, will emerge at a higher level as a result [19, 31, 100, 147, 157, 170, 184, 223]; in this type of simulation, the investigated property is not explicitly coded in the model, but is supposed to emerge [100, 170, 184]. A fundamental assumption behind the approach taken by ALife is that the essence of biological complex systems can be captured using (relatively) simple models [19, 20].

Compared to mathematical models, ALife models typically enable a finer-grained description of the systems being modelled. Thus, for the purpose of this thesis, ALife models are likely to be better suited to the investigation of interactions between multiple levels within a hierarchical complex system [100].

2.2.1 Why should artificial life models be used?

If life could be restarted from the beginning, it is possible many characteristics would evolve differently; for example, it is conceivable we might have a number of digits in our hands and feet which is not five. Yet it is also possible many characteristics would evolve as before; for example, there may always be animals that can swim, fly or walk. Even though these are among the most fascinating questions, traditional science generally cannot resolve whether certain aspects are present because they are necessary or are merely the result of a particular historical development. There are many such open questions in biology that are unlikely to ever be answered using traditional methods. Some of these questions require creating conditions that cannot be made empirically; others require experiments that would take time scales too vast for scientists to perform [147] or involve biological data that is too complex and incomprehensible to be used [19, 147].

The primary advantage of Artificial Life models is that they enable investigating hypotheses that would be difficult or even impossible to test in other ways [19, 54, 100, 147, 157]. In addition, ALife models can be used to test the coherence of existing theories: examine the underlying assumptions of existing models [54, 100, 147, 158], as well as the consequences of altering these assumptions [100]. Perhaps the most novel usage of ALife models is that they can be used to examine fundamental concepts of life such as self-organisation, natural selection, the theory of complexity [100]; ALife enables exploring not just models of biological life as we know it, but can also explore life-like systems that only exist in theory [237]. In fact, as mentioned in the previous section, one of the goals of ALife is to look for unifying principles that can govern living systems [19, 100, 237] (though some doubt whether this can be achieved [219]). Even if none of ALife's achievements are considered, at the very least the tools and methods created by its practitioners can be used by other fields [237].

Unlike biological experiments, every aspect of ALife experiments has the potential of being fully controllable [41]. The scientist can also have complete access to every component of the simulation and its behaviour over time (i.e. dynamics of evolution) – yet he need not fear that gaining these observations affect the results of the simulation [41, 170]. Every experiment can be repeated as many times as the researcher wants [147], and he is at liberty to alter the starting conditions, and restart the experiment to see how these affect the system's behaviour [147]. Furthermore, by explicitly modelling evolution using a computer simulation, it is possible to view evolution as a computational process, specifically, analyse it from a novel, computational perspective, e.g. measure the 'information' contained in a population and understand how this information eventually is used to increase fitness [147] (in one such study by Bergstrom and Lachmann, the fitness value of information of the environmental state within the model was calculated [28]. In another study by Chu and Adami, the relationship between fitness and mutation rate and the propagation of information within an ALife simulation was examined [47]).

Although ALife models often cannot be used to make precise predictions of real world data [147, 170], they are very good at displaying a system's dynamics, and observing the conditions and mechanisms that result in unexpected behaviours; thus, can be used to provide users with an intuition of the system: which events are normal and which are not [147, 170].

2.2.2 Criticisms of artificial life

Even though ALife is a promising field, it certainly has its share of problems. It is hoped that as the field matures, its problems will be resolved.

A common criticism of ALife researchers is that they have been running experiments without any clear hypothesis and lacking theoretical frameworks [41]. Indeed, its practitioners have been generally accused of not always being very rigorous when it comes to methodology [54, 223]. This is certainly not made easier by the fact that, as all computational models, ALife models are difficult to verify; it is not easy to identify the extent that each of the rules of the model contributes to the global behaviour of the system, and whether these rules are based on valid assumptions [100, 170]. At times it can also be difficult to explain a system's behaviour: decide whether its behaviour is a result of the model or is caused by unknown and irrelevant elements, such as conceptual or programmatic errors [41, 100, 170].

With regards to practical problems, ALife models frequently have to be simplified in order to be computationally feasible and for their results to be comprehensible [147]. Furthermore, because they are often too abstract, it is difficult to relate their dynamics to the behaviour of the real world phenomena they simulate [147, 219].

In order to do good research in ALife, it may be advisable to follow guidelines on building good models (next section). In addition, it has been suggested that cooperation between ALife researchers and biologists be made for the work to be biologically significant [100]. Finally, whenever possible ALife models should incorporate real world data [100, 170] – it is particularly important to incorporate real world empirical constraints into the model [31].

2.3 Modelling biological systems

2.3.1 Agent-based modelling or equation-based modelling

As briefly mentioned in the introduction chapter, there are two main ways in which researchers model complex systems: agent based models (ABMs) and equation-based models (EBMs). ABMs comprise many individual agents that encapsulate the behaviours of the various components of the system. EBMs consist of a set of equations that are evaluated when the model is executed [171]. Although each type of model has its advantages and disadvantages, and it cannot be said that one type is superior to the other [41], it seems that ABMs are more suitable to modelling systems of the type this thesis is focusing on.

Equation-based models consist of a set of equations that describe the relationship between system variables [171]. EBMs capture only the global dynamics of the system, the collective behaviour of many elements, and cannot be used to look at individual components of the system and their interactions [147, 149, 156, 169, 171]. In order to be solvable, this type of model often has to be greatly simplified – at times, enough that the model becomes unrealistic and does not provide any useful insights about its target [147]. EBMs are particularly unsuitable when modelling systems which have different hierarchical levels [100], spatially distributed phenotypes [41], small populations [221], as well as when there are complex, non-linear interactions between components [41]. In fact, according to Taylor and Jefferson [221], modelling biological systems using EBMs is completely impractical, as even simple models of an organism's behaviour require hundreds of equations – a feat modern mathematics cannot perform. That being said, an advantage of EBMs is the maturity of the supporting mathematical sciences (statistics, dynamical systems theory, etc) [41] as well as the availability of several popular tools for construction and analysis of system dynamics models [171].

Agent-based models consist of many individual agents, each encapsulating the behaviours that make up the various elements of the system. ABMs enable access to all the components and processes of the system: these can be analysed at any given moment [170]. However, like EBMs, ABMs also capture the global variables of the system – these simply emerge from the interactions of all components and are not simply calculated; this also makes verification of ABMs easier, as there are is more than one level of variables that can be compared [171]. In addition, ABMs are not susceptible to the limitations of EBMs mentioned above, and so, can be used for a wider range of problems [100].

Construction of ABMs is easier, their usage tends to be more intuitive, and comparing their results with their targets is easier [171]. That said, like EBMs, ABMs frequently have to be simplified in order to be computationally tractable and for the results to be understandable – thus, run the risk of modelling the target incorrectly, and not being able to provide any useful insights about it [147]. One disadvantage of ABMs is the lack of universal tools for creation and analysis, which usually must be developed by researchers independently [157].

ABMs are particularly appropriate for usage in ALife simulations for two reasons. First, since ALife experiments attempt to recreate a desired phenomena through the collective interactions of many components, ABMs are the perfect match [157]. Second, being able to analyse the components and behaviour of the simulation is a primary concern in ALife simulations.

2.3.2 On the design of models of biological phenomena

Even though computational models are built and used in many different fields, there does not seem to be one methodology which is agreed by all on being the ideal one [233], nor is there an agreement on the proper role of models [185]. In fact, there is even no agreement on what is meant by the word 'model' in science [122]. In her excellent review, Webb [233] surveyed seven dimensions which simulation models can vary in and provides a comprehensive framework that can be used. This thesis supplements this framework with definitions made by other authors. Throughout the thesis, every expansion to the model is thoroughly analysed using this methodology. Note that only six dimensions – those relevant to this thesis – are mentioned; the seventh dimension, 'medium', which deals with the physical material used for implementation of the model, is clearly only relevant for models that are implemented in hardware and not the software models used in this thesis.

Definitions

A model is the representation of a hypothesis underlying an explicit real world phenomenon [223, 233]. The model's hypothesis clearly specifies the components and interactions thought to be sufficient to generate the desired behaviour [233]. Thus, by implementing the model, the researcher is able to view the consequences of the assumptions underlying the hypothesis

[41, 233]. If the behaviour of the model is similar to that of the target, then it is reasonable to assume that the model's assumptions are in fact true [157, 233].

Ideally, the model implements the hypothesis and nothing besides, so that the generated behaviours can in fact only be attributed to the hypothesis [223, 233]. However, the process of implementation normally requires elaborations or simplifications of the hypothesis for it to be tractable, and these may not have an underlying theoretical justification, and so, the actual model is likely to contain some elements that are not a part of the hypothesis [233].

If the model does not generate the target behaviour, then it is assumed that the underlying assumptions are not enough to generate the target; it is possible to alter the assumptions and try again [223]. It is important to remember that a model that correctly generates the desired behaviour may still erroneously explain the target behaviour for one reason or another – the correctness of the assumptions is not guaranteed [233].

Dimension 1: Biological relevance

This dimension defines the degree in which a model is biologically relevant, meaning, it is a model that is useful towards improving our understanding of the modelled biological phenomena. These type of models can be used to test hypothesis that are relevant to a biological system; however, the extent of which these models can be used to ask questions varies: some models aim to represent biological phenomena more or less closely than other models, for example, one model makes specific empirical claims about a biological system while the other only generally describes its dynamics.

Dimension 2: Level

This dimension describes the hierarchy of processing levels – the levels of organisation – that the model represents, specifically, the rudimentary elements. Deciding the appropriate levels to represent is problem specific – there is no one 'correct' level: levels that provide relevant details towards gaining an understanding of the system should be included. However, for the purpose of this dimension, it is not crucial that every level is 'anatomically' accurate, as long as its functionality and behaviour are correctly replicated [208, 233].

Dimension 3: Generality

This dimension describes the generality of the model: the more general a model is the more real systems it applies to.

Dimension 4: Abstraction

This dimension describes the level of abstractness of the model: the degree of which the modelled phenomenon's components and processes are described. A detailed model is less abstract. There are advantages and disadvantages for both complex and abstract types of models. Complex models are more difficult to implement, understand and verify. However, abstract models are in danger of ignoring aspects that are crucial towards understanding the system. Segev suggests that complex models are required at first to discover what the appropriate simplifications are [202]; it is possible to 'simplify' in the 'wrong way', particularly when the system is not well understood.

Dimension 5: Accuracy

This dimension describes the level of accuracy of the model: whether the mechanisms and process of the model mirror those in the real system. When the accuracy dimension of the model is high, it can be said the scientific content of the model is justified. Even models with some inaccuracies can be biologically relevant, that is, useful towards increasing our understanding of the system as long as the erroneous assumptions are well understood. Some models that are very inaccurate can still be very biologically relevant [233].

Dimension 6: Match

This dimension describes the degree which the model behaves like the target phenomenon; only the behaviour is considered (and not the mechanisms). There are many different ways in which a model can behave like its target ranging from being able to produce roughly similar dynamics to being able to provide precise predictions. If the target behaviour does not match the model's behaviour then the hypothesis can be rejected or possibly altered; otherwise, the underlying hypothesis is strengthened to an extent that depends on the model's mechanisms matching the target's [233].

2.4 Evolutionary computation

The field of Evolutionary computation (EC) deals with algorithms for solving computational problems using principles from evolutionary biology and genetics. Evolutionary algorithms (EAs), as these types of algorithms are called, include Genetic Algorithms, Evolutionary Programming, Evolutionary Strategies and Genetic Programming [27]. EAs have been shown to be among the most flexible, efficient and robust of all search algorithms [68], thus, are now used to solve a wide range of different problems [27]. EAs are particularly suitable for problems that require programs are adaptive: continue operating even when the environment changes (e.g. controlling a robot in a dynamic environment). EAs are also useful for researching aspects of evolution and nature [27, 147]. A computational and conceptual advantage of EAs is their simplicity: incorporating the principles of random variation (mutation, recombination) and selection (survival of the fittest) together with reproduction effectively defines an EA [147].

There are several principles which are true for all EAs. All EAs primarily deal with search: they enable finding a useful solution for a problem within a huge collection of potential solutions (called the 'search space') [27]; this is accomplished by evolving a population of candidate solutions to a given problem using operators inspired by the principles of genetic variation and natural selection [12]. The fact that EAs use a population of solutions grants them the benefits of parallelism: they effectively search many different parts of the search space simultaneously and do not focus on a single point [147]. However, even though they are good at global search, EAs are relatively inefficient in fine-tuned local search [238, 245]. EAs aim to find a good solution in a reasonable amount of time, but not necessarily the optimal solution [147].

2.4.1 When should an evolutionary algorithm be used?

There are many types of search algorithms. Good search algorithms operate by using an intelligent strategy in order to pick the next area of the search space to examine [147]. According to the no-free-lunch theorem, there is no single algorithm which is on average superior to any other algorithm [241]. Consequently, EAs are better for some types of problems and worse for others.

There are several situations where EAs are particularly appropriate:

- When the search space is large and is not perfectly smooth or is not well understood. In such situations, EAs are appropriate since they do not need additional information – unlike other types of search algorithms which require a lot of additional information to work properly (e.g. gradient techniques need derivates) that may not be available or is difficult to obtain [68, 238, 245]. In other situations, EAs may not do as well as other search algorithms.
- When the fitness function is noisy.
- When the global optima is not required, and a good solution will be sufficient [147].
- When it is less crucial to understand the way which the evolved solution works. Evolved solutions often have a lot of irrelevant components [147]; consequently, it may be very hard to understand how they work. When it is crucial to understand the operation of the solution (e.g. for medical applications), EAs are probably not the best choice.

2.5 Genetic algorithms

Genetic algorithms (GAs), which were invented by John Holland in the 1960s and 1970s [86], are search algorithms based on the principles of natural selection and natural genetics [68]. GAs operate by balancing exploration (discovering new components of solutions) and exploitation (usage and incorporation of the known components) [147]. GAs are probably the most widely used of all of the evolution based search algorithms [27], and are known for their ability to deal with many types of optimisation problems and produce excellent results [27, 68, 86].

GAs, like other evolutionary algorithms, require maintaining a population of candidate solutions. Each of the potential solutions has a genotype, which encodes all the traits of a phenotype in genes. Using a fitness function, every candidate solution is assigned a fitness value. This value assesses the quality of the phenotype for the purpose of the solving the problem; it is crucial that the fitness function accurately determines the quality of the phenotype [147].

The operation of the GA starts by generating an initial population of random candidate solutions. The candidate solutions are then evaluated using the fitness function: the fitter ones are kept, while the unfit ones are removed. The solutions that remain are allowed to reproduce, and using the genetic operators of mutation and crossover, create new offspring to maintain the population [147]. This process is called a generation, and is repeated a number of times, often between 50 and 500. As long as the selection criteria relate to actual fitness, there will be selection pressure towards areas in the search space with increasingly better solutions [27, 147].

A genetic algorithm is a type of a complex system; the genetic operators and the various parameters of the system interact nonlinearly to generate the global behaviour of the GA. Although GAs are conceptually simple, their behaviour is complicated, and understanding how they work, and what type of problems are appropriate is still unresolved [147].

2.5.1 Encoding a candidate solution

A candidate solution is frequently implemented using bit strings, but other encodings, such as real numbers or characters, can also be used when more appropriate (e.g. when evolving the weights of neural networks) [147]. Fixed-length, fixed-order, binary encodings are the most common encodings for GAs. This has mainly been the case for historical reasons: a large portion of GA theory, such as the Schema theorem, is based on the assumption of using these encodings [147] (however, Schema theorem has been extended later on to include real numbers encoding as well [243]). The way in which candidate solutions are encoded is extremely important and may in fact be the most important element that affects the success of the GA [147].

It is also possible to adapt the encoding: instead of using a fixed size genome, its size can grow or shrink as needed. This approach has a lot of potential, since it enables evolution to find the ideal size for the genome. However, there are also some disadvantages: the genome may grow extremely large [147].

2.5.2 Fitness landscapes

It is possible to create a visual representation of the entire space of genotypes with their corresponding fitnesses: this is called a fitness landscape. It can be said that a GA is a method for searching fitness landscapes for highly fit strings [147]. For problems with very 'hilly' fitness landscapes, finding the globally optimal solution (the highest peak) can be very difficult [27] since it is possible to be trapped in a local optima – a candidate solution whose immediate neighbours are all worse than it is – and thus, not be able to find the global optima. However, the fact that GAs (and other EAs) use a population of solutions decreases the likelihood of this occurring [68].

For most types of problems GA deal with, the fitness landscape is static; this is biologically unrealistic – in the real world, the fitness landscape cannot be separated from the organisms that inhabit it [147]. That said, for some problems, particularly for those where the quality of one solution affects the fitness of the others (such as ecological simulations), the fitness landscape constantly changes.

2.5.3 Genetic operators

The simplest form of a genetic algorithm has at least three operators: selection, crossover and mutation. However, some problems require creating custom operators. Deciding which genetic operators to use and how to implement them greatly depends on the encoding of the problem [147].

It is very important that the effect of genetic operators is not too disruptive: the phenotypes of generated offspring should not be too dissimilar from their parents' phenotype [27]. In addition, enabling the GA to adapt its own rates of mutation and crossover, as well as other parameters and aspects of selection (such as the population size) during a run has the potential of improving its effectiveness [147]. See section 4.2 for a more thorough discussion of these issues.

Selection

Selection determines which candidate solutions in the population are selected to reproduce – create offspring for the next generation – and the number of offspring created. The purpose of selection is to allow the fit solutions to survive; the fitter the solution, the more likely it is to be selected. Selection has to be carefully balanced: too strong a selection will result in a loss of diversity and convergence on a local optima, too weak a selection will result in slow evolution. Selection works on the phenotypes and not on the genotypes – it does not 'care' how a trait is encoded [147].

There are many types of selection methods, including but not limited to:

- Tournament selection: two individuals are randomly chosen from the population, and at a predefined probability, one of them is selected to reproduce. This is repeated until the number of necessary offspring is created [69].
- Rank selection: the fitnesses of the candidate solutions are sorted, and each is given a rank. The rank effectively becomes its new fitness. The advantage of this method is that it prevents premature convergence. Its disadvantage is that it eliminates the relative differences in fitness, which may be large [147].
- Elitism: in every generation, some of the best individuals are kept [53].
- Fitness-proportionate selection: every candidate solution is given a probability of being selected to reproduce directly related to its fitness. This method is very popular, but can decrease variability and as a result can often result in premature convergence [86].

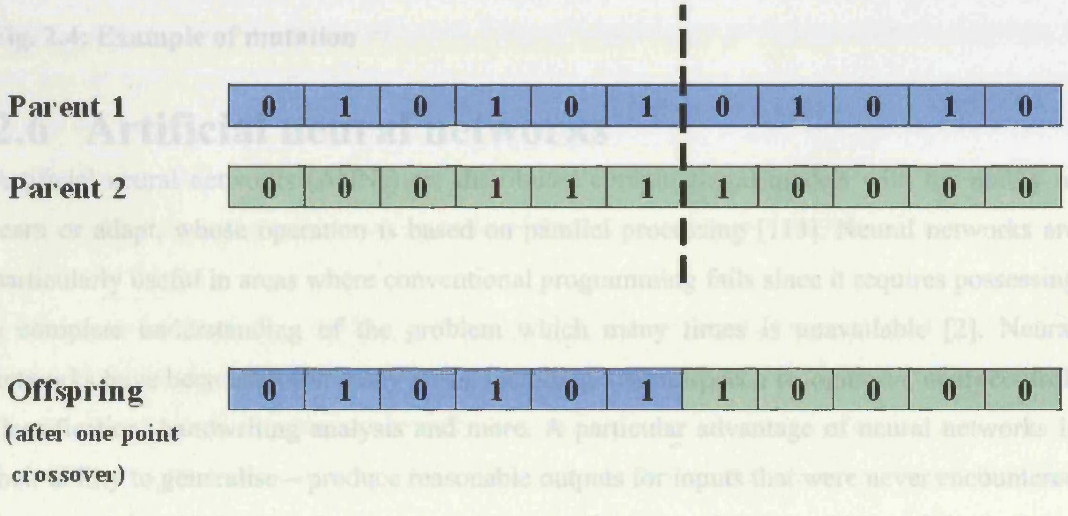


Fig. 2.3: Example of one-point crossover.

Crossover

Crossover causes the exchange of genetic material between the two parents. The conventional theory of GAs states that the power of GAs is derived by recombining good 'building blocks' of solutions to form better solutions, thus, it is believed that crossover is a primary reason why GAs are successful [147]. Single point crossover is implemented by selecting a random crossover point, and the before and after parts of the two parents are exchanged and form two new offspring. Two point crossover works in a similar way, except two crossover points are selected. See fig. 2.3 for an example of crossover.

Mutation

Mutation randomly changes the value of some of the genes of a solution; every gene has a probability, normally very small, of being mutated. When genes are represented using bit strings, mutation is normally done by flipping a bit (see fig. 2.4 for an example). When genes are real numbers, a Gaussian function changes the value of the number or a new value is randomly created. Holland suggested that the role of mutation is to prevent diversity loss for a given gene, thus, it is significantly less important than crossover [86]. However, other EC methods, such as evolutionary programming use mutation without crossover [147], and so, evidently for some systems the role and importance of the mutation operator are different.

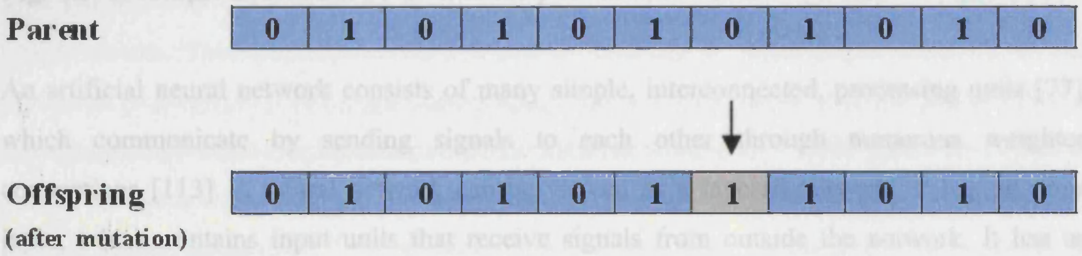


Fig. 2.4: Example of mutation

2.6 Artificial neural networks

Artificial neural networks (ANNs) are distributed computational models with the ability to learn or adapt, whose operation is based on parallel processing [113]. Neural networks are particularly useful in areas where conventional programming fails since it requires possessing a complete understanding of the problem which many times is unavailable [2]. Neural networks have been useful in many areas, including vision, speech recognition, neurocontrol, classification, handwriting analysis and more. A particular advantage of neural networks is their ability to generalise – produce reasonable outputs for inputs that were never encountered during training [77]. Neural networks were partially inspired by the ability of the brain to make complex decisions quickly despite the slow speeds of biological neurons [151]. That said, neural networks are only loosely based on biological nervous systems; there are many biological complexities which are ignored [151].

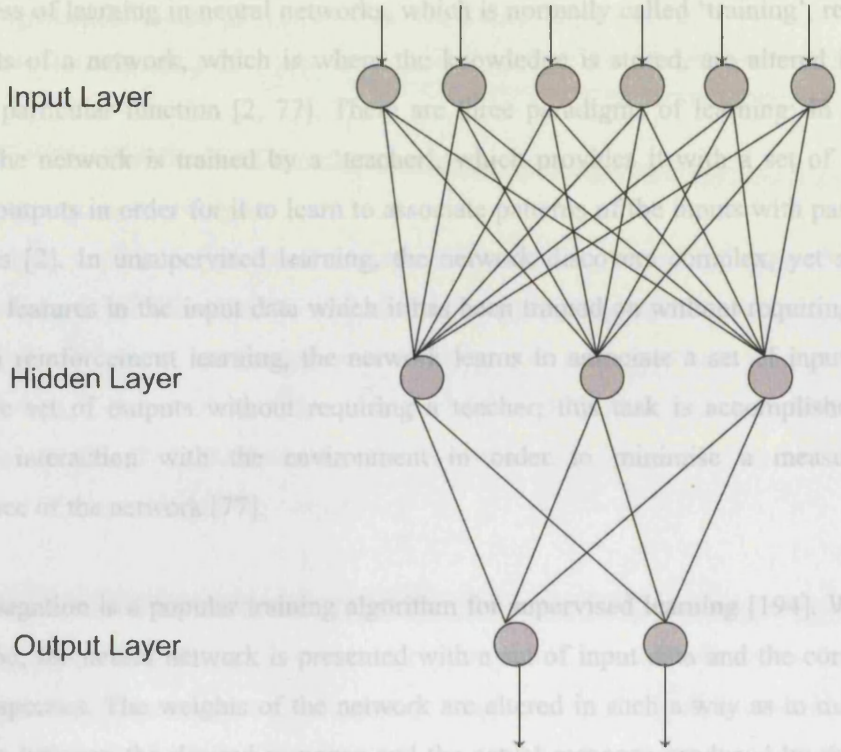


Fig. 2.5: A sample neural network with 6 input units, 3 hidden units and 2 output units.

An artificial neural network consists of many simple, interconnected, processing units [77], which communicate by sending signals to each other through numerous weighted connections [113]. A neural network can be viewed as a layered network. It has an input layer, which contains input units that receive signals from outside the network. It has an output layer, which contains output units that send signals out of the network. In between, it has one or more hidden layers that contain hidden units whose input and output signals stay within the network (see fig. 2.5 for a sample neural network). It has been shown that a single hidden layer suffices to approximate any function with many discontinuities to arbitrary precision as long as the activation functions of the hidden units are non-linear [76].

Feed-forward networks are neural networks with no closed loops [2], meaning, the data flow is one directional: units receive their input from the immediately preceding layer and send their output to units in the immediately succeeding layer. In such networks there are no connections within the same layer [113]. This type of network can be fully connected; in this case, every input unit is connected to every output unit [2], or they can be partially connected – some connections are missing [77]. A recurrent neural network is similar to a feed-forward network, but the flow of the data is bidirectional: it may have at least one feedback loop, meaning, it may have at least one unit whose output connects to input of a unit from the same or a preceding layer – or even itself [2, 77].

This process of learning in neural networks, which is normally called 'training', requires that the weights of a network, which is where the knowledge is stored, are altered in order to achieve a particular function [2, 77]. There are three paradigms of learning: In supervised learning, the network is trained by a 'teacher', which provides it with a set of inputs and matching outputs in order for it to learn to associate patterns of the inputs with patterns from the outputs [2]. In unsupervised learning, the network discovers complex, yet statistically persistent, features in the input data which it has been trained on without requiring a teacher [2, 77]. In reinforcement learning, the network learns to associate a set of inputs with the appropriate set of outputs without requiring a teacher; this task is accomplished through continued interaction with the environment in order to minimise a measure of the performance of the network [77].

Back-propagation is a popular training algorithm for supervised learning [194]. When using this method, the neural network is presented with a set of input data and the corresponding desired responses. The weights of the network are altered in such a way as to minimise the differences between the desired response and the actual response produced by the network. This procedure is repeated many times, until there are no further significant changes in the weight values. This way, the network learns by creating an input-output mapping for the presented problem [77]. Although back-propagation is a very powerful technique, at times it does not always work. For instance, when the network is trapped in local optima and is never able to escape and find the global optima (this can happen if the error function is multimodal or non-differentiable) [147, 245]. An additional limitation of this algorithm is the necessity of having a teacher [147].

A neural network can also be trained by evolution. Using evolutionary algorithms, the network weights and topology can be evolved [147]. This type of training has its own set of advantages and disadvantages (see next section).

2.7 Evolving artificial neural networks

Standard training algorithms for neural networks, such as back-propagation, have many limitations; using evolutionary algorithms, such as genetic algorithms, it is possible to overcome many of these. It is, therefore, unsurprising that there has been a lot of work on using evolutionary algorithms to evolve neural networks. The evolution of neural networks using genetic algorithms (also called Neuroevolution [70] and Evolutionary Artificial Neural Networks [245]) is a useful method of combining the benefits of evolution with learning.

2.7.1 Aspects of neural networks that can be evolved

There are several ways in which genetic algorithms can be used to evolve aspects of neural networks.

Evolving the connection weights

It is possible to evolve the values of the connection weights of a neural network [147, 238, 245]. One benefit of this process is that it enables training of neural networks without requiring differentiable or continuous error functions – or even that there is an error function at all; therefore, it is less likely to become stuck at local optimas and more likely to find a good global solution [245]. Additionally, the network does not require a 'teacher' to supply it with pairs of inputs and matching outputs.

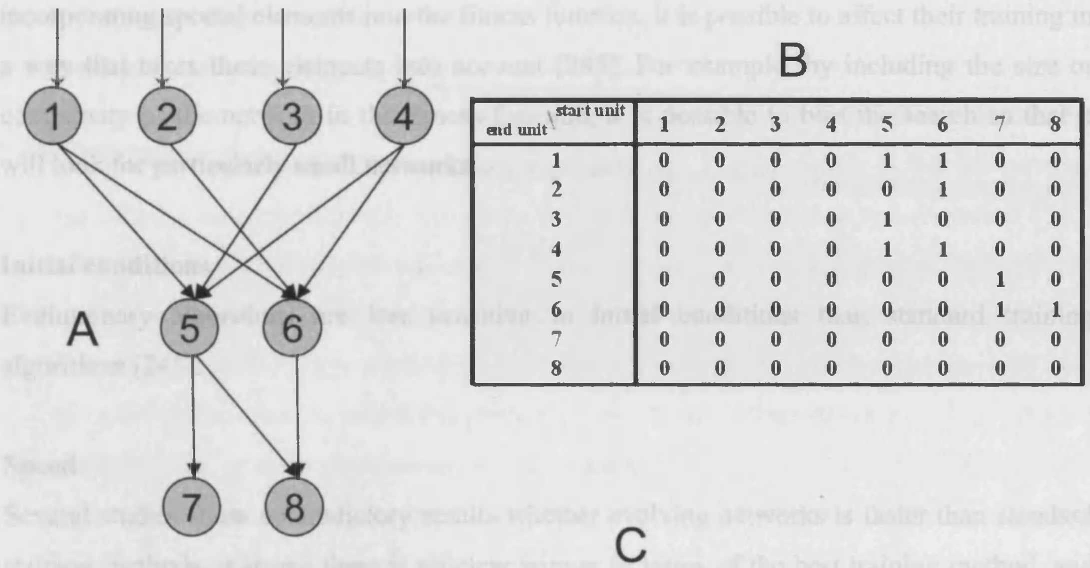
Evolving the network's architecture/topology

It has been shown that altering the structure of a neural network affects its functionality, particularly its speed and accuracy of learning; however, it is difficult to determine the ideal architecture of a neural network for the problem at hand, and there is no systematic way to find it [147, 215, 245]. This can be solved by evolving the network's topology; it is possible to evolve any parameter related to the structure of the network, including: number of units (hidden, input), number of layers, connectivity of the network (number and location of connections, and whether to include recurrent connections), as well as the activation function of potentially every hidden and output unit in the network [147, 238, 245]. See fig. 2.6 for an example of an encoding of a network's topology.

Many methods are limited to evolving only the connection weights and the connectivity of the network and do not evolve other aspects (such as the number of units or layers) [214, 238, 245]. Other methods enable the evolution of most or all aspects. It has been shown that evolving both structure and weights greatly improves performance since finding a suitable structure decreases the dimensionality of the search space of connection weights [215].

Evolving input features

The possible inputs a neural network receives can be potentially very large. However, it is possible some are redundant or unimportant. By determining through evolution which inputs to consider, performance can be improved and the network size reduced. An interesting benefit is that the researcher also discovers which input features are important and which are not [238, 245].



end unit \ start unit	1	2	3	4	5	6	7	8
1	0	0	0	0	1	1	0	0
2	0	0	0	0	0	1	0	0
3	0	0	0	0	1	0	0	0
4	0	0	0	0	1	1	0	0
5	0	0	0	0	0	0	1	0
6	0	0	0	0	0	0	1	1
7	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0

Genome: 00001100 00000100 00001000 00001100 00000010 00000011 00000000 00000000

Fig. 2.6: An example of an encoding of a network's topology. (A) The network's structure and connectivity. (B) The connectivity matrix (1 indicates units are connected) (C) The final genome.

Evolving learning rules

Traditional neural network training algorithms use a learning rule that determines how the weight updating takes place. There are many possible weight updating rules with many variations (different value for the rate of learning parameter, using momentum, etc). Choosing the right rule can greatly improve the learning ability of the network. Instead of empirically searching for the ideal value, it is possible to use a genetic algorithm and evolve the learning rules; this can greatly facilitate the process [147, 245].

In addition, modular neural networks/ensembles can be evolved (see section 7.1).

2.7.2 Additional considerations

There are several additional issues relevant to the decision whether the evolution of neural networks should be used or not.

Generality

One advantage of using genetic algorithms is that it is possible to evolve different types of networks (recurrent, feed-forward) using the same algorithm [245].

Special elements

It may be desirable that the training of the network includes additional elements. By incorporating special elements into the fitness function, it is possible to affect their training in a way that takes these elements into account [245]. For example, by including the size or complexity of the network in the fitness function, it is possible to bias the search so that it will look for particularly small networks.

Initial conditions

Evolutionary algorithms are less sensitive to initial conditions than standard training algorithms [245].

Speed

Several studies show contradictory results whether evolving networks is faster than standard training methods, it seems there is no clear winner in terms of the best training method, and that the best method is always problem dependent [245] (an unsurprising conclusion according to the no-free-lunch theorem [241]). That said, since evolutionary algorithms are relatively inefficient in fine-tuned local search but are good at global search [238, 245], and traditional training methods are not ideal at finding global solutions, hybrid methods that combine the advantages of both appear to be ideal [238, 245]: the GA is used for global search, and a standard method is initialised with the results found and performs the local search [245].

2.7.3 Encoding and genetic operators

There are several issues regarding the encoding and genetic operators to consider when evolving neural networks, in addition to those mentioned in section 2.5.1 on encoding a GA.

Encoding: when evolving topology

When a network's structure is evolved, the decision how to encode the network's genome becomes significant. There are two different ways in which a network can be encoded:

(a) **Direct encoding**: using this encoding, every aspect of the network is specified in the genome. One disadvantage of this encoding is its scalability: when evolving very large networks, the genome becomes very large, and consequently, the search space is likely to be intractable [216]. An additional disadvantage is that repeated structures cannot normally be reused, thus, they effectively have to be continuously rediscovered by evolution [147]; for example, attempting to evolve the shape of a hand with five digits would be very challenging using direct encoding as each digit would have to be evolved separately – a far more sensible approach would be to evolve the design for one digit and allow evolution to reuse it (see next item). Note that using custom operators, it is possible to enable some reuse of structures – this is demonstrated in chapter 7.

(b) **Indirect/developmental encoding:** using this encoding, the network is generated using developmental rules which can be evolved. Unlike direct encoding, the information that is encoded does not specify every trait in the network explicitly but rather specifies the information required in order to construct the network. The advantage is that the genome can be very compact because not every unit and every connection are described [215, 245]; this is also more biologically plausible [216, 245]. Additionally, this method enables structures to be reused [147]. There are several disadvantages: the connectivity patterns generated by this method are not very accurate [245] (because the genome only describes the manner in which the phenotype is created, unlike direct encoding where a complete and precise description of the phenotype is encoded in the genome), and because the generated phenotypes do not map directly to genotypes, they can affect the search in unpredictable ways [215].

It was shown that direct encoding is at least as good as indirect encoding with regards to the creation of smaller neural networks [209].

Genetic operators

Deciding how to implement the search operators (mutation, crossover), and whether to add custom operators, can have a very large effect on network training [245], and the evolvability of the phenotype [196]. The choice of search operators greatly depends on the representation used and on the aspects of the network that can be evolved; certain search operators are more suitable than others for some representations [215]. See section 4.2 on evolvability.

Crossover problem: competing conventions

One consistent problem when evolving neural networks is the competing conventions problem, also called the permutations problem: during the evolution of neural networks, when two genomes that represent identical networks (in terms of solution) that are encoded differently cross over, the offspring is likely to be unfit [215, 238]. This problem occurs because the networks represent the solution differently: the same genes (same position in the genome) may express different traits, and the same traits may be in different locations of the parent genomes. Thus, crossover would disrupt the functionality of the offspring: its structure may have duplicated traits or omitted traits – with both variants being unfit [215, 238].

In order for crossover to work, it is crucial that the right genes are crossed over with their counterparts [215, 238]. Some methods solve this problem by eliminating crossover completely, and only using mutation [238], others use historical information that keep track of related genes, and so, know which genes to pair together during crossover [215], and others identify functional aspects of units in order to be able to perform intelligent crossover [153]. Regardless of the mechanism, the important element remains the crossing over of related genes [238].

2.8 Summary of chapter

This chapter reviewed the field of complex systems, with a particular focus on hierarchical complexity. The result of this review indicated that although it is a well known fact that complex systems in the real world tend to be hierarchical, scientific models rarely incorporate this aspect, furthermore, a systematic investigation of the interactions that occur between different levels of a hierarchical complex system model has never been performed. Indeed, the importance of these interactions, which were labelled 'complex interactions', was further reaffirmed by a survey of work conducted in many different fields that has repeatedly shown that often the overall behaviour of hierarchical complex systems is dependent on complex interactions.

Since a systematic exploration of complex interactions has never been conducted, the work in this thesis introduces Mosaic World, a hierarchical complex system model that comprises a population of evolving neural network agents, for the investigation of complex interactions.

In order to understand the context and usefulness of such models, and be able to create one which correctly accomplishes its aims, a review of the field of artificial life, and a useful methodology for the design of models of biological phenomena, were presented. The rest of the chapter surveyed the practical matters involved in the creation of Mosaic World. Thus, a description of the usage of neural networks and genetic algorithms was given, and an evaluation of the issues – advantages and disadvantages – involved with the evolution of neural networks using genetic algorithms was provided.

Chapter 3

System: Mosaic World

3.1 Introduction

In order to explore complex interactions, a model that possesses the necessary characteristics must be created and investigated. This chapter introduces Mosaic World, a hierarchical complex system model that can be used for the investigation of complex interactions as well as for the exploration of other computational and biological hypotheses.

3.2 System overview: concept and goals

The investigation of complex interactions required that a hierarchical complex system model is created. This could be accomplished by selecting a hierarchical complex system seen in nature and systematically modelling its components across all levels. Although this approach would result in a model which possesses many complex interactions that could be investigated, it was determined that it would be too limiting in terms of the range of possible interactions and hypotheses that could be explored. Thus, in the early stages of the project it was decided to select several interesting biological systems and universal principles for modelling; in this type of model, every part is biologically plausible, however, the overall model is only partially accurate from a biological point of view. On the other hand, such a model enables investigating a much larger range of interactions and hypotheses, and so, its computational and biological relevance and overall usefulness is considerably greater. This is justified because the model is biologically relevant – its results are plausible and realistic – consequently, it is mostly irrelevant that the model is not biologically accurate in its entirety (this viewpoint is supported in Webb's review [233]). More importantly, since the ultimate goal is the detailed investigation of complex interactions in a hierarchical complex system, the precise nature of the overall system is of secondary importance.

As a result, several versions of Mosaic World have been used for the work described in this thesis. The initial version is described in this chapter. Additional versions are expanded and examined in later chapters. All versions of the model are hierarchical complex systems that enable the exploration of the interactions that occur between the various levels of the model and the examination of interesting hypotheses. That said, the more advanced versions are more hierarchical than their predecessors, and as a result, the study of complex interactions becomes more informative in the later versions (and later chapters) as the hierarchical complexity of the model is incrementally increased.

The visual environment is a suitable environment for modelling. Although this may not be immediately obvious, the stimuli that the visual system receives are inherently ambiguous. This ambiguity is a result of the unknown contributions of the three elements that make up the visual stimuli: the reflectance of the viewed objects, the quality of the illumination and the effect on the passing light of the surrounding medium. Thus, because the visual system has no direct way to ascertain the source of the image, it can be argued that disambiguating the received stimulus is the most basic challenge of all visual systems [131, 132, 133, 182]. For this reason, a visually ambiguous environment is an appropriate context for the study of complex interactions, and also provides a useful model for exploring other interesting computational and biological hypotheses.

Therefore, the initial version of Mosaic World (which is equivalent to the system described in [197]) was created and is described in this chapter; note that this version is used for the studies described in chapters 4, 5 and 6 – though each of these chapters required several additional minor features whose proper place is in the relevant chapter and not here. This version of Mosaic World consists of a two dimensional grid of coloured surfaces under one or more simulated light sources, and aims to emulate key characteristics of natural scenes. This environment is inhabited by virtual agents, 'critters', that survive by consuming positive resources and avoiding negative resources. Every surface's value is determined from its reflectance – its colour. Every critter starts out with a certain amount of energy and dies if it runs out of energy. The critter population is maintained by the critters themselves; critters can reproduce both sexually and asexually. Critter behaviour is determined using a modified 3D feed-forward neural network.

Mosaic World naturally comprises many levels of abstraction: genes, neurons, receptors, networks, critters, population and species; figure 3.1 illustrates the object model of the initial version of Mosaic World. The construction of Mosaic World enables the investigation of interactions between components at each level, and between levels, see figure 3.2. In subsequent chapters, the model will be expanded and interactions table updated accordingly. These interactions and their effects on the overall system are investigated by presenting a series of challenges to Mosaic World, each designed to affect key interactions within the system and enable their study. Note that the exploration of complex interactions includes not only these key interactions, but also the cascade of interactions that takes place in the system, across its various levels, following the original perturbation.

3.2.1 The methodology behind the initial version of Mosaic World

In this chapter, the methodology behind the initial version of Mosaic World is examined using Webb's methodology for the design of models of biological phenomena (which was introduced in section 2.3.2). Subsequent chapters will examine the additions to the model.

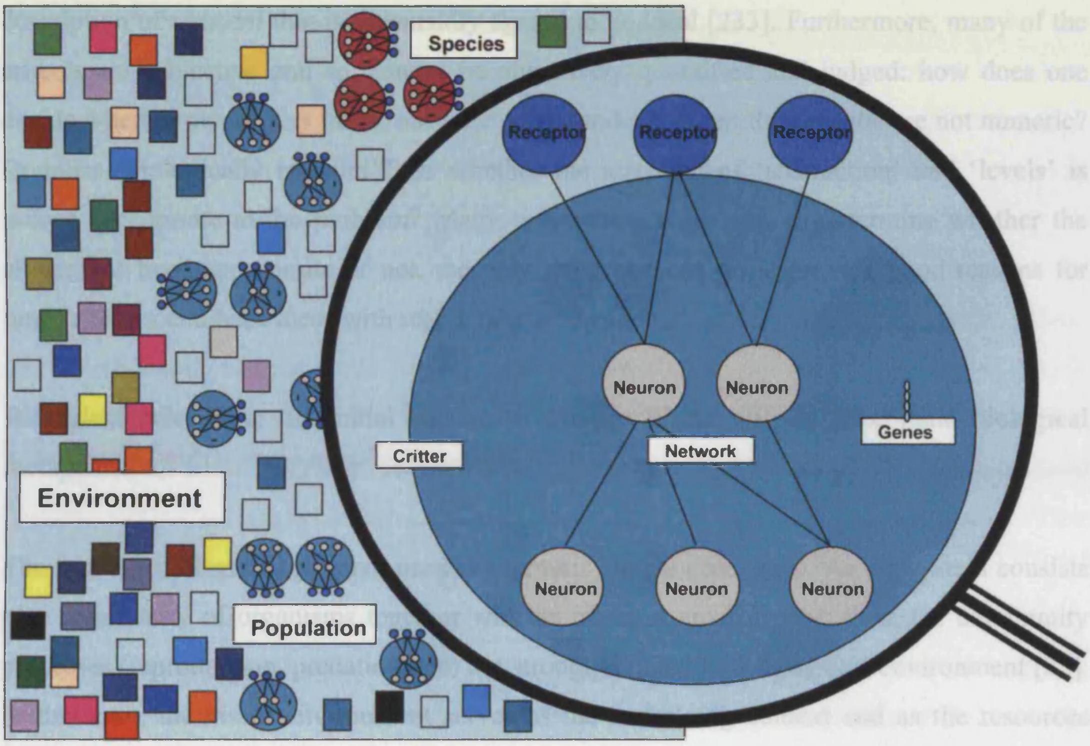


Fig. 3.1: Object model of the initial version of Mosaic World

				Affecting level				
Affected level	**Environment**	**Genes**	**Neuron**	**Receptor**	**Network**	**Critter**	**Population**	**Species**
Environment	External effect					Depletion of environment	Depletion of environment	Depletion of environment
Genes	Selection pressure	Epistasis, Evolution/ Reproduction, Selection pressure	Selection pressure	Selection pressure	Selection pressure	Selection pressure	Selection pressure	Selection pressure
Neuron	Phenotype	Network communication	Network communication	Network communication				
Receptor	Perception of the environment	Phenotype			Network communication	Perception of self/other critters, Perception of critter state		
Network		Phenotype	Network communication	Network communication				
Critter	Consumption of environment, Movement in environment	Phenotype			Control	Competition, Reproduction		
Population	Consumption of environment, Movement in environment	Extended phenotype					Competition Cooperation	Competition, Cooperation
Species	Consumption of environment, Movement in environment	Extended phenotype					Competition, Cooperation	Competition, Cooperation

Fig. 3.2: Major interactions within the initial version of Mosaic World. For example, the critter→environment interaction denotes the depletion of the environment whereas the environment→critter interaction refers to the critter's consumption of the environment.

Before the methodology is examined, it is important to emphasise that Webb's framework provides guidelines for the construction of good models rather than presents a list of statements that determines what a good model is and what is not; in fact, there is no single description of a model that is universally agreed to be ideal [233]. Furthermore, many of the criteria are subjective and so, cannot be objectively quantified and judged: how does one decide whether model X is more 'accurate' than model Y when their results are not numeric? Or more 'biologically relevant'? Or whether the selection of 'abstraction' and 'levels' is indeed appropriate to the problem? Many times there is no way to determine whether the choice has been appropriate or not, the only thing one can do is provide good reasons for one's choices and back these with real data when available.

Biological relevance: the initial version of Mosaic World utilises three main biological metaphors.

The primary biological metaphor used is a generic simple ecosystem. An ecosystem consists of a community of organisms together with its physical environment; thus, the community processes (reproduction, predation, etc) are strongly related to the physical environment [23]. In this case, the visual environment serves as the underlying context and as the resources available for the critters, the inhabitants of the ecosystem. In this ecosystem there are many types of resources, and one type of organism which has the potential of speciating into different species; however, all critters must be herbivores (at this stage). Therefore, the dynamics of the evolving ecosystem should resemble the dynamics of natural ecosystems.

In addition, the biological metaphor used for the environment is an abstract visual environment, and the critter visual system is based on biological cone photoreceptors. The usage of such an environment forces evolving critters to deal with one of the most fundamental challenges faced by all organisms which rely on vision, namely the inherent ambiguity of visual information. The usage of this visual system increases the likelihood of biologically relevant results (and this is indeed the case, as the 'match' section shows).

Therefore, this version of the model is biologically relevant because:

- it can be used to examine complex interactions. This claim is backed in all the data chapters (ch. 4-8) where a complex interactions analysis is performed.
- it can be used to examine hypotheses that relate to visual evolution (shown in ch. 5).
- it can be used to gain insights about simple ecosystems (demonstrated in ch. 6),
- it can be used to examine other computational and biological hypotheses (in ch. 4 it is used to explore evolvability).

Level: in this version the model consists of several levels: genes (level 1), neurons and receptors (level 2), networks and critters (level 3), population and species (level 4). This selection of levels was chosen in order to provide a sufficient initial framework for exploring complex interactions while creating a realistic challenge for evolution that is not easy but not prohibitively difficult. Although even in this version the system is hierarchical and thus, useful for exploration of complex interactions, the study of complex interactions becomes increasingly more informative as the number of levels increases. Such an increase in hierarchical complexity occurs in chapters 7 and 8.

Generality: the main purpose of the model is the investigation of complex interactions which can be achieved using many types of hierarchical complex system models, and does not require modelling a specific biological system. Furthermore, as stated in section 3.2, the fact that the model was designed to enable the investigation of a large range of hypotheses, and does not focus on a single biological system, suggests that it is general and not specific. That said, the model can be used to examine many specific hypotheses.

Abstraction: the modelled ecosystem, visual environment and critter visual system can be said to be fairly abstract. Although many aspects of the real world have been modelled – and as the accuracy section discusses, these features are based on real world mechanisms – clearly many aspects have been omitted. The rest of the model can be said to be complex. Since this thesis deals with the investigation of complex interactions within a hierarchical complex system, the minimal hierarchical complexity of the model has to be relatively high (thus, in ch. 9 it is shown that a minimum of 6 levels was necessary in order to obtain *all* the insights discovered in this thesis).

Accuracy: although the model is relatively abstract and does not describe complete real world mechanisms, the aspects that are based on the real world are accurate. As stated at the beginning of this section, it is difficult to back this claim; the only way to do so is describe the model's mechanisms that are used and show their similarity (and point out the differences) to the real world phenomenon that is modelled. This will be done in the following chapters as well. The following aspects are based on natural phenomena:

- the model's ecosystem is based on real world ecosystems (as discussed in the 'biological relevance' section).
- the abstract visual environment is strongly based on the visual characteristics of the natural environment, including: the usage of the human visual spectrum, the implementation of multiple illuminants, environment and perceived stimuli.
- The critter visual system is based on the biological cone photoreceptor.

In addition, a caveat which applies to many computational models applies here as well: the algorithm for artificial neural networks used is based on a standard feed-forward artificial neural network and not on the biological neural network.

Match: in the next chapters, the behaviour of the model will be compared with the behaviour of the real world phenomena it aims to capture. That said, it can be said that the version of the model described in this chapter matches the real world behaviours that it aims to capture because its generated behaviours are similar to the behaviour of the target phenomena. Therefore:

- In chapter 5, it will be demonstrated that the evolved visual systems are not only similar to biological visual systems, but also utilise mechanisms reminiscent of those used in nature.
- In chapters 6, it will be shown that the model's ecosystem greatly resembles many real world behaviours that are examined in the chapter.

3.3 Definitions

Three elementary concepts are frequently used in this thesis: reflectance, illumination and stimulus.

3.3.1 Reflectance

Real world objects have a reflectance: a physical constant which determines the percentage of light the object reflects for any given wavelength [225]. In Mosaic World, every object has a reflectance function: the percentage of reflected light in the human visual range (400nm to 700nm [182]) that the object reflects. This is modelled using 31 real numbers between 0 and 1, each representing the percentage of reflected light for a specific wavelength in increments of 10nm.

Although in some experiments the values of all wavelengths are randomly determined, in most experiments only 7 wavelengths are randomly created (referred to as the 7 major wavelengths: 400,450,500,550,600,650,700nm) – all other wavelengths are linear combinations of the two major wavelengths around them (e.g. 460nm = 0.8*450nm+0.2*500nm). This was done in order to generate a set of possible reflectance values that is very large, yet is not too large to be computationally impractical. A sample reflectance is illustrated in figure 3.3.

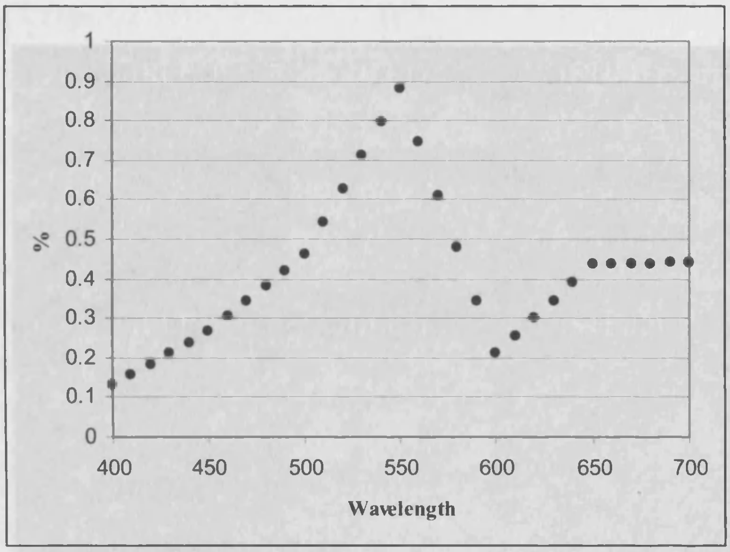


Fig. 3.3: a sample reflectance; a reflectance can be defined using 31 real numbers that describe every wavelength between 400 and 700nm in increments of 10nm.

3.3.2 Illumination

Illumination is the light that shines on a scene [182]. In Mosaic World, every object has an illumination function: the intensity of the light source (in the human visual range) that reaches the object. This is modelled using 31 real numbers between 0 and 1, each representing the intensity of the light for a specific wavelength in increments of 10nm. Essentially, this defines the colour of the light source.

The values of the illumination function are generated precisely the same way as the reflectance function – in most experiments, only the 7 major wavelengths are randomly generated; however, an additional limitation is that illumination intensity values are normally limited to values between 0.2 and 1 (to avoid creating environments that are often too 'dark' for recognition).

3.3.3 Stimulus

As in natural environments, the perceived stimulus for every object is determined by the relative contribution of its reflectance and the shining illumination (in the human visual range). Note that, similarly to the real world, there is no direct way to discern the underlying reflectance and illumination. See fig. 3.4 for visual examples of the creation of stimulus using reflectance and illumination.

$$St(i) = \sum_{i=400}^{700} \mathrm{Re}(i) Il(i) \tag{3.1}$$

Where St(i) is the stimulus value of wavelength i, Re (i) is the reflectance value of wavelength i and Il(i) is the illumination value of wavelength i.

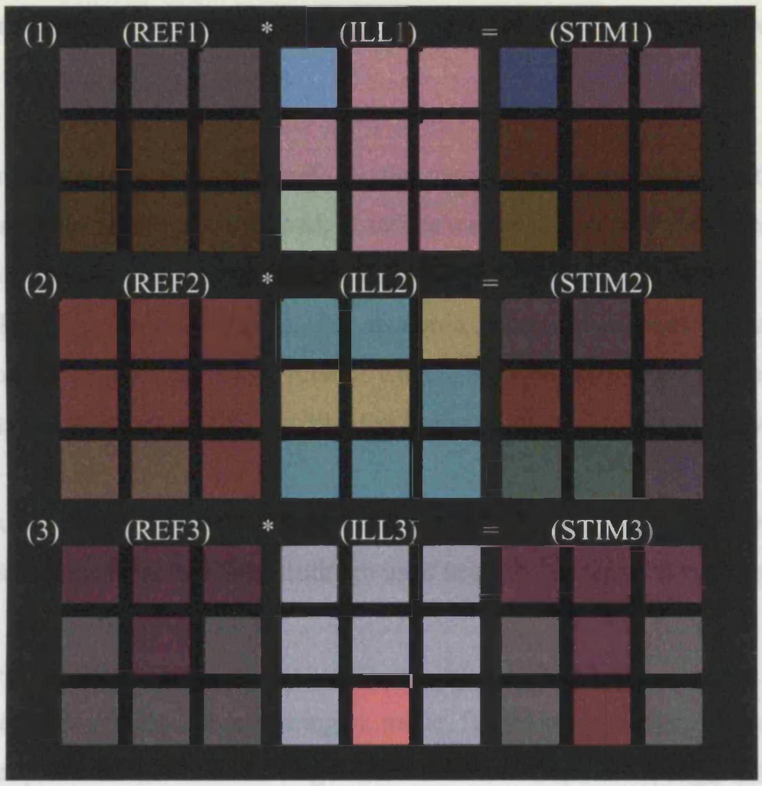


Fig. 3.4: Three examples, each displaying a set of 3x3 reflectances that are illuminated by a 3x3 varied light source; the result is a set of 3x3 stimuli.

3.4 Environment

Mosaic World's environment is a 2D grid that consists of a customisable number of surfaces, normally a 100x100 (empirically determined to be a sufficient size that is computationally feasible). One or more simulated light sources of various qualities and sizes illuminate the surface matrix. A number of holes are present in the world. Nothing exists beyond the edges of the world; a critter that attempts to move more than one surface away from the edges dies instantly.

3.4.1 Surfaces

Surfaces are the most fundamental element of Mosaic World. Every surface has a reflectance function which determines the way it reflects simulated light, and a resource value which determines its behavioural significance: the energy it grants or detracts from a critter that consumes it.

Surfaces are the critters' source of nourishment. Critters 'eat' the constituent wavelengths of a surface's reflectance function. When a critter takes a 'bite' out of a surface, every wavelength in the surface's reflectance function is decreased by the bite size; if a bite reduces a wavelength to a negative value, it is instead set to zero. This implementation was chosen because it was reminiscent of natural consumption: a critter may only eat the wavelengths that are actually there.

A surface's current resource value depends on the percentage of wavelengths that remains from its maximum value. As it is consumed, a surface's resource value diminishes and it also becomes increasingly transparent, eventually becoming invisible. The value of a surface that has been completely consumed is zero. For example, if a surface that has a maximum resource value of 30 has 50% of its constituent wavelengths eaten, its current value is 15; if the surface's maximum resource value is -30, after being consumed its value becomes -15.

Mosaic World uses two methods to determine a surface's resource value: dynamic value function and predefined value function. Both are used in different types of experiments.

Dynamic Value Function

This value function operates by assigning a value for every wavelength in the visual spectrum; normally this is determined using a linear function (equation (3.2)); this essentially defines the behavioural 'worth' of a wavelength. The surface's value is calculated by summing the multiplication of every one of the wavelengths that constitute its reflectance with its behavioural value (equation (3.3)). By altering the values of *a* and *b* in equation (3.2), different values can be assigned for equivalent surfaces. Note that using this type of value function, some wavelengths are worth significantly more than other wavelengths. In fig. 3.5, a sample value function is illustrated; using this value function, the value of the reflectance displayed in fig. 3.3 is -17.43, thus, when such a surface is consumed, it detracts energy.

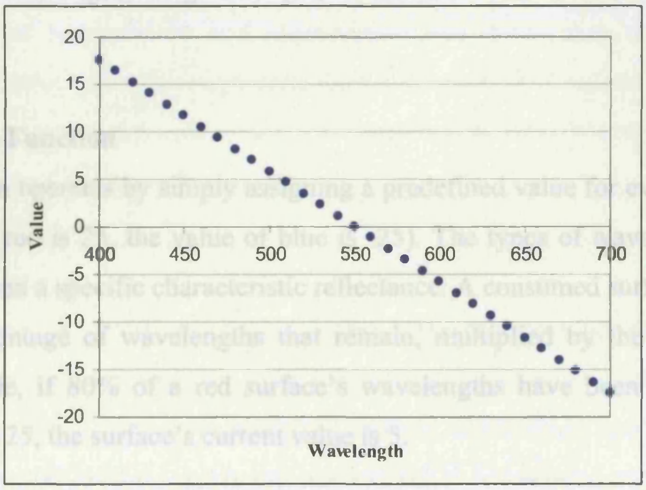


Fig. 3.5: A sample value function. In this example, a = -1.1666 and b = 17.5. The chart illustrates how much every wavelength contributes to the surface's overall value

In addition, complex value functions can be created by using different functions for describing individual wavelengths – this means that equation (3.2) is replaced with other functions.

$$V(i) = \frac{a(i-400)}{10} + b \tag{3.2}$$

Where V(i) is the behavioural value of wavelength i using the value function, and a and b are predefined constants.

$$S = \sum_{i=400}^{700} \mathrm{Re}(i)V(i) \tag{3.3}$$

Where S is the surface's value, Re(i) is the reflectance value of wavelength i, and V(i) is the behavioural value of the wavelength.

This type of value function has been adopted because it provides a useful model of natural phenomena: using this function, similar colours have similar values, and different colours normally have different values as well. Furthermore, it assigns different values to different wavelengths, and thus, may encourage critters to evolve strategies that require them to identify specific wavelengths, which is a desirable goal because it may enable comparison of evolved visual strategies with their natural counterparts. Last, another appealing advantage of this value function has been the fact that every surface is likely to possess both positive wavelengths and negative wavelengths, with the overall value dependent on the proportions of each; this enables creating surfaces with extremely diverse value structures: e.g. the following surfaces are all equivalent and are equal to zero: (i) a surface with few short wavelengths (400nm, highly positive) and many long wavelengths (600nm, mildly negative) (ii) a surface with many medium wavelengths (500nm, mildly positive) and few very long wavelengths (700nm, highly negative) (iii) a surface with a uniform amount of all wavelengths.

Predefined Value Function

This value function operates by simply assigning a predefined value for every type of surface (e.g., the value of red is 25, the value of blue is -25). The types of wavelengths have to be predefined and given a specific characteristic reflectance. A consumed surface's current value is worth the percentage of wavelengths that remain, multiplied by the maximum surface value. For example, if 80% of a red surface's wavelengths have been consumed, and its maximum value is 25, the surface's current value is 5.

This value function is useful but only infrequently used (specifically, in the colour vision experiments – chapter 5); even though it offers far greater control than the dynamic value function – similar colours can have radically different values, and different colours can have identical values – there is a serious limitation to this mechanism: all the possible colours have to be predefined and a specific value must be assigned. This is a serious constraint, since some of the environments used in experiments have thousands of randomly defined shades of colour. Thus, this value function is suitable for experiments that require only a small number of colours.

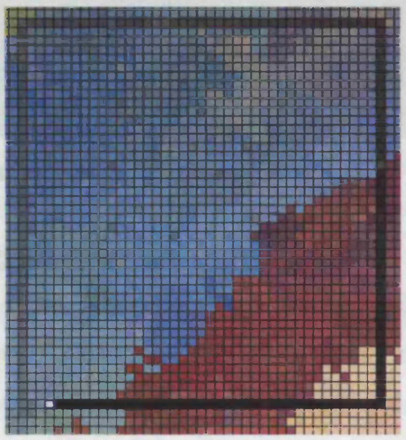


Fig. 3.6: A demonstration of surface regeneration: this image shows the trajectory of a critter that consumes all surfaces in its path. The coloured squares are surfaces, and the white square outlined by blue is a critter. The less that remains of a surface, the more transparent it is. As can be seen, the surfaces the critter recently consumed have not regenerated whereas the surfaces it consumed a while ago are almost fully restored.

Regeneration

A surface that has been consumed slowly regenerates; this is necessary – otherwise, the environment will quickly run out positive resources and the population will become extinct. Two parameters affect regeneration: regeneration speed determines the amount of time steps between intervals of regeneration and regeneration rate determines the percentage of a wavelength's maximum value that regenerate during an interval of regeneration. The value of the surface that regenerated depends on the wavelengths that actually grow. See fig. 3.6 for a visual demonstration of surface regeneration.

Surface display

There are two modes of surface display. The first accurately portrays the surface's current status, meaning, a surface that has 11% of its reflectance's wavelengths remaining will appear like a very weak shade of its full, unconsumed, colour. The second mode displays surfaces that have more than 10% of their maximum value as full (unconsumed surfaces) – the rest are displayed as consumed surfaces (completely transparent). Unsurprisingly, the first mode presents a more difficult challenge than the second – each is used in different experiments.

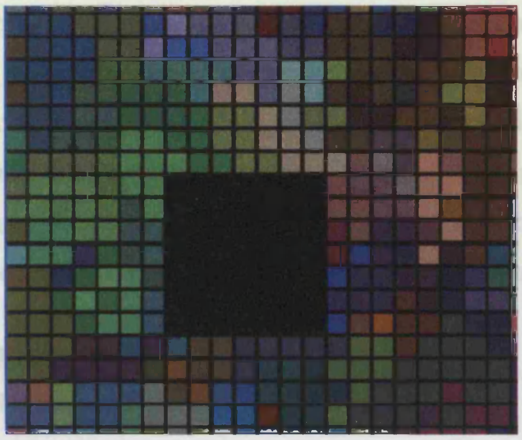


Fig. 3.7: A sample hole: this hole is 7x7 surfaces across.

3.4.2 Light sources: illumination matrix

In order to emulate natural illumination conditions, an illumination matrix that shines on every surface has been created. This simulates the presence of one or more light sources which vary in terms of quality (spectral distribution) and size, and frequently change. The illumination does not affect the value of a surface, however, it affects the way the surface is perceived by critters.

Depending on the experiment, the illumination matrix changes every predefined amount of time, normally 50 time steps (this duration was empirically determined to be the most challenging; shorter durations are simply ignored, while longer durations cause critters to adapt to the specific illumination). This change occurs gradually: an incremental shift between the old and the new illumination matrices takes place. At any given moment, the current illumination matrix is a weighted average of both the new and the old illumination matrices. This attempts to emulate natural scenes, which rarely change completely in a short amount of time.

3.4.3 Perceived stimuli

As in natural environments, the stimuli – the colour – that is perceived by the critters and external viewers (us) depends on the relative contribution of the reflectance (the surface) and the shining illumination, as described in equation (3.1). It is this ambiguous stimulus that is presented to the critters, with the consequence that there is no direct way for a critter's sensors to estimate a given surface's type from the stimulus alone. Thus, a way must be found in order to correctly determine the type of resource – discover whether a surface is 'food' or 'poison'.

3.4.4 Holes

In most experiments, a number of holes, normally 3-9, are present in the surface matrix. A hole's size is customisable, but is often selected to be 7x7 surfaces across (these dimensions are usually a percentage of the dimensions of the surface matrix). Holes are equivalent to the world's edges: they are completely black (thus, are not affected by illumination), and a critter that attempts to move more than one step into them, falls and dies immediately. Holes were added in order to increase the difficulty of the environment and force critters to evolve a strategy of dealing with edges. See fig. 3.7 for a screenshot demonstrating a hole.

3.4.5 Background colour

The surface matrix includes a background colour – a reflectance that is not seen unless surfaces are consumed and consequently become transparent. Therefore, as less of a surface remains, it becomes increasingly similar to the background colour. The chosen background colour is normally grey; it is identical for all surfaces and it is static – it never changes as a result of an action initiated by a critter.

The background colour was incorporated in order to increase the level of difficulty for critters. In early runs, before this feature has been implemented, it was discovered critters learned to recognise good surfaces by the fact they were frequently at least partially eaten. This behaviour was undesirable, as the intention was that critters learn to recognise specific surfaces and not only pursue surfaces that have been eaten. The solution was the creation of the background colour: as a surface gets eaten, it becomes increasingly similar to the background colour; however, since the background colour is grey, and so, similar to all colours, seeing it gives no clue whether a partially eaten surface is good or not. Therefore, the background colour feature increases the difficulty for critters as they are forced to evolve mechanisms for surface recognition and cannot rely on other information to determine whether a surface should be eaten or not. In theory, critters could still use the status of a surface – i.e. whether it is eaten or not – to determine whether it should be consumed; however, because an eaten surface is transparent, and thus, appears like the background colour which is similar to all surfaces, this becomes a very challenging task in its own right.

3.5 Environment creation

In nature, because objects and illuminants are extended in space, two neighbouring points in any image are more likely to have the same physical characteristics than are two points further away from each other. To model this statistical relationship in Mosaic World, an algorithm was created that enables complete control over such clustering across the surface and illumination matrices, as well as the relative proportion of negative and positive wavelength resources in the world. Thus, the generated matrix can be customised in terms of surface/illumination cluster size, which can vary from one surface to the entire surface matrix, as well as each clusters' shading, which can be gradual changes to random transitions.

Specifically, the algorithm must be able to create random surface and illumination matrices, where certain fundamental parameters can determined in advance, including: the number of clusters and their size (very small – one surface across to very big – entire surface matrix), the degree of shading (very gradual changes between clusters to random transitions), the average value of surfaces and the distribution of positive and negative clusters – the last three are only applicable to the creation of the surface matrix.

The algorithm is described in figure 3.8 and four sample environments are displayed in figure 3.9. In addition, in figure 3.10, a sample surface matrix is displayed four times: once with a uniform illumination and three times with different illumination matrices. Note that although the same algorithm is used for the creation of the surface and illumination matrices, different parameter values are used for each.

Constants:
CLUST = the probability (0-100%) of new surfaces being identical to neighbouring surfaces.
SHADE = similarity factor (0-100%) of non-identical surfaces to neighbour surfaces.
POS_RES = the probability (0-100%) of generating a positive surface/resource.
NEG_RES = the probability (0-100%) of generating a negative surface/resource.
SEEDS = the number of random seeds used to initialise the matrix.

Method of operation:

(1) An empty surface matrix is created.

(2) A number of surface seeds (SEEDS) are generated. Every seed is placed in a random location in the matrix and is initialised in one of the following two ways (predefined):
   - (a) The reflectance function is randomly generated (described in 3.3.1, 3.3.2).
   - (b) Using POS_RES and NEG_RES, the surface's type is determined: whether the surface is positive (desired value greater than 3), negative (desired value less than -3) or neutral (desired value is between -3 and 3).
      - i. A reflectance function is randomly generated and its value is calculated using the value function (3.4.1).
      - ii. If the reflectance function's value is of the correct type, proceed. Otherwise, repeat step (i).

(3) A new surface is generated at a random location in the matrix. If there are no adjacent surfaces near this surface, it is removed from the matrix and this step is repeated.

(4) If there are one or more adjacent surfaces, a reflectance function is generated for the surface; this reflectance function is based on a randomly selected neighbouring surface. Using CLUST it is determined whether the new surface is identical or not to the selected neighbour, i.e. with a CLUST value of 0, there is 0% chance it will be identical to one of its neighbours, and 100% it will be different.
   - (a) If the new surface is determined to be identical to its neighbour, the neighbour's reflectance function is copied and used.
   - (b) If the new surface is determined to be different from its neighbour, using SHADE it is determined how similar it would be; this parameter randomly changes all the major wavelengths of the reflectance function, i.e. a SHADE value of 0 causes every major wavelength in the reflectance function to be copied and randomly changed by 0 (so it will be identical to its neighbour), a value of 1 causes major wavelengths to be randomly changed by -1 to +1 (so it will be very different from its neighbour).

(5) Steps (3) and (4) are repeated until all surface positions have been filled.

(6) This step is used only for surface matrix creation. Measure world statistics: unless the average surface value and the distribution of positive and negative clusters are within predefined ranges, go back to step (1).

Fig 3.8: the algorithm for environment creation

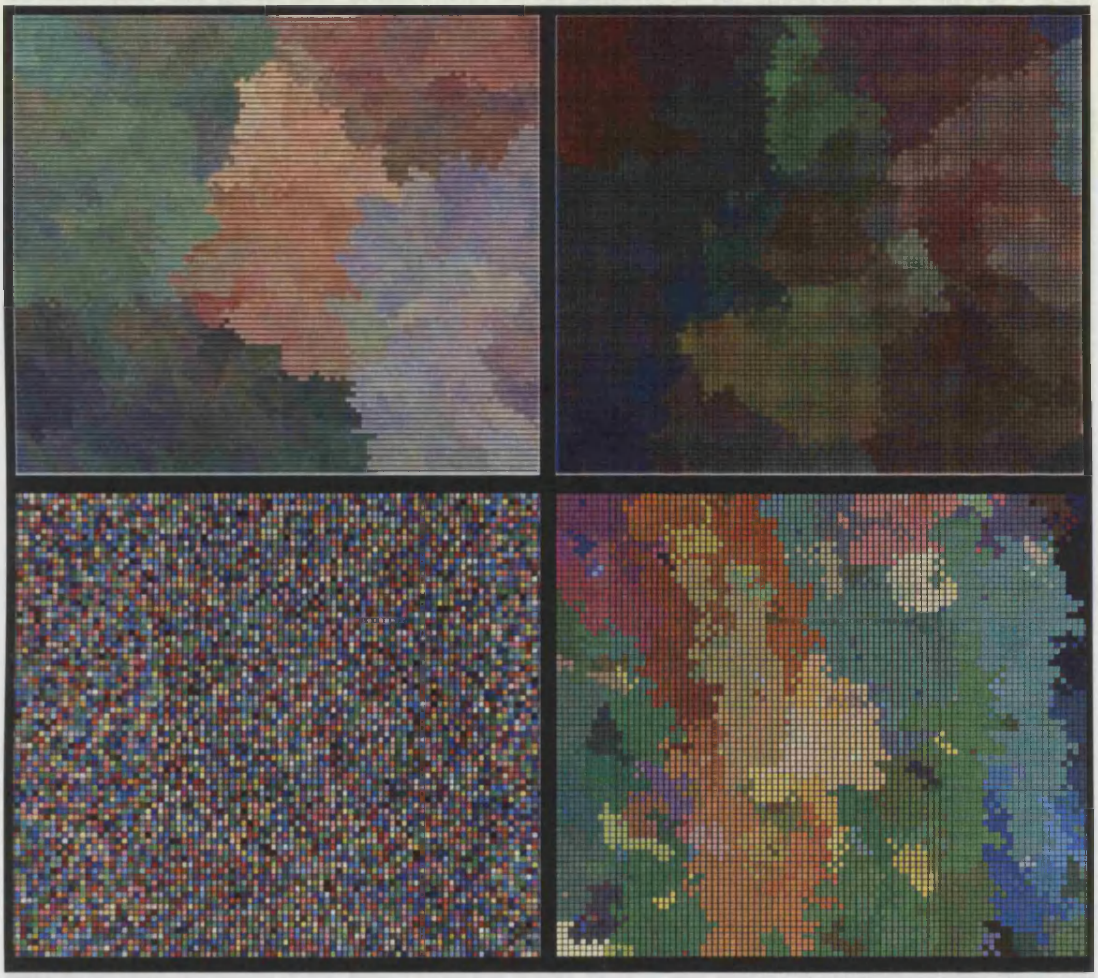


Fig. 3.9: the two top matrices: CLUST set to 0.7, SHADE to 0.2. Lower left matrix: CLUST set to 0, SHADE to 0. Lower right matrix: CLUST set to 0.99, SHADE to 0. Note that certain settings of CLUST may cause the SHADE parameter to have no effect on the surface matrix (e.g., in the lower left image, the fact CLUST is set to 0, defining all surfaces to be different from their neighbours, causes SHADE's setting of 0, which determines the similarity of neighbouring surfaces, to have no effect)

3.6 Critters

Critters are the inhabitants of Mosaic World. Every critter has field of view which is the area it receives stimuli from the environment, and an orientation - a direction it is facing. All critters are created with a certain amount of energy, which decreases in time; this models the flow of resources in and out of biological organisms. If a critter runs out of energy, it dies, giving it a strong incentive to gain energy by consuming surfaces. The amount of energy lost every time step is also dependent on the actions the critter performs (see section 3.6.1). Finally, critters have a limited life span – a critter that manages to survive longer than 15,000 time steps dies immediately; this feature prevents particularly fit critters from taking over the environment and gives new critters with novel behaviours an opportunity to thrive. Figure 3.11 displays a snapshot of Mosaic World with multiple critters.

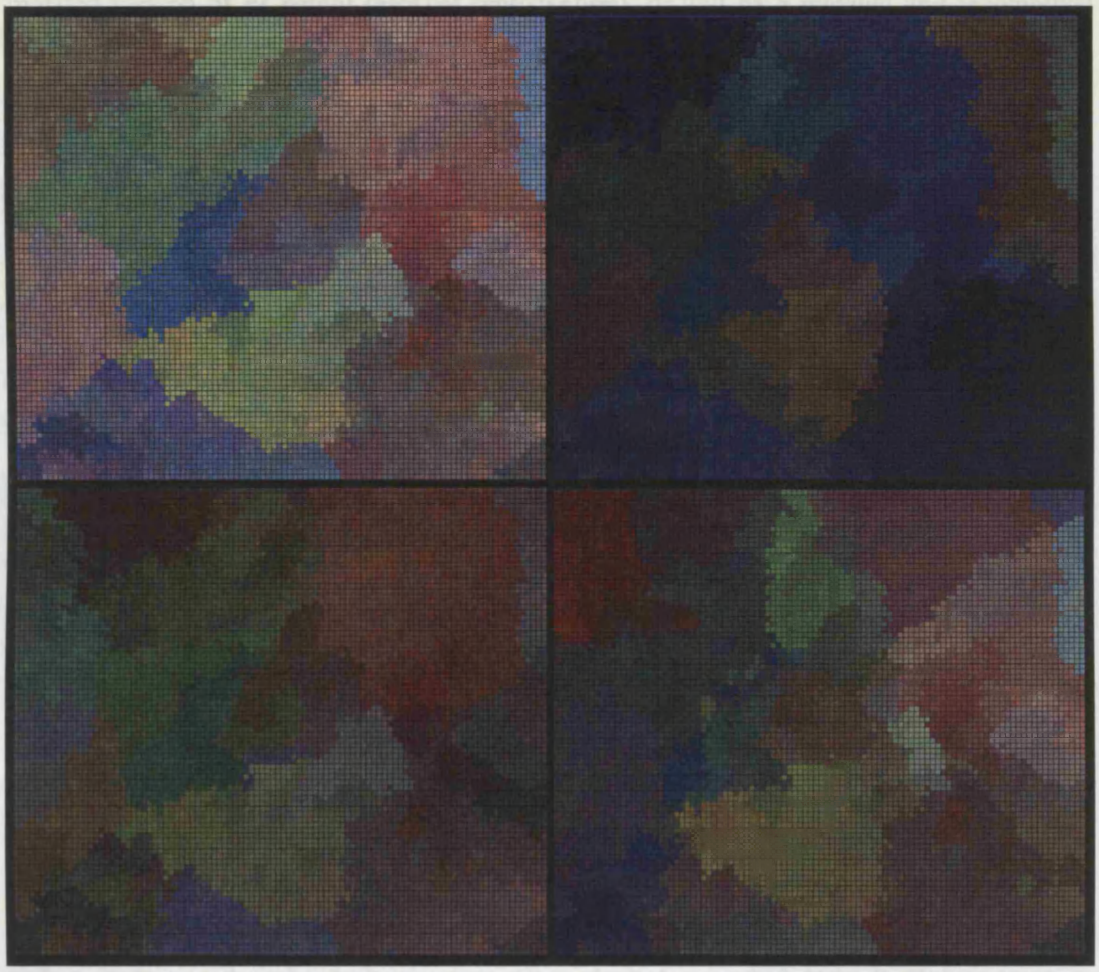


Fig. 3.10: Top left: a surface matrix (without a light source). Top right and the two lower images: the same surface matrix lighted by with different illumination matrices.

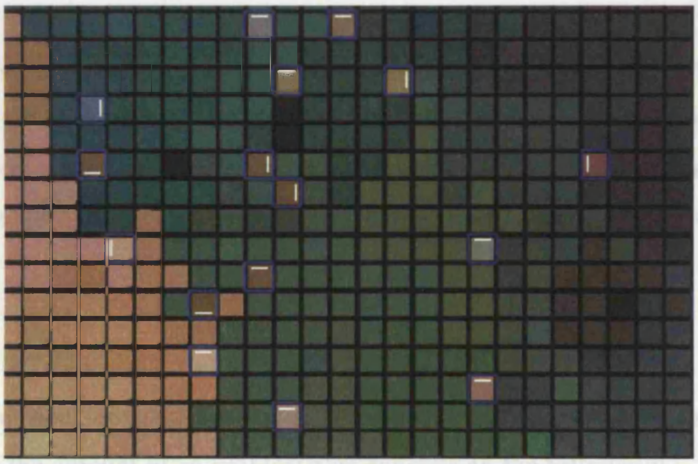


Fig. 3.11: A close-up on a section of Mosaic World with many critters. The critters are the squares surrounded by a blue frame; the white line indicates the direction they are facing.

The critter population is maintained in Mosaic World through sexual and asexual reproduction. Depending on the mode of reproduction, an offspring's genome will either be a mutated version of its parent (asexual reproduction), or will be a mutated and recombined version of its parents' genomes (sexual reproduction).

Although the environment is two dimensional, it can be said that critters hover above the surface matrix and underneath the illumination matrix.

3.6.1 Energy

Upon instantiation, all critters are given a certain amount of energy which decreases in time. If a critter's energy level drops to zero, it dies immediately. This feature models an organism's metabolism, specifically, the fact that some required internal processes cost energy. Furthermore, the addition of this feature prevents critters from simply standing and forces them to forage (and indirectly, to find a way of finding positive resources).

Gaining energy

A critter can gain energy by consuming a surface. For consumption to occur, a critter needs to be in contact with the surface for a predefined amount of time (2 time steps). The critter determines on its own the size of its bite (using the 'bite' output unit in its artificial neural network). A critter's bite decreases the surface's reflectance function by the bite size and the critter gains/loses energy depending on the amount and value of the wavelengths consumed. A critter may only consume wavelengths that are actually present (i.e. it cannot cause a reflectance's wavelengths to become negative through repeated biting). Biting costs an amount of energy that is relative to the bite size; however, there is a fixed component to this cost as well (meaning, biting costs energy even if its size is infinitesimal).

The bite size feature was implemented in order to encourage critters to evolve biting strategies, thus, the cost relative to the bite size was determined to be appropriate. However, in order to prevent situations where critters take infinitesimal bites to sample surfaces and thus, avoid the need to recognise surfaces, an additional fixed component was added to the cost.

Losing energy

Even a critter that does not perform any action loses a certain amount of energy every time step. In addition, the amount of energy lost also depends on the following:

- Rate of motion
- Turning

- Surface consumption
- Reproduction: sexual and asexual
- Failed attempts of reproduction (sexual and asexual)

3.6.2 Movement and turning

A critter may move between 0 and 4 surfaces every time step; similar to the real world, moving faster costs considerably more energy in terms of energy per surface moved. A critter may only move forward. The critter's movement depends on its orientation, which is the direction it is facing. By activating the 'move' output unit in its artificial neural network, the critter determines whether it wants to move, and if it does, the speed of movement.

A critter can turn in increments of 90 degrees. When a critter turns, its orientation and field of view turn with it. A critter turns by activating two output units: 'left' and 'right'. If the difference in activations between 'left' and 'right' is greater than a given value (0.25), the critter turns right; if it is lesser than a negative value (-0.25), the critter turns left; if in between these values, the critter does not turn. In early runs, movement was controlled by a single output unit, however, there was a noticeable bias towards turning in one direction; this bias was eliminated by using two output units.

3.6.3 Genome

Every critter has a genome which defines all its traits: its brain (visual layer/receptors: position, sensitivity, peak and state), brain structure (number and position of hidden units), brain contents (all information regarding the connection weights: weight values, starting coordinate, ending coordinate and state, and all the information regarding partial connections: weight values, ending coordinates) and the critter's transmittance. There is a one to one relationship between the genes in the genome and a critter's phenotype. Similar to natural evolution, when critters reproduce their offspring inherits traits from them using the genetic operators of mutation and crossover.

Each physical attribute of the critter is treated as an object, and each object can either mutate, or parts of it can be recombined with comparable objects from other critters during sexual reproduction. Thus, the only time the genome is explicitly displayed is when a critter is saved for analysis and is stored in a text file (see summarised genome in Figure 3.12).

This specific representation for the genome was selected because it is easy for a human to read and modify it, and also because it is unambiguous: only one possible phenotype can be constructed using this genome.

Transmittance: 0.33, 0.35, 0.37, 0.40, 0.42, 0.44, 0.45, 0.46, 0.46, 0.47, 0.48, 0.50, 0.52, 0.54, 0.56, 0.58, 0.57, 0.5, 0.53, 0.51, 0.49, 0.51, 0.52, 0.54, 0.55, 0.57, 0.58, 0.58, 0.59, 0.60, 0.61

3D Neural network (partially connected):

Visual layer: 3 units:

- Health unit
- Receptor 1: coordinate: [0,-1], peak: 680nm, tuning: 0.01226, active.
- Receptor 2: coordinate: [0,0], peak: 400nm, tuning: 0.02868, active.

Hidden layer: 4 units:

- Hidden unit 1: coordinate [-1,-1]
- Hidden unit 2: coordinate [0,0]
- Hidden unit 3: coordinate [2,0]
- Hidden unit 4: coordinate [-1,1]

Output layer: 7 units

Active Connections: 33

Partial connections: 1

Fig. 3.12: Summarised sample of a critter genome.

3.6.4 Reproduction

Critters can reproduce both sexually and asexually. In both types of reproduction, the parent(s) must have at least a minimum amount of energy (20% of maximum energy), otherwise reproduction fails. In addition, the parent(s) must not move for a predefined amount of time (3 time steps). The created offspring is spawned in the vicinity of its parent(s), with decreasing probability of spawning farther away.

Sexual reproduction was implemented to be able to examine the strategies critters evolve in order to recognise and attract mates; however, early runs demonstrated that using only sexual reproduction is simply too difficult for an untrained critter – learning how and when to reproduce is hard enough even when there is no need to also identify a potential mate. Thus, asexual reproduction was created in addition.

Sexual reproduction

In order to sexually reproduce, two critters need to be in contact – they must be on the same surface. At least one of the critters involved must 'want' to reproduce sexually: the 'sexual reproduction' output unit in its artificial neural network must be activated; this enables critters to determine when may be a good time to reproduce (e.g. currently have a lot of energy resources).

Once sexual reproduction occurs, an offspring spawns. The offspring's initial energy is transferred from both its parents: 25% of a critter's maximum energy is transferred from each parent. If the partner (the critter that did not initiate the reproduction) does not have this amount of energy, mating fails. If as a result of mating, the initiating critter's energy level drops below zero, reproduction is still successful; however, the offspring only gets the initiating critter's available energy, and the initiating critter dies at the end of this process.

If a critter tries reproducing sexually but fails because there's no other critter next to it, or it has not waited the required number of time steps, it pays an energy penalty: this was done to discourage critters from constantly trying to reproduce sexually.

Asexual reproduction

A critter can reproduce asexually without requiring a partner. The critter must 'want' to reproduce asexually (the 'asexual reproduction' output unit in its artificial neural network must be activated). Once asexual reproduction occurs, an offspring is created. The offspring's initial energy, 40% of a critter's maximum energy, is transferred from its parent. If the parent does not have this amount of energy, whatever energy it possesses is transferred to the offspring, and afterwards, the parent dies.

If a critter tries reproducing asexually but fails because it has not waited the required number of time steps, it pays an energy penalty: this was done to discourage critters from constantly activating the 'asexual reproduction' output unit and effectively using the 'movement' output unit to initiate reproduction.

The offspring's genome

There is a predefined probability (70%, determined using [147]) that an offspring's genome that is created through sexual reproduction will be a recombined version of both its parents' genomes, using the custom crossover operator described in 3.7.3 (note that the actual percentage of crossover is lower since asexual reproduction does not utilise crossover). As part of the process, the offspring's genome is also mutated. If crossover does not occur, the offspring's genome is cloned from one of its parents (randomly determined) and mutated in the process.

An offspring's genome that is created through asexual reproduction is cloned from its parent and mutated in the process.

3.6.5 Transmittance

Transmittance describes the percentage of light that passes through an object [182]. Every critter possesses a transmittance; this property defines the percentage of light for every wavelength in the human visual range that passes through the critter, and effectively defines the critter's colour. The critter's transmittance is defined in the critter's genome and is evolvable – thus, critters have the potential of using transmittance as a way of recognising conspecifics or as camouflage; this is the reason this feature has been added.

The critter's transmittance affects the stimulus that is perceived by other critters and external viewers – a critter cannot see itself. Therefore, when critters hover above a surface, equation (3.4) should be used instead of equation (3.1). There are two elements to this change:

(i) Some of the light source passes through the critter, which acts as a filter. The resulting light reaches the surface and gets reflected.

(ii) The rest of the light source is reflected of the critter and thus never reaches the surface.

The resulting stimulus is a sum of (i) and (ii).

For the sake of simplicity, when more than one critter is present in the same physical location, the transmittance of the critter that arrived first dominates the transmittances of the other critters.

$$St(i) = \sum_{i=400}^{700} \mathrm{Re}(i) Il(i) Tr(i) + \sum_{i=400}^{700} Il(i)(1 - Tr(i)) \tag{3.4}$$

Where *St(i)* is the stimulus value of wavelength *i*, *Re(i)* is the reflectance value of wavelength *i*, *Il(i)* is the illumination value of wavelength *i* and *Tr(i)* is the critter's transmittance value of wavelength *i*. The left side of the equation, which characterises the light that passes through the critter, is described by item (i) above. The right side of the equation, which characterises the light that is reflected of the critter, is described by item (ii) above.

3.7 Critter Brain

Every critter possesses a brain that determines its actions according to the stimuli received from the environment. The brain comprises a 3D neural network, which is essentially a modified feed-forward artificial neural network. See figure 3.13 for a sample critter brain.

The 3D network is composed of multiple 2D layers. The visual layer is equivalent to a standard input layer and contains receptors (which are effectively modified input units). The hidden layer contains standard hidden units. The output layer contains output units, which determine the critter's behaviour: turn left or right, move forward or stay in the same position, sexually reproduce with a nearby critter, asexually reproduce and bite surface.

Every unit in the network has an [x,y] coordinate relative to the critter's centre, which defines its location in the layer it is placed in – only a single unit can be placed at any given location. Thus, networks of vastly different architectures can be crossed over during sexual reproduction, as each network possesses the same virtual coordinate reference frame; this deals with the competing conventions problem in crossover of neural network (described in 2.7.3), and is the reason why this structure has been selected.

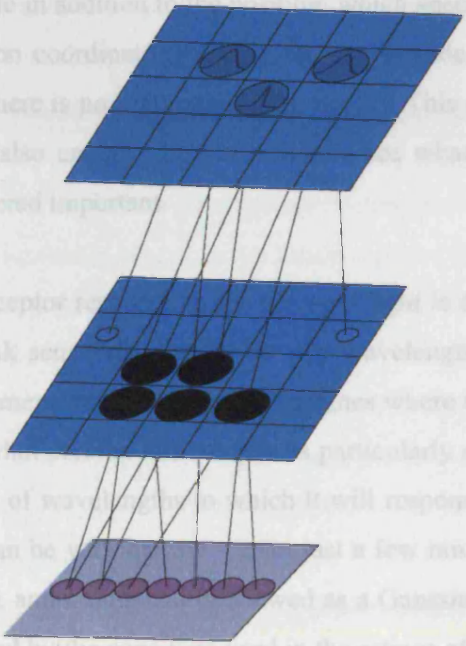


Fig. 3.13: Sample critter brain which has three layers. The visual layer contains three receptors (one highly tuned, the other two possess lower tuning values). The visual layer is connected to the hidden layer, specifically to five hidden units and two empty coordinates (partial connections). The hidden layer is connected to the output layer.

The units of the network communicate through connection weights that extend between units from higher layers to lower layers. Connections can be active, inactive, or completely nonexistent. In addition, partial connections may be present in the network; these connections extend from a unit to a coordinate instead of terminating at a unit. Inactive or partial connections do not participate in the feed-forward process; however, they are passed on to a critter's offspring where they may be reactivated or reconnected as a result of crossover – this offers the potential of creating novel patterns of connectivity that existed in neither parent. Connections are discarded if inactive or partial for long periods of evolutionary time (this was implemented to prevent bloat: without this feature a large number of inactive connections quickly accumulate).

3.7.1 Visual Layer

The visual layer, which contains receptors, is equivalent to the input layer in a standard neural network. Like all units in the network, every receptor has a spatial *position*, an [x,y] coordinate in the visual layer. In some experiments, the receptor's position in the visual layer also determines the location – relative to the critter's centre – where it detects light from Mosaic World (i.e., its visual 'receptive field'). For example, a receptor located in [-1,0] receives stimuli from a surface that is to the left of the critter. In other experiments, a receptor has another [x,y] coordinate in addition to the position, which specifies the *critter's receptive field* instead of the location coordinate. Viewing an area outside of Mosaic World returns nothing but darkness (as there is no light outside the world). This enables evolution to select what the critter sees and also enables the researcher to see what locations (relative to the critter's centre) are considered important.

The manner in which a receptor responds to the received light is determined by its *peak* and *tuning*. The receptor's peak sensitivity can be for any wavelength within the human visual range (400-700nm at increments of 10nm); this determines where the receptor's sensitivity is greatest, and effectively, what colours this receptor is particularly sensitive to. The receptor's tuning defines the number of wavelengths to which it will respond around its peak (its 'half bandwidth'). A receptor can be very narrow – span just a few nm – or it can span the entire visible spectrum. The peak and tuning can be viewed as a Gaussian function. This particular design was strongly inspired by the cone type used in the retinas of biological eyes [182, 225] and attempts to emulate this mechanism – the goal was to discover whether evolved structures (peak and sensitivity) bear any resemblance to their biological counterparts.

A receptor can be either *active or inactive*. Inactive receptors do not participate in subsequent processing, but are nonetheless inherited by offspring; these are discarded if inactive for a long period of evolutionary time (and so are all connections leading out of this receptor) – this was implemented in order to avoid bloat – many inactive receptors for every critter.

In addition to receptors, every critter also has a health monitor unit, a special type of input unit which is located in the visual layer; this unit receives the percentage of the critter's remaining health. This unit cannot be removed or disabled through evolution; however, leading connections can be disabled. This feature was implemented in order to enable critters to evolve behavioural strategies that depend on their current level of health (see chapter 6, challenge: behaviour).

3.7.2 Genetic operator: mutation

Mutation takes place during sexual and asexual reproduction. There are several types of mutations.

Value Mutation affects the values of the connection weights through a Gaussian function: small changes are much more likely to occur than large changes.

Structural Mutations are mutations which alter the brain's topology.

- *Add unit mutation* enables addition of units (receptors, hidden) (2%). When a receptor is added, it is randomly placed in the visual layer with a bias towards the centre; this receptor's design is based on an existing receptor (randomly picked): its peak and connectivity, as well as its outgoing connections are copied. When a hidden unit is added, it is randomly placed in the hidden layer with a bias towards the centre and forms connections with units in the adjacent layers – it is fully connected; all new connections are initialised with random values.
- *Delete unit mutation* enables deletion of units (receptors, hidden) (0.5% per unit). When any type of unit is removed, all its outgoing connections are deleted. If as a result of a unit being deleted a connection now has no end destination, it remains in the network as a partial connection.
- *Add connection mutation* enables addition of connections (1%). Connections can only be added between units that do not already have an existing connection. New connections are initialised with random values
- *Delete connection mutation* enables deletion of connection weights (0.1% per connection).

Receptor mutations are mutations that change properties of receptors.

- *Drift Receptor* mutation (0.3% per receptor) changes a receptor's location in the visual layer; all its outgoing connections move with it. The receptor's new position is random yet biased: it is more likely to be closer to the critter's centre than farther away.
- *Drift Receptive Field* mutation (0.3% per receptor) changes the location of the receptor's receptive field (the area it receives stimulus from). The new receptive field is random yet biased – it is more likely to be closer to the critter's centre than farther

away. In experiments where the receptive field is dependent on the receptor's position, this mutation does not exist.

- *Alter Peak* mutation (2% per receptor) randomly changes the receptor's peak to another wavelength (400 to 700nm, in increments of 10nm)
- *Alter Tuning* mutation affects the receptor's tuning value through a Gaussian function: small changes are much more likely to occur than large changes.

State mutation has a given probability of activating or deactivating a connection (0.3% per connection) or a receptor (0.3% per receptor). If a connection or a receptor has been inactive for a large period of evolutionary time (15,000 time steps), it gets discarded.

Transmittance mutations alter the critter's transmittance (10% for each of the seven major wavelengths). The wavelength's value changes by up to ±0.05, however, it cannot increase above 1 or below 0.2. The minor wavelengths are automatically adjusted.

The initial values of the parameters were determined using available literature on genetic algorithms [147] and the evolution of neural networks (particularly [215]). Afterwards, a considerable amount of preliminary experiments was conducted in order to discover useful values for the used parameters. Since the number of possible permutations and the amount of interactions going on between some of the parameters is quite large, it is possible that some of these values are not ideal.

3.7.3 Genetic operator: crossover

Crossover takes place during sexual reproduction at a predefined probability (70%). During crossover, a random point is selected on each network layer of both mating critters. All 3D layers of each critter brain are 'sliced' at this point. These two parts are copied, and the result is combined to form the offspring's genome. This process may cause partial connections to reconnect, for instance, if a partial connection is obtained from one parent, and a hidden node at the corresponding coordinate that previously lacked a connection is obtained from the other parent, the partial connection is converted to a standard connection.

This method of crossover has been selected because it has the potential of overcoming the competing conventions problem encountered in crossover of neural network (described in 2.7.3).

Crossover also recombines the transmittances of both mating critters; a random major wavelength is randomly picked and divides the transmittance to two parts: a part is copied from every parent. Thus, the offspring critter's colour is similar to both its parents' colours.

3.8 Evolution

To maintain an open-ended system, Mosaic World's evolution utilises a genetic algorithm with no fixed population size and no explicit fitness function. The critters themselves decide when to reproduce (sexually or asexually) by activating the appropriate output neurons. Critters survive if they can eat good resources and stay on the world. Thus, there's an implicit evolutionary selection pressure to improve all traits that increase such skills. For the population to survive, the critters must balance reproduction with resource consumption. Otherwise, there may be too many critters for the world to sustain, or too few critters to maintain the population. This implicit version of selection has been implemented because it is closer to biology than the explicit selection algorithms used in standard genetic algorithms. Note that there is no maximum population size; however, the environment can only sustain more than a certain number of critters (around 700 critters) for short periods of time.

Because at time-step 0 all critters are randomly instantiated, a statistical consequence of this is that the initial population sometimes dies. When this happens, a new population of random critters is instantiated, with the caveat that 20% are mutated clones of critters that showed general promising surviving skills (a combination of survival age and mating amount).

3.9 Technical Aspects

- Programming language used: Mosaic World was written in C++ under the Windows environment (Visual C++).
- Computational requirements: the vast majority of experiments were designed to run approximately 15 hours (overnight experiments). However, several difficult experiments (most notably, those in chapter 5 part 1) were designed to run over longer periods of time (approximately 2 days).

3.10 Chapter Summary

This chapter introduced Mosaic World, the model used in this thesis for the investigation of complex interactions and other computational and biological hypotheses. Because an abstract visual environment was picked as the underlying context of the model, the chapter began by outlining the essential fundamental concepts of reflectance, illumination and stimulus.

Afterwards, a detailed description of the environment was given: the resources it provides (surfaces), the dangers that are present (holes and edges) and the inherent ambiguity that is incorporated into the environment (the light sources that illuminate the environment). In addition, the algorithm used for environment creation (surface and illumination matrices) was given.

The chapter concluded by giving a thorough description of the inhabitants of Mosaic World: the critters. This included a description of critter capabilities and behaviour (movement, reproduction and consumption), critter operation (brain and genome), and the evolutionary process that takes place.

Chapter 4

Challenge: evolvability

4.1 Introduction

Evolvability is the ability of a population to continually produce offspring fitter than any currently in existence. Since genes directly determine the organism's phenotype, it can be said that that the way in which the genome is altered through the course of evolution by way of mutation and recombination, in addition to epistasis, the effect that some genes have on the operation of others, is essentially the cause of higher or lower evolvability. Therefore, it can be said that evolvability is the ability of genes in the population to change in a way that produces fitter offspring. Consequently, the study of evolvability involves interactions that occur between genes (genes→genes interactions).

There are several ways in which the interaction of genes can affect the fitness of the phenotype. When a gene gets altered, the value of the trait it encodes is changed. In Mosaic World, this means that a neuron, a receptor or a trait gene is expressed differently the next time the phenotype is created from the genome, and consequently, the network controlling the critter (and possibly even the population the critter is a member of) is affected by this change. This change to the phenotype may have an indirect effect on traits encoded by other genes; for example, in Mosaic World, consumption of a resource requires standing still for a period of time, thus, a gene that makes a critter constantly move would indirectly affect the gene that controls consumption, effectively neutralising it. In addition, a gene may affect other genes in a more straightforward manner: when a gene that controls the peak or tuning of a receptor is altered, the stimulus that is perceived by the network may be very different, and thus, the network's behaviour – which depends on many other genes – may be completely changed. A gene may also affect other genes during the process of reproduction: for example, the gene controlling the distance parameter, explained later in this chapter, would affect the number and identities of units that connect to a newly added hidden unit.

Later chapters investigate the effect of evolving genes on the major aspects of critters (e.g., receptors, neural networks, population-level behaviours). However, it can be argued that the most fundamental effect of genes on other genes is during reproduction: children inherit their parents' genes with some mutation, and so it is the interaction of parent genes, and parent and child genes, that produces a new and potentially better solution. A useful interaction between parent and child genes implies an evolvable population, so an understanding of the evolvability of a population provides knowledge on useful parent and child gene interactions. It is this evolutionary genes→genes interaction that forms the focus of this chapter. Therefore, the experiments described in this chapter investigate the resultant effect on evolvability as a consequence of the process used to evolve the neural networks used in critter control. The challenge posed for Mosaic World in this chapter is:

Can appropriate genes→genes interactions occur that improve the effective and resilient evolution of critters that adapt to an environment which becomes increasingly more difficult through time?

To enable Mosaic World to address this challenge, several different ways of transferring parent genes to child genes (focusing on the genes responsible for the topology of the critters' neural networks) will be examined, allowing the investigation of the way different forms of genes→genes interactions affect the evolvability of neural network agents.

4.2 Investigating evolvability

Evolvability is generally defined as the capacity to evolve [136], or more specifically, as the ability of a population to produce offspring fitter than any yet in existence [4], and not to produce less fit variants [212]. Evolvability is also known as evolutionary adaptability [107] and as such, a major element of evolvability is the capacity to adapt to changing environments by learning to exploit commonalities over time in those environments. Thus, by understanding evolvability and how to promote it, not only will it be possible to solve increasingly complex problems, but one may also better understand the process of evolution generally.

Evolvability should not be confused with fitness. It is possible to have two populations of solutions, both with identical levels of fitness. However, if one is more evolvable than the other, then its offspring are more likely to be fitter in relation to those in the less evolvable population in subsequent generations [227]. This can prove to be crucial when the environment is dynamic.

The key properties required to generate systems exhibiting high evolvability are still not completely understood, particularly in the context of artificial life simulations. The evolvability of a system appears to be strongly linked to the representation of the problem – the way genetic variation is mapped onto the phenotype [22, 228], as well as the choice of search operators [4]; these parameters determine the distribution of local optima in the search space, and as a result affect the difficulty in finding fitter offspring [67]. It was shown that for the search to be successful, the mapping should put similar phenotypes close to each other in solution space [116], or in other words, the search operators' effect should be gradual [5].

A necessary precondition for high evolvability would involve a many-to-one genotype-to-phenotype mapping. This redundant mapping would enable many mutations to have no effect on the phenotype, and as a result, better explore the search space through neutral networks [58]. It can be argued that evolution of neural networks, particularly those that are used for control and classification, qualifies for the complex mapping condition; Fogel [61] defined an evolved neural network's phenotype as its behaviour, and not its constituent weights. Using this definition, changing many aspects of a neural network would not necessarily change its phenotype (behaviour).

Modularity has been recognised as an element that increases evolvability [228]. It has been suggested that the ability to reuse structures in neural networks should increase evolvability as well [160]. It has also been proposed that adaptive evolution, the ability of evolution adapting elements of itself, promotes evolvability [22, 67]; this was theorised to enable evolution to tune search operators as needed during various evolutionary stages.

Even though there are many issues to consider when evolving solutions using standard genetic algorithms, there are many more challenging issues one must consider when it comes to the evolution of neural networks, for example, evolving network topology requires adding and removing elements from the network. This does not sound like a terribly complicated procedure, but then, how are these network elements added? Are new units fully connected? Are they connected at all? Can we allow evolution itself to make this decision? Each of these decisions may have a huge impact on the evolution process by affecting the genes that determine the network structure and the interactions that occur between them. Inevitably, these changes to the genome affect the entire hierarchy of the phenotype – which influences many additional parameters including likelihood of runs being successful as well as the variability and quality of evolved solutions; consequently, it is crucial to pick a good method.

While a lot of research focused on evolution of neural networks, including topology, it is difficult to predict whether a method will be superior to others and understand why that is the case. The problem is there are no clear guiding principles as to what will work better, and this becomes more complicated when trying to evolve neural networks in artificial life models, where even measuring the quality of the evolved solution becomes problematic. The answer to this problem largely depends on the system's evolvability, which in turn depends on numerous parameters – all essentially relating to the interactions that go on between genes.

In this chapter, the question of the process by which network elements are to be added (and removed) is addressed by focusing, not on the evolved solutions as such, but on the evolvability of the critters themselves. (The work described here has been published in [196]). This investigation of evolvability is conducted using several different types of structural mutations which affect the interactions between genes in different ways. For a mutation type to be useable, it must have the ability to completely alter a neural network's structure by adding and deleting elements. In order to be able to test the effects of the suggested principles thought to increase evolvability, every mutation type used in the experiments incorporated some of these principles. The three principles tested are:

- *Incremental changes to network topology*, where every change made to the network structure is very small.
- *Adaptive evolution*, where evolution can modify some aspects of itself.
- *Structural duplication*, where existing substructures of the network are copied and can be reused.

4.3 Additions to Mosaic World

The investigations described in this chapter required that initial version of Mosaic World be expanded in several minor ways.

4.3.1 New types of structural mutations

The investigations of evolvability were performed using several different types of structural mutations in order to evolve the topology of the neural networks that form the critter brain. Therefore, the following five types of structural mutations are added to the model and replace the relevant types described in section 3.7.2 (see fig. 4.1 for an illustration). All structural mutations must be able to add and remove units and connections from the networks; the only difference is the manner in which this change is accomplished – the way the genes interact. All new connections to the network are initialised with random values. The probabilities of occurrence of these mutations are identical for all types. The tested principle appears in parenthesis.

Structural mutation type 1 – fully connected (non-gradual changes): when using this mechanism, new receptors and hidden units that are added to the network connect to all units in adjacent layers. Using this method, every mutation makes a potentially large change to the networks.

Structural mutation type 2 - single connection (gradual changes): when using this mechanism, new receptors and hidden units connect to a single, randomly chosen, unit in every adjacent layer – exactly two new connections are added to the network in case of a hidden unit addition, and one new connection for the addition of a receptor. In addition, the Delete Unit mechanism is disabled – units are automatically removed when they have no outgoing or incoming connections. Using this method, every mutation makes a small change to the network.

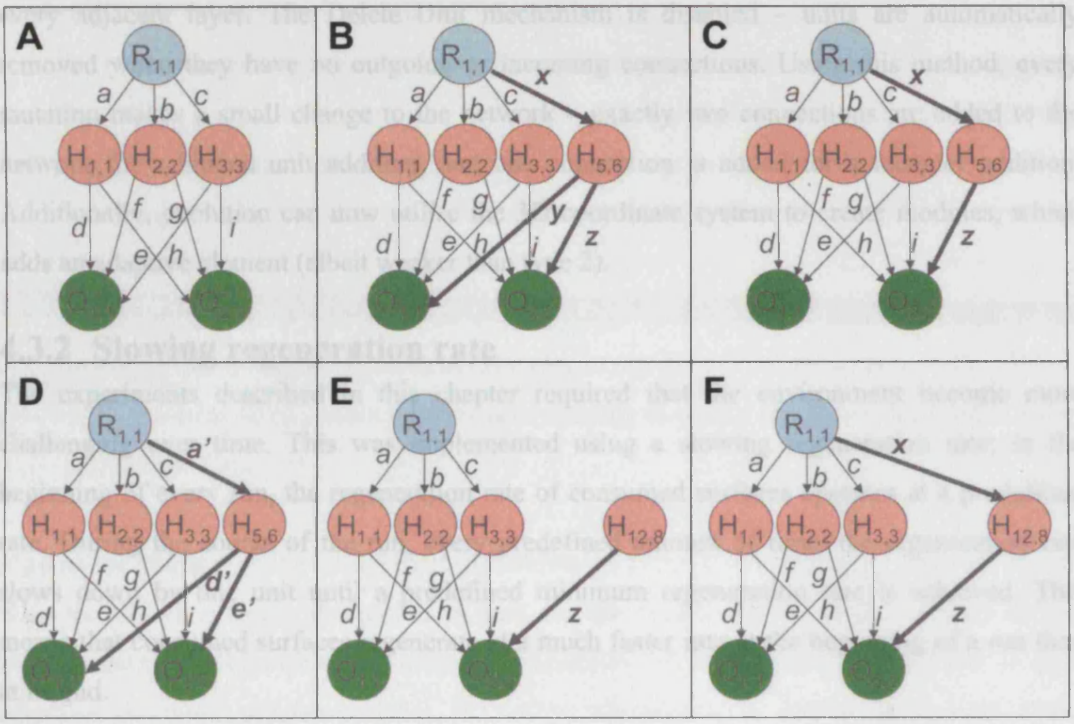


Fig 4.1. A visual illustration of addition of a hidden unit using the five types of structural mutations. [A] The original neural network with 1 receptor, 3 hidden units, and 2 output units. [B] Using mutation type (i), new unit (H5,6) is fully connected through 3 random connections. [C] Using mutation type (ii), new unit (H5,6) connects to (R1,1) and (O2,2). [D] Using mutation type (iii), new unit (H5,6) is a clone of (H1,1). [E] Using mutation type (iv) new unit (H12,8) only connects to (O2,2) as the distance parameter is very high. [F] Using mutation type (v) new unit (H12,8) connects to the closest receptor (R1,1) and closest output unit (O2,2).

Structural mutation type 3 – reuse of structures (structural duplication): When using this mechanism, added receptors and hidden units are cloned from a random unit in the same layer. The new unit possesses a copy of every incoming and outgoing connection of the original.

Structural mutation type 4 – distance dependent (adaptive evolution, gradual changes): When using this mechanism, added receptors and hidden units connect to all units in adjacent layers within a given distance (which is calculated using the coordinate scheme described in section 3.7). The distance parameter is an evolvable gene of a critter. By evolving a low distance parameter, the change to the network can be very small or very large.

Structural mutation type 5 – shortest connection (adaptive evolution, gradual changes): when using this mechanism, added receptors and hidden units connect to the closest unit in every adjacent layer. The Delete Unit mechanism is disabled – units are automatically removed when they have no outgoing or incoming connections. Using this method, every mutation makes a small change to the network – exactly two connections are added to the network for a hidden unit addition, and one connection is added for a receptor addition. Additionally, evolution can now utilise the 3D coordinate system to create modules, which adds an adaptive element (albeit weaker than type 2).

4.3.2 Slowing regeneration rate

The experiments described in this chapter required that the environment become more challenging over time. This was implemented using a slowing regeneration rate; in the beginning of every run, the regeneration rate of consumed surfaces operates at a predefined rate. During the course of the run, every predefined amount of time, the regeneration rate slows down by one unit until a predefined minimum regeneration rate is achieved. This means that consumed surfaces regenerate at a much faster rate at the beginning of a run than at its end.

4.3.3 The methodology behind these additions

Biological relevance: the changes to the model enable to directly examine the effects of structural mutations (which operate by changing the underlying genes) on the evolvability of the agents. The five types of structural mutations that are examined incorporate three principles believed to affect evolvability in nature: adaptive evolution, the ability of evolution of altering elements of itself, incremental changes, the size of the changes caused by genetic operators and structural duplication, the ability of evolution to reuse existing genetic structures. Thus, these changes to the model are both computationally relevant (as indicated by various computational literature on the subject [4, 136, 212, 227]) and biologically relevant (as indicated by various biological literature on the subject [42, 87, 107, 228]).

Level: the changes to the model do not affect this parameter.

Generality: the changes to the model do not affect this parameter: the model can still be said to be a general model despite the fact it is used in this chapter to examine specific hypotheses.

Abstraction: the examined principles which are believed to affect evolvability are fully implemented using the five types of structural mutations; however, even though these changes are relatively simple and do not require significant alterations to the model they are detailed enough to completely capture the modelled phenomenon.

Accuracy: the additions to the model implement the examined real world principles concisely (without a lot of overhead) and accurately:

- Incremental changes: this is implemented directly, e.g. in the case of mutation type 2, by forcing the search operators to make minimal changes to the phenotype.
- Adaptive evolution: this is implemented directly, e.g. in the case of mutation type 4, by allowing evolution to evolve elements (the distance parameter) that affect the process of evolution.
- Modularity: this is implemented directly, e.g. in the case of mutation type 3, by allowing the mutation operator to duplicate existing network structures. Albeit, this is only one form of modularity, whereas modularity in nature can span structures of many different scales.

Match: the changes to the model that are believed to affect evolvability in nature are shown to in fact affect it within the model as well. As the results section in this chapter shows, incremental changes are shown to increase evolvability (expected from [5, 116]) and so does adaptive evolution (expected from [22, 67]). Modularity is shown to indeed affect evolvability (expected from [160, 228]), but at least in the way it has been implemented here, it decreases evolvability rather than increase it which is an interesting observation by itself. This is elaborated more broadly in section 4.2 of this chapter.

4.4 Measuring evolvability in Mosaic World

Mosaic World is more than just a population of individual critters – it is a dynamic ecosystem in which critters survive if their genomes enable them to interact with each other and their current environment effectively enough to gather resources.

Previously suggested measurements of evolvability (for example, Altenberg's evolvability measure using Price's theorem [4] and Smith et al's evolvability metrics [212]) do not take into account conditions specific to the ecologically relevant conditions of Mosaic World (and potentially other artificial life systems), and as a result they could not be used. These methods require accurately measuring fitness, which is not feasible for three reasons: first, no one statistic encapsulates all the required behaviours a critter must possess to be termed fit, and there is no universal method of combining all statistics to create a true fitness measure.

Second, the fitness of all critters is linked, as critters compete against each other on resources; a fit critter, effectively, decreases the fitness of other critters; this effect is difficult to measure. Third, although reproduction does not directly contribute to a critter's fitness, controlling reproduction is crucial to the species' collective fitness: the population, as a whole, must replenish itself at a rate that is sustainable by the available resources of the world. Thus, a critter must share some of this collective fitness.

Therefore, the evolvability measurement used in this chapter is based on the evolvability measure used in the Avida ALife environment [162]. This measurement was expanded by factoring in the environment difficulty. It can be argued that evolvability can either be expressed by demonstrating that a population gradually improves over time, or alternatively, by showing a population adapting to an environment that gradually becomes more challenging. By quantifying these aspects, it is possible to define the total evolvability indicator in Mosaic World, E_{total}, using equation (4.2) – its range of possible values is 0 to 1, and the *evolvability function through time*, using equation (4.1). Both measures incorporate four different elements: survivability, population success, environment difficulty and time variance. Note that a similar definition of evolvability appeared in [204] a year after the original paper describing this work was published [196].

Survivability: the critter's survival ability is the closest thing to fitness, and is best expressed by its age. A critter that can survive for long obviously managed to learn important skills required to survive in the world and managed to overcome many of the difficulties (e.g. it is able to recognise positive resources and negative resources, it managed to avoid falling from the edges or into the world's holes). Furthermore, by surviving longer, a critter may get more opportunities to reproduce and as a result spread fit genetic material to its offspring.

Population success: a population's 'fitness' is best expressed by its size at a given time. A population that managed to maintain itself through time, collectively learned how to balance resource consumption and reproduction through its constituent critters. Also, a larger population has more individuals that pass on traits to offspring, and is more likely to survive a 'catastrophe' purely because of its greater size.

World difficulty: in certain Mosaic World experiments the environment is altered over time to make it more challenging for a critter to survive. A population that manages to survive under conditions in which the selection pressure continuously grows shows an indication of adaptability, and thus, evolvability. This aspect of the equation is controllable by the researcher and must be directly tied in, from a numerical point of view, to the difficulty of the world in order to measure evolvability, i.e. if survival in the world at time t is twice as hard as the initial conditions, the difficulty factor at time t is 2.

Time: only by looking at the relative changes of survivability, population success and world difficulty over time, it is possible to precisely obtain the total evolvability measure.

In conclusion, these four elements provide useful measures of the capacity of Mosaic World's population to evolve. A population that maintains large numbers, where each agent survives for long periods of time, despite an increasingly difficult environment, consistently through time – can be said to be a population with a great capacity to evolve. Therefore, this function can be said to measure the capacity of a population to generate fit offspring through time.

$$E(t)=\frac{D(t)}{D_{\max}}\frac{\sum_{i=0}^{P_t}\left(\frac{A_{t,i}}{A_{\max}}\right)}{P_{\max}} \tag{4.1}$$

$$E_{total}=\frac{\sum_{i=0}^{t}E(t)}{t_{\max}} \tag{4.2}$$

$$Resilience=\frac{\sum_{i=0}^{t}iE(i)-n\overline{E(t)t}}{\sum_{i=0}^{t}i^2-n(\bar{t})^2} \tag{4.3}$$

$$Stamina=\overline{E(t)}-\left(\text{Resilience}\times\bar{\text{t}}\right) \tag{4.4}$$

Where: E_{total} is a population's evolvability indicator, E(t) is the evolvability at time t, D(t) is the difficulty factor at time t, D_{max} is the maximal difficulty of D(t), P_t is the size of the population at time t, $A_{t,p}$ is the age of a member of population p at time t, A_{max} is the critter maximum life span, P_{max} is the maximal population the environment can support, t_{max} is the total length of time of the experiment, n is the number of data values available.

Explanation for both equations: The top right part of equation (4.1) calculates the average survivability for all critters, the bottom right part factors in the population success, and the left part of the equation incorporates the world difficulty. Thus, this characterises the evolvability function through time. Equation (4.2), which calculates the evolvability indicator, simply averages the total evolvability (as measured using eq. (4.1)) per time unit.

Example: With a population size P of 400 at time 10000, all critter ages A are 1500, the difficulty factor D at time 10000 is 100, using maximum difficulty D_{max} of 350, maximum population size P_{max} of 10000, and maximum age A_{max} of 15000, evolvability at time 10000 is $E(10000) = 100/350 * (400*1500/15000)/10000 = 0.00114$.

In addition, figure 4.2 demonstrates the evolvability function through time, Resilience and Stamina values for a sample population.

By extracting the height and the slope of a linear trendline of the evolvability function through time (using equations (4.3) and (4.4)), two extra indicators can be gained:

(i) *Resilience (slope)*: this indicator defines the resilience of the population to change. Lower values indicate populations more tolerant to change.

(ii) *Stamina (height):* this indicator defines the population's ability to thrive when conditions are easy.

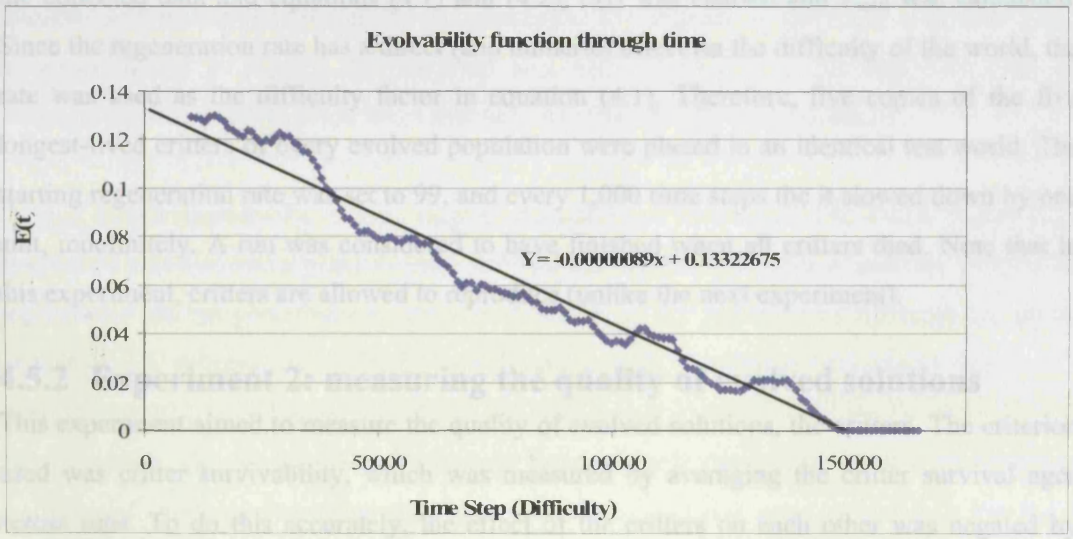


Fig 4.2. The evolvability function through time for a sample population. Using a linear trendline of the evolvability function through time, the Resilience and Stamina values for the population can be calculated: Resilience = -0.00000089, Stamina = 0.13322675.

4.5 Experiments

The main objective of the experiments was to investigate the conditions necessary to overcome the challenge. This required measuring the evolvability function through time, E(t), and the total evolvability, E_{total}. A secondary objective was to obtain additional statistics examining effects other than evolvability of the structural mutations used: variability of evolved forms (average structure), quality of critter solutions and the percentage of successful runs (a run is considered to have failed when no population of critters successfully evolved without the need for a restart).

To this end, two sets of experiments were performed. Each of the experiments required multiple populations that were evolved using the five structural mutations. Therefore, at least eight successfully evolved populations were collected for each of the mutation types (using the same randomly generated world). Each run started with identical population characteristics (all critters possessing fully connected networks: 3 receptors, 3 hidden units and 8 output units, 33 connections), and was stopped after 550,000 time steps. During each run, the regeneration rate of consumed surfaces was slowly reduced to increase challenge and force critter populations to adapt. Initially, consumed surfaces regenerated every 13 time steps 3% of their maximal value. Every 3,500 time steps regeneration slowed down by one unit, until the regeneration rate of 99 was reached. To analyse the effects of the mutation operators only, crossover was disabled during all runs and experiments.

4.5.1 Experiment 1: measuring evolvability through adaptation

This experiment aimed to test the maximum difficulty that a population can adapt to. Using the collected data and equations (4.1) and (4.2), E(t) was charted and E_{total} was calculated. Since the regeneration rate has a direct (and numeric) effect on the difficulty of the world, the rate was used as the difficulty factor in equation (4.1). Therefore, five copies of the five longest-lived critters of every evolved population were placed in an identical test world. The starting regeneration rate was set to 99, and every 1,000 time steps the it slowed down by one unit, indefinitely. A run was considered to have finished when all critters died. Note that in this experiment, critters are allowed to reproduce (unlike the next experiment).

4.5.2 Experiment 2: measuring the quality of evolved solutions

This experiment aimed to measure the quality of evolved solutions, the critters. The criterion used was critter survivability, which was measured by averaging the critter survival ages across runs. To do this accurately, the effect of the critters on each other was negated by prohibiting reproduction, and by placing a very small number of critters in every world. Furthermore, the difficulty of the world was made static by fixing the regeneration rate (to 99). Therefore, five copies of the five longest lived critters of every run were placed in an identical test world. Critters were left to survive as long as they could. All runs were stopped after 10,000 time steps, and were each repeated 3 times. Critters that survived until the end of the run were 'killed': marked as if they had died then (a necessary assumption, otherwise long lived critters might have a non proportional effect on the average survival age).

4.6 Results

In table 4.1, the E_{total} for each type is shown (as a percentage of the maximum E_{total} of type 4), as well as the resilience and stamina for each type (using equations (4.3) and (4.4) and divided by type 4's resilience for comparison purposes). In fig. 4.3, the evolvability function (weighted average) through time is shown with E_{total} appearing in the legends for every type. Table 4.2 shows the minimum, maximum and average of the maximum regeneration rate a population could adapt to and of critter average survival age, as well as the percentage of successful runs and the average critter structure per type.

When comparing the E_{total} of all types, it is clear that adaptive evolution and gradual changes to networks increase E_{total}, whereas non-gradual changes, and structural duplication decrease it. Types 4 and 5, both utilising adaptive evolution and gradual changes, had the highest E_{total} with type 4 the higher of the two. Their evolvability functions were, however, very different: Type 5 had – on average – a higher stamina, but it was less resilient than type 4, and its populations quickly weakened as difficulty increases. Type 4 was more resilient, as evident in its average adaptation rate. Overall, the data suggests that the type 4 structural mutation is slightly more evolvable [note that type 4's average survival age was also the best of all runs; type 5's was lower, but still very good]. It could be said, however, that type 5, having a higher stamina, and lasting the longest in the adaptation experiment, is the most evolvable type. However, it can be argued that the total area under the curve is the best indication of evolvability, since this measure takes into account both stamina and resilience.

Type 2, which operates by making only gradual changes to the network, had a higher E_{total} than type 1's. It also had a better average survival age and the best rates of success. Despite its populations' decent performance, once the difficulty of the environment becomes too great, its evolvability decreases considerably which results in its populations becoming extinct.

Type 1, which operates by making only large (non-gradual) changes to the network, had low (and second worst) average adaptation rate and average survival ages, as well as a low E_{total}. Generally, it seemed unable to utilise the structural mutations to alter the network's size: on average, only one receptor, and no hidden units, were added at all. This appears to be another indication of its low evolvability.

Table 4.1. The evolvability elements incorporated, the obtained E_{total} as a percentage of E_{total} of type 4 and the extracted resilience and stamina values using a linear trendline of E(t) for every type (divided by type 4's resilience for comparison purposes)

Mutation type	Element incorporated	E_{total} (%)	Resilience	Stamina
4	Adaptive evolution, Gradual changes	100.00%	-1.00	5.68
5	Adaptive evolution, Gradual changes	98.12%	-1.13	6.39
2	Gradual changes	78.50%	-0.98	5.53
1	Non-gradual changes	71.47%	-0.94	5.29
3	Structural duplication	41.58%	-0.41	2.34

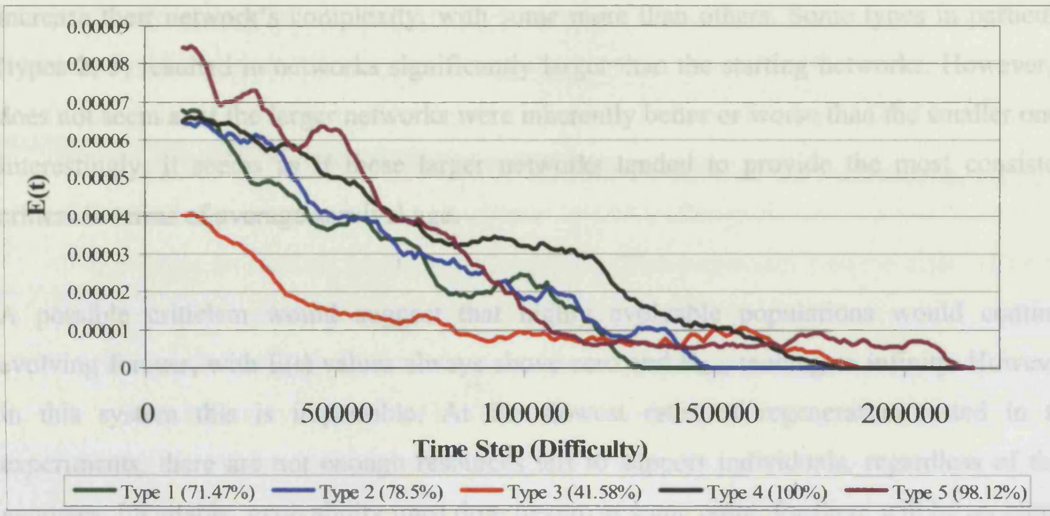


Fig. 4.3. The evolvability function (weighted average) through time for the five types of structural mutations and their relative evolvability indicator (of the E_{total} for type 4)

Table 4.2. Several statistics (average, minimum, maximum) describing the maximum regeneration rates the tested populations adapted to and the critter survivability, in addition to the average critter structure, and percentage of successful runs; broken down according to mutation types

Mutation type	Maximum adapted regeneration rate: Ave. (Min.-Max)	Survival age: Ave. (Min.-Max.)	Ave. critter structure: Receptors, Hidden (Connections)	Successful runs (%)
Random critter		57.36 (56.08-59.48)	3, 3 (33)	
1	191.14 (119–222)	3182.37 (1277.23-4600.12)	4.03, 3.13 (29.47)	64%
2	197.12 (159–237)	3733.34 (2781.13-4801.6)	8.32, 10.74 (108.70)	73%
3	163.87 (109–277)	2388.49 (893.44-5339.6)	4.86, 4.51 (41.45)	50%
4	224.36 (171–272)	3905.31 (1625.16-5021.96)	4.98, 6.26 (55.48)	69%
5	202.62 (167–305)	3651.06 (2613.92-5321.28)	10.39, 12.21 (144.25)	62%

Type 3, utilising structural duplication, had the lowest E_{total} as well as the lowest scores on all other tests. It would be easy to dismiss this method of evolution as completely non-evolvable, except for the fact that, despite having the low results of the vast majority of type 3 runs, some of its individual runs scored the *highest* average survival age and the near highest adaptation rates. The weakness of this approach is that cloning a fully connected hidden unit usually results in very large changes to the network (in some instances, 10+ connections being added at once), so it is possible this negative evolvability promoter far outweighs the positive evolvability gained by the structural duplication aspect. Thus, it can be deduced that this method has potential, but its weakness often far outweighs its strength.

Looking at the evolved forms, it is obvious that all types utilised the structural mutations to increase their network's complexity, with some more than others. Some types in particular (types 2, 5) resulted in networks significantly larger than the starting networks. However, it does not seem as if the larger networks were inherently better or worse than the smaller ones. Interestingly, it seems as if these larger networks tended to provide the most consistent critters in terms of average survival age.

A possible criticism would suggest that highly evolvable populations would continue evolving forever, with E(t) values always above zero and E_{total} tending to infinity. However, in this system this is impossible. At the slowest rates of regeneration tested in the experiments, there are not enough resources left to support individuals, regardless of their genomes. Inevitably, evolvability must drop to zero at some point, for there will be no critters left in the population to evolve. Such eventual resource limitation leading to extinction is inevitable in all real and modelled systems (time will always be limited, if nothing else), so an infinite E_{total} may be impossible to achieve.

4.7 Complex interactions analysis

The work described in this chapter primarily deals with genes→genes interactions and their effect on evolvability. The required expansions to the model consist of five types of structural mutations; each of the mutations incorporates principles believed to affect evolvability positively or negatively. These effects on evolvability occur through genes→genes interactions and essentially determine the likelihood that the offspring created during reproduction would be fitter or not. Therefore, these interactions are crucial towards accomplishing the challenge set for this chapter. It is interesting to note that although these changes take place at the lowest level of the hierarchy, the level of genes, their effects reach all levels in the critter phenotype (receptor, neuron, network), and because the critters interact (through competition on resources and reproduction), these affect the population level as well (population, species):

The interaction(s) that takes place are in parenthesis at the end of each sentence.

1) Every critter attempts to survive – this requires several different behaviours:
    (a) **Perception:** stimuli are perceived by the critter's receptors *(environment→receptor)*. Naturally, the ability to perceive the environment may be affected by the underlying changes to the genes.
    (b) **Communication:** the receptors relay this information to the network through neurons *(receptor→neuron, neuron→network)*. The ability to relay the information may be affected by the changes to the genes as well.
    (c) **Control:** the networks control the critter's behaviour *(network→critter)*.

   (d) **Consumption:** the critter may consume surfaces *(critter→environment)*; and in this case, positive or negative energy is transferred from the environment to the consuming critters *(environment→critter).* This decision may be affected by the underlying changes to the genes.
   (e) **Movement:** the critter may choose to move (forage for food, avoid the world's edges and holes) *(environment→critter).* This behaviour may be affected by the underlying changes to the genes.
   (f) **Reproduction:** the critter may choose to reproduce *(critter→critter).* This decision may be affected by the underlying changes to the genes.

2) **Selection (to evolve appropriate behaviour):** many critters die during stages 1-d to 1-f, either by consuming negative surfaces, or by falling from the edges/into a hole, or by moving too quickly (and running out of energy), or by reproducing when not possessing enough energy. Because critters that possess appropriate behaviours are more likely to survive, and thus, pass on genes that define them, the advantages these behaviours confer directly affect the selection of these genes *(network→genes).*
3) **Selection (to better compete):** the critters that survive compete on resources (critter→critter). Consequently, critters that are fitter are more likely to win in such a competition, thus, features which increase fitness (this includes both evolved behaviours and other aspects of the critter such as transmittance) affect the selection of genes which define these features (*network→genes, critter→genes).*
4) **Selection (to survive in a more difficult environment):** the surface regeneration rate slows down, thus, the environment effectively becomes more difficult, as per the conditions of the experiment. Therefore, features which increase a critter's fitness in any way (including behaviours and structures) affect the selection of genes which define these features (*network→genes, critter→genes).*
5) **Reproduction:** continuing (1-f), the critters that survive past steps (2) to (4) and are now able to reproduce are fitter and more adaptable than those that died (genes→genes). Because the selection pressure is becoming increasingly stronger, in the long run the only offspring that survive are those that are more evolvable and so, more adaptable. As the results show, the different structural mutations affect evolvability, thus, affect the fitness of the resulting offspring. Therefore, the resulting changes to genes affect the phenotype of the critters across all levels *(genes→receptor, genes→neuron, genes→network, genes→critter)* and eventually the population *(genes→population).*
6) Steps (1) to (5) are repeated until the run ends. As was shown, the five structural mutations result in critters and populations with different characteristics. As elaborated in section 4.2, evolvability is the ability of genes in the population to change in a way that produces fitter offspring across generations. This occurs by changing the offspring's

genome which affects existing genes→genes interactions or creates new ones in certain ways that are more likely to create fit offspring; these differences in offspring fitness are a result of the various principles that are incorporated into each structural mutation, each affecting evolvability in a different way. For example, when making a large (non-gradual) change to the offspring's genome using mutation type 1, which has been shown to decrease evolvability, the change is prone to creating unfit offspring because the large change is more likely to damage structures in the genotype than to create useful ones. The changes to the genes affect the entire hierarchy of objects in Mosaic World: genes affect neurons and receptors, which affect the networks and critters, which affect population and species, and of course, this effect goes downward as well – the critter's altered behaviour affects receptors and neurons, and eventually genes, through selection pressure. According to the results:

(a) *Non-gradual changes to network decrease evolvability*: during reproduction, the offspring inherits its parent(s)'s genes with some mutations (genes→genes). For populations that use the mutation types that incorporate this principle, this interaction between parent and child genes results in a new genome that differs by a large amount from the parent genome. These changes are more likely to disrupt existing structures than they are to increase innovation and produce useful structures in the genome, thus, the offspring's fitness is likely to be lower and the population's evolvability decreases when incorporating this principle (genes→genes).

(b) *Gradual changes to network increase evolvability*: during reproduction, the offspring inherits its parent(s)'s genes with some mutations (genes→genes). For populations that use the mutation types that incorporate this principle, this interaction between parent and child genes results in a new genome that only differs by a small amount from the parent genome. These changes are more likely to increase innovation and produce useful structures than they are to disrupt existing structures in the genome, thus, the offspring's fitness is likely to be higher and the population's evolvability increases when incorporating this principle (genes→genes).

(c) *Usage of modular elements decrease evolvability*: during reproduction, the offspring inherits its parent(s)'s genes with some mutations (genes→genes). For populations that use the mutation types that incorporate this principle, this interaction between parent and child genes results in a new genome that contains one extra copy of an existing structure from the parent's genome. Because an entire structure is copied, these changes are likely to be large, and the new genome will differ by a non-trivial amount from the parent genome. Thus, (in

Mosaic World) these changes are more likely to disrupt existing structures than they are to add useful structures in the genome. Consequently, the offspring's fitness is likely to be lower and the population's evolvability decreases when incorporating this principle (genes→genes).

(d) *Adaptive evolution increases evolvability*: during reproduction, the offspring inherits its parent(s)'s genes with some mutations (genes→genes). For populations that use the mutation types that incorporate this principle, this interaction between parent and child genes results in a new genome that only differs by an amount whose size depends on a gene in the parent genome. Consequently, during stages of evolution where large changes are appropriate (exploration), a large change may be performed, and vice versa, when small changes are appropriate (exploitation), a small change may be performed. Therefore, these changes are more likely to increase innovation and produce useful structures than they are to disrupt existing structures in the genome, thus, the offspring's fitness is likely to be higher and the population's evolvability increases when incorporating this principle (genes→genes).

Consequently:

(i) Mutation type 1, which only comprises element (a), results in populations that are not very adaptable and perish quickly when the environment changes. In these populations, the changes to genes tend to result in critters that are not fit to survive in an increasingly more difficult environment. In fact, considering the small network structure, it appears that most additions to the network result in unfit critters.

(ii) Mutation type 2, which only comprises element (b), results in populations that are not very adaptable and perish quickly when the environment changes. In these populations, the changes to the genes tend to result in critters that are not fit to survive in an increasingly more difficult environment. However, considering the large network structure, the additions caused by the structural mutations are likely to be neutral.

(iii) Mutation type 3, which comprises elements (c) and (a), results in populations that are not very adaptable, and perish quickly when the environment changes. In these populations, the changes to the genes tend to result in critters that are not fit even in unchanging environments.

(iv) Mutation type 4, which comprises elements (b) and (d), results in populations that are adaptable and are resistant to environmental change. In these populations, the changes to the genes tend to result in critters that are fit to survive in an increasingly more difficult environment. Considering the medium network structure, these changes are relatively small.

(v) Mutation type 5, which comprises elements (b) and (d), results in populations that are adaptable and are resistant to environmental change. In these populations, the changes to the genes tend to result in critters that are fit to survive in an increasingly more difficult environment.

4.8 Conclusions

The aim of this study was to investigate the genes→genes interactions taking place in the system by setting a challenge to Mosaic World that necessitated useful parent-to-child gene interaction. Since useful evolutionary interactions imply evolvability, these genes→genes interactions were investigated by exploring the evolvability of neural networks within an artificial life simulation. In the described experiments, the effectiveness of five different types of structural mutations, which incorporate different general principles thought to be important for network evolvability, was tested. Two experiments were performed, and the resulting E_{total} and evolvability function over time were calculated and compared.

The experiments conducted indicate that certain principles increase evolvability when used to evolve neural network artificial agents. The inheritance of genes through the process of gradual changes to networks appeared to promote evolvability. Another promoter of evolvability was the presence of genes that enabled evolution to adapt elements of itself, by actively affecting the process of genome copying from parent to child. However, when the inheritance of genes occurred through the duplication of network structures from parent to child, evolvability appeared to be hindered; that being said, despite exhibiting on average very low evolvability, this process showed some potential by evolving some of the best individual runs. Finally, when the inheritance of genes occurred through the process of non-gradual changes to the networks, evolvability appeared to be inhibited as well (or at least, did not seem to be promoted).

To conclude: this chapter has demonstrated that the method used in the evolution of neural networks for artificial life simulations plays a significant factor in all elements of the evolved runs.

Given that the results of the experiments indicated that usage of structural mutation type 4 results in the most evolvable populations, it was decided that subsequent experiments will use this type instead of the equivalent mechanisms which were described in chapter 3.

Chapter 5

Challenge: colour vision

The previous chapter explored the lowest level – the gene level – of the Mosaic World model, by investigating genes→genes interactions and their effect on evolvability. This chapter continues this narrative, and moves to the next level in the model: receptors. For that reason, this chapter describes a set of experiments that were conducted in order to further investigate the complex interactions that occur in Mosaic World, specifically, those interactions that occur between receptors and the environment. The challenge posed for Mosaic World in this chapter is:

Can receptors suitable for specific environments evolve in a population of critters, and how do the characteristics of visually different environments affect the resulting visual systems? (i.e., can critters evolve colour vision?)

In order to achieve this, two separate studies were conducted. The first examined the effect of physical and behavioural similarity and dissimilarity on the evolution of visual systems in abstract environments. The second explored the hypothesis that the need to survive in ambiguous environments is a possible reason for evolving visual systems that possess colour vision.

5.1 Introduction

Colour vision is the capacity of a visual system to distinguish between light of different wavelengths. The perceived colour is a subjective feeling generated by the brain – it is not an aspect of the physical world.

Vision requires three stages. In the first, light from the image is projected onto the retina. The second requires light-sensitive visual cells to absorb photons and generate electrical signals. In the third, these signals are analysed in the brain [134]. Although there is a great diversity in the design of eyes between different species, there is also a great convergence in the ability of these eyes to extract crucial aspects from light such as contrast, colour, shape and motion [176].

Many species have two different visual systems that are used in different conditions: one enables dim light vision, and another enables daylight and colour vision. In vertebrates, these two systems are represented by the two types of photoreceptors: rods and cones [176]; both are light sensitive receptor cells in the retina that transform the received pattern of light into a pattern of neural activity that represents the image [225].

Rods are particularly sensitive to light, thus, are mostly effective at night or other situations where there is a minimal light level. Rods enable only low-acuity monochrome vision, so cannot be used to tell colours apart. During the day the rods are ineffective as they become saturated.

Cones are more suited for use during the day, as they are less sensitive than rods to low light levels. Cones can differentiate between different spectral distributions, so are mainly used for colour vision. At night, or other situations where there is a minimal light level, colour vision generally cannot be used [82]. At intermediate light levels, both rods and cones contribute to vision [172].

There are three cone types used by humans and Old World primates [225], thus, these species have the potential to possess trichromatic colour vision. Each of the cone types has different spectral sensitivities; the short wavelength photoreceptor peaks at 420nm ('bluish' light). The medium wavelength photoreceptor peaks at 530nm ('greenish' light). The long wavelength photoreceptor peaks at 565nm ('reddish' light) [225]. Many reptiles and birds possess four cone types; thus, have the potential for tetrachromatic colour vision. Most mammals possess two cone types, and so have the potential to possess dichromatic colour vision [172].

A photoreceptor's sensitivity only defines the region of the spectrum that it is activated by, i.e. the rate at which photons are caught [65]. Using only a single photoreceptor gives no information about the spectral distribution of the light, its direction or its intensity. A single photoreceptor cannot differentiate between changes in wavelength and changes in the intensity of light [225]. A weak light at a wavelength it is sensitive to may cause an identical activation to a strong light at a wavelength it is less sensitive to [134]. In order to support colour vision, a comparison of activations from at least two photoreceptors that differ in spectral sensitivity is required [134, 225]; this comparison – or opponent interaction [232] – can take place in the eye or more centrally [91, 93]. The signal coming from the photoreceptors must be kept segregated for the postreceptoral circuitry, so that they could be compared [172].

Some computational models that investigate vision

Liese et al created an ALife simulation in which a population of visual agents evolved sensors to survive. In their system, survival required that the agents' sensors become sensitive to the spectral characteristics of lamps, energy giving elements present in the environment. To avoid collision with other agents, additional sensors sensitive to agent emitters were evolved as well [129].

In another ALife model, Menczer and Belew evolved a population of agents to study the evolution of sensory systems. In their system, recognising and consuming a specific combination of resources was required to survive; however, recognition required evolving two types of sensors: a type to perceive the external environment, and a type for the internal environment [141]. Kortmann et al evolved a population of visuo-motor systems to investigate the trade-off between spatial and temporal resolution that occur in biological systems [109]. Aleksander and Morton have created a model that investigates the cause of certain visual deficits in patients of Parkinson's disease [3]. Olsson et al investigated a developmental control system for a robot that creates on its own a model of its sensors and actuators. By learning to associate sensor readings with possible actions, the robot is able to perform motion tracking and simple imitation [165].

In this chapter, the interactions between the environment and receptors, as expressed in visual evolution, are examined. In the first part of the chapter, two sets of experiments are conducted; in these experiments, a population of critters is evolved in simple, conceptually abstract, environments. These experiments examine the effect physical similarity, the similarity of the wavelengths that describe an object, and behavioural similarity, the similarity of the behavioural significance of the object, have on visual evolution and also explore how varying degrees of similarity differently affect the evolution of the visual system. In the second part of the chapter, another set of experiments is conducted; these experiments examine the hypothesis that environmental ambiguity – the one-to-many relationship between perceived stimulus and its behavioural significance – is a possible reason for the evolution of colour vision in nature. The chapter is concluded with a complex interactions analysis of the experiments.

5.2 Additions to Mosaic World

The experiments that were conducted in this chapter required that the model is expanded in several minor ways.

5.2.1 Simple environments

The ability to create simple, conceptually abstract, environments was added to Mosaic World. These simple environments enable precise control of many environmental aspects (i.e. number of colours and their distribution, environmental statistics). In these environments, normally up to 4 colours are used and each is assigned a specific value using the predefined value function (see section 3.4.1). The colours are distributed in grids, and the size of each region is customisable (e.g. each region can be 3x3, 4x4, 5x5 surfaces across). See fig. 5.1 for two sample environments.

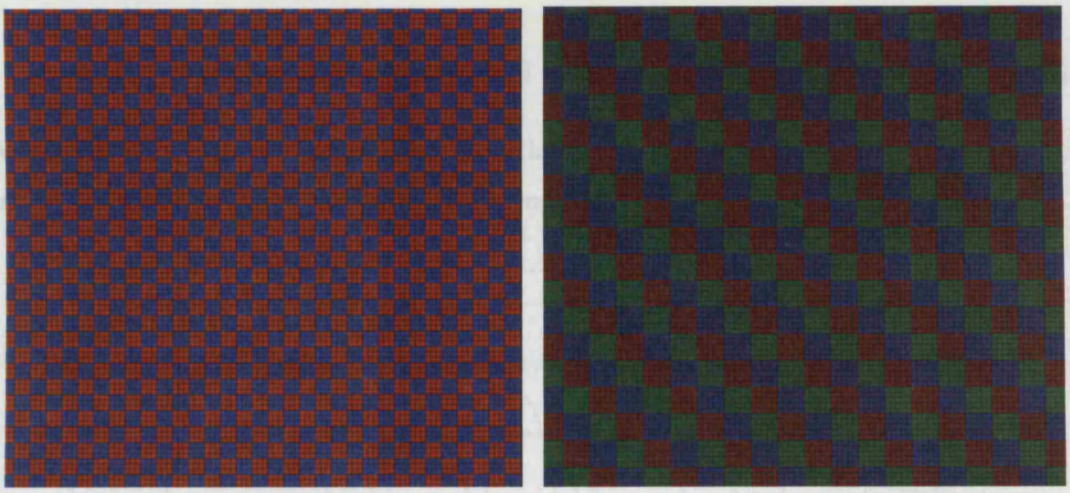


Fig. 5.1. Two simple environments. The left environment contains two types of resources divided into regions that are 3x3 surfaces across. The right environment contains three types of resources divided into regions that are 5x5 surfaces across.

5.2.2 Ambiguous value function

A new ambiguous value function is created by expanding the dynamic value function which is described in section 3.4.1. This value function creates a one-to-many relationship between stimuli and their behavioural value, as every stimulus may have different values (and therefore, different behavioural meanings) at different time steps. Thus, the stimuli can be said to be ambiguous.

Similarly to the dynamic value function, this value function operates by assigning a value for every wavelength in the 400-700nm range which is determined using a linear function and essentially defines the behavioural 'worth' of a wavelength. However, in each time step, every element in the function is altered by adding or subtracting a random value in a predefined range (see equation (5.1)). The surface's value is calculated by summing the multiplication of every one of the wavelengths that constitute its reflectance with its behavioural value (equation (5.2)). Note that using this value function, the value of every wavelength may change in every time step. However, on average, the wavelengths that provide the best nourishment continue doing so despite the random element; this particular aspect is crucial, as evolution may be able to exploit this statistical regularity in order to enable critters to survive. In figure 5.2, two sample value functions are illustrated.

$$V(i) = \frac{a(i-400)}{10} + b + (RAND(2r+1) - r) \tag{5.1}$$

Where V(i) is the behavioural value of wavelength i using the value function, RAND() is a random number generator function, and *a*, *b* and *r* are predefined constants; *a*, *b* are constants in a linear function and *r* is the range constant for the random number generator.

$$S = \sum_{i=400}^{700} \mathrm{Re}(i)V(i) \tag{5.2}$$

Where S is the surface's value, Re(i) is the reflectance value of wavelength i for the surface, and V(i) is the behavioural value of the wavelength.

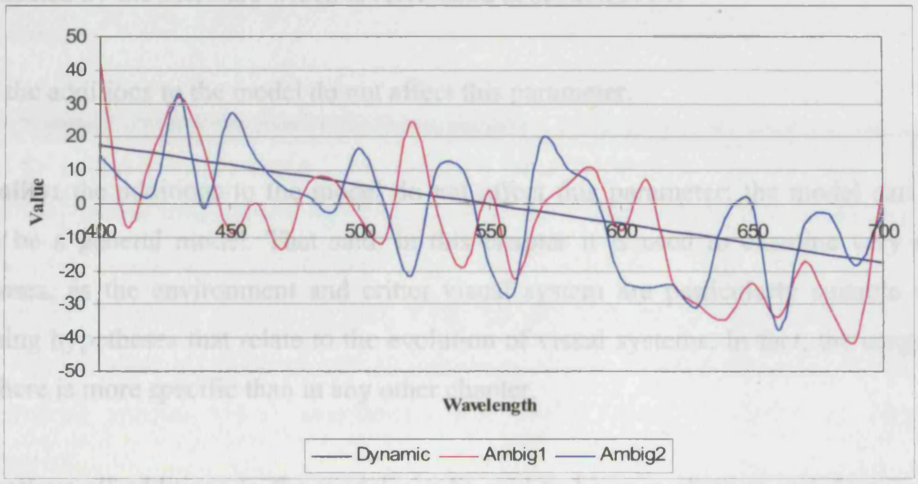


Fig 5.2. Two examples of the ambiguous value function and the dynamic value function they are based on (from fig. 3.5). In this example, *a* = -1.1666, *b* = 17.5 and *r* = 25. The figure demonstrates that in two different time steps the value function can be very different.

5.2.3 Ambiguous perceived stimuli

In section 3.4.3, it was described that the stimuli that is perceived by the critters depends on the relative contributions of reflectance and illumination. In this section, a new ambiguity mode, ambiguous perceived stimuli is added. When this mode is active, the standard dynamic value function is used (defined in section 3.4.1); however, in each time step, a random value is added to or subtracted from the constituent wavelengths of the stimuli. An individual wavelength cannot be set above the maximum intensity (1) or below the minimum intensity (0). This effectively creates a one-to-many relationship between stimuli and their source, as every stimulus can be generated by many different types of surfaces. Thus, the stimuli can be said to be ambiguous.

5.2.4 The methodology behind these additions

Biological relevance: all additions to the model are conceptually very simple and are meant to represent abstract principles; nonetheless, they enable running experiments that are useful towards improving our understanding of biological phenomena:

- The simple environments feature enables examining abstract principles such as the effect of physical similarity on visual evolution. Although the environments are extremely simple, the results of the experiments (sections 5.3.4 and 5.3.5) are biologically relevant as indicated by the literature which is referenced in sections 5.3.1 and 5.3.2.
- The ambiguous value function and the ambiguous perceived stimuli features are particularly abstract. Although these do not have corresponding biological phenomena, the results of the experiments (sections 5.3.3, 5.3.4, 5.3.5) are biologically relevant as indicated by the literature which is referenced in section 5.4.1.

Level: the additions to the model do not affect this parameter.

Generality: the additions to the model do not affect this parameter: the model can still be said to be a general model. That said, in this chapter it is used to examine very specific hypotheses, as the environment and critter visual system are particularly suitable towards examining hypotheses that relate to the evolution of visual systems. In fact, the usage of the model here is more specific than in any other chapter.

Abstraction: all additions to the model can be said to be very abstract and do not emulate any specific feature of a real world phenomenon except for the overall concept.

Accuracy: In this chapter, the additions to the model emulate two overall principles:

- Abstract concepts, such as the effects of physical similarity and behavioural similarity: this is implemented using the simple environments feature.
- Ambiguity: this is implemented using the ambiguous value function and the ambiguous perceived stimuli features.

Both types of additions capture well the overall concept, but are abstract enough that the question of 'accuracy' does really not apply here.

Match: as both results sections of the chapter show, the additions to the model result in behaviours that are very similar to their real world counterparts.

- In part 1, it is shown that evolved visual systems evolve to perform tasks similar to their biological counterparts (specifically, detect the presence of positive resources: food). Another biological parallel is the exhibited increase in sensitivity and specialisation as a result of challenging visual conditions.

- In part 2, it is shown that when exposed to ambiguity, critters evolve visual systems that can be characterised as colour vision, and utilise mechanisms that are similar – in principle – to their biological counterparts.

5.3 Part I: similarity and visual evolution

Two sets of experiments were conducted in order to investigate the relationship between the similarity of the environment and visual evolution. In both experiments, it is anticipated that environment→receptor interactions that take place will result in the visual system of the critters becoming better adapted to the environment in the course of evolution; the experiments are conducted in order to confirm this and investigate the precise nature of the adaptations.

5.3.1 Visual systems and environments

In order for vision to be beneficial to an organism that possesses it, it must be able to perceive relevant and useful information that is present in the environment. That being said, many environments – such as dim environments with very low levels of light – offer a considerable challenge for the visual system. In fact, it can be said that the greatest challenge of visual systems in dim areas is capturing enough light to be able to reliably see [121]. Many species have evolved special visual adaptations that enable them to thrive in challenging environments.

The intensity of the illumination during a full moon night is roughly a million times dimmer than illumination during the day [232]; in moonless nights, the light is further 100 times dimmer [134]. Consequently, nocturnal animals that wish to rely on vision must evolve visual mechanisms that enable them to overcome these difficulties. Similar difficulties are faced by animals that reside in the ocean, where light levels drop very quickly with depth: after 600-700m the level of illumination drops to starlight levels. However, the ocean creates additional difficulties, such as a limited spectrum of light in deeper water, e.g. in the first 100m of the ocean, virtually all of the orange-red part of the spectrum (>550nm) is absorbed, as well as the direction of the light source: in the depths of sea, virtually all the light comes from above [232].

There are numerous kinds of adaptations evolved by nocturnal animals or animals that live in deep-sea that enable them to detect the light in such challenging environments. One way to adapt is to evolve very sensitive eyes; the eyes of invertebrates in the deep sea are considered to be some of the most sensitive eyes found in the animal kingdom [142]. Eyes can be made sensitive by being very large, thus, they can capture as many photons that are available – e.g.

the eyes of a giant deep-sea squid were reported to be 37cm in diameter [232]. Alternatively, the visual signal can be summed in space and time by neurally integrating signals in the visual system; this has the potential of drastically improving vision in dim light at the cost of a decrease in spatial resolution (when using spatial summation) or a decrease in visual response time (when using temporal summation) [232]. Another adaptation is used by superposition eyes, a type of compound eyes that are known for their high sensitivity; this type of eye – possessed by nocturnal insects and deep-sea crustaceans – enables light from a narrow area of space to be collected by a large number of lenses and be focused onto a single photoreceptor [232]. Finally, some arthropods adapt to the dark by widening the receptive fields of their photoreceptors at night and narrowing them during the day [118].

Low levels of light are not the only issue that requires specific adaptations: organisms can evolve visual specialisations for specific purposes. For example, some organisms need to detect the presence of a bright point source of light. A point source of light could be a star in a clear night sky, the occasional flash of bioluminescence in deep sea or a bioluminescent signal that is used by fireflies to attract potential mates [232]. Many deep sea organisms that are faced with this challenge, for survival and reproduction, have large pupils and long photoreceptors that are very sensitive [230, 231], thus, can recognise whether a point source of light is present. Of course, if this light source must be located (rather than just identified) then more adaptations are necessary.

Rather than solve a general problem, some visual systems resort to simply solving a specific problem that is faced; this can be said to be analogous to the engineer term known as 'matched filters' (a matched filter is a filter that maximises the signal-to-noise ratio for a known signal when noise is present [78]). Normally this is enabled by limiting the amount of information that is perceived from the environment and looking for a specific visual signal which serves a cue to perform a specific task. Naturally, this severely limits the general usefulness of the system, but it relieves the visual system and brain from the need to do considerably more complicated work [234]. For example, Ocypode crabs overcome the problem of size constancy (the ability to reliably estimate an object's size regardless of its distance) without estimating the distance and size of objects; instead, these crabs treat objects that stimulate a certain number of vertical rows in the equator of their eyes as if they are in the correct size; whereas in humans, this is done in a much more complicated way, by measuring the absolute distance to the object and using the retinal image size. The crab's visual strategy works – but only when its visual environment is very predictable, as is normally the case in its flat environment [247]. A somewhat similar strategy is used by the toad; toads stick their tongues out and snap at any small, dark, moving object that is nearby, even if it is a piece of small dark paper that is thrown at it [188]. Although the toad's ability to perceive its prey is very limited, in its environment it is sufficient for its purposes: in nature, any small, dark, moving object is essentially prey for the toad.

5.3.2 The usefulness of colour vision

Colour vision is a commonly evolved mechanism for perceiving useful information that is present in the environment. Animals use colour to detect, identify and distinguish between objects, and normally possess visual systems that are adapted to the colour of objects of importance, such as conspecifics, predators and food sources (prey, fruits, leaves, etc) [232].

The benefits colour vision provides are numerous; most often, colour vision has been considered a specialisation for finding food [92, 213]. In the context of primates, who include some fruit in their diets, trichromatic colour vision may grant a distinct advantage in detection of yellow and orange fruits in green foliage [152, 213]; it certainly becomes very difficult to detect fruit without colour vision against mottled foliage when the light source varies randomly, a situation which may occur when the illuminant is interrupted by foliage [152]. This hypothesis is strengthened by the observation that primates tend to forage on colourful fruit, unlike non-primate diurnal mammals (e.g., squirrels eat brown and grey nuts) [137]. Interestingly, it has been suggested that yellow and orange tropical fruit have coevolved with the trichromatic colour vision of Old World monkeys [152]. Trichromacy also evolved in several species that only eat leaves, and can be used in this case to differentiate between different types of leaves [55]. Similarly, bee, wasp and moth colour vision has been demonstrated to be ideal for the task of flower discrimination [46].

Some animals use colour as a cue for orientation. For example, honey bees and ants use a chromatic signal as a compass [235]. Similarly, in water environments, the colour of the illumination can serve as an indication of the current depth and the orientation [97]. Although it is likely that colour vision is used for mate recognition, no conclusive proof has been found so far; however, with many types of animals, existing evidence strongly suggests that colour vision is used for this purpose, for example, jumping spiders, dragonflies and firefly squids [232].

As described in previous section, dim environments require specific adaptations. In the case of colour vision, colour discrimination is limited because of the inherent photon noise [232]. Until recently, it was believed that true colour vision has not been evolved under starlight conditions; however, Kelber et al have shown that a type of nocturnal hawkmoth possesses trichromatic colour vision at light levels a 100 times dimmer than the dimmest which can be perceived by humans [101]; this is believed to be possible using temporal and spatial summation [101, 119].

5.3.3 Experiments

Two sets of experiments were conducted. In the first set, it is examined how 'physically' similar/dissimilar environments that are behaviourally similar/dissimilar affect visual evolution. The aim is to discover whether there are common recurring characteristics to the evolved visual systems and whether there are similarities between these and the corresponding natural analogies. In the second set, it is examined how increased similarity of environments affects visual evolution. The aim here is to discover whether any particular visual strategy is required to deal with the increased similarity (and consequently, increased difficulty of the environment), and whether this strategy bears any resemblance to the visual strategies evolved by natural organisms.

In all experiments simple environments with four colours were utilised. The colours used are: red, green, blue and grey (see fig. 5.3 for their reflectance functions); however, different predefined values were assigned for every colour in the various experiments. The used environments consist of regions that are 3x3 surfaces across and all surfaces within a region are of the same colour. Although the regions were placed randomly, a predefined distribution of resources was used. In all experiments a random population of 2,200 evolving individual critters was placed in the environment for 1,100,000 time steps (roughly 40-45 hours). Afterwards, the critter population was stored and analysed. Each experiment was repeated at least 3 times – reported results were averaged across runs. In every set of runs, the same randomly generated environment was used. In these experiments, a receptor's position also specified its receptive field, that is, the area it is sensitive to (see section 3.7.1). Therefore, only a single receptor may detect any given surface relative to the critter's centre.

Experiment 1: the effect of physical and behavioural resource similarity on visual evolution

The purpose of this experiment was to see how physical similarity, which is the similarity of the wavelengths that describe each surface (e.g. blue is different from green because blue has a reflectance function that peaks at 470nm and green peaks at 550nm) and behavioural similarity, the similarity of the meaning of a surface from the critter's perspective, affect the evolution of the critter visual system. The surface matrix was illuminated by a static uniform illumination source. Four different categories of experiments were run (see table 5.1).

Table 5.1. The four types of run in experiment 1.

Experiment #	Surface type	Value of blue surface	Value of red surface	Value of green surface
1.1	Saturated	25	-25	0
1.2	Saturated	-25	25	0
1.3	Saturated	-12.5	-12.5	25
1.4	Saturated	12.5	12.5	-25

Note: the purpose of the grey surface is to provide additional difficulty for critters because a critter that examines a grey surface cannot tell whether this is a grey surface or a consumed positive surface (which becomes transparent when consumed and shows the grey background colour). Additionally, the values of ±25 were picked because consuming a full surface with a value of 25 brings a starved critter roughly to 80% of its maximum health, and consuming a full surface with a value of -25 will bring a healthy critter to roughly 20% of its health.

Table 5.2. The four types of run in experiment 2.

Experiment #	Surface type	Value of blue surface	Value of red surface	Value of green surface
2.1 (identical to 1.1 – same results used)	Saturated (level 3)	25	-25	0
2.2	Saturated (level 2)	25	-25	0
2.3	Saturated (level 1)	25	-25	0
2.4	Unsaturated	25	-25	0

Experiment 2: the effect of increased resource similarity on visual evolution

The purpose of this experiment was to discover the effect of greater physical similarity on the evolution of visual systems. These experiments utilised the concept of saturation. Saturated colours are closer to pure colours whereas unsaturated colours look like pure colours mixed with neutral grey. The significance of saturation lies with the fact that unsaturated colours are harder to tell apart: the more unsaturated a surface is, the flatter its reflectance function. A saturated red and a saturated blue can be very easy to distinguish as their reflectance functions might not even overlap. However, an unsaturated red and an unsaturated blue might have significant overlaps, making the recognition of both a more difficult task. Thus, the effects of decreasing levels of saturation on the visual system, which result in recognition of resources becoming increasingly difficult, are examined in this set of experiments.

In this set of experiments, three additional versions of experiment 1.1 were performed (see table 5.2); in each subsequent run type, the used colours were less saturated than the previous run type. See figure 5.3 for an illustration of the reflectance functions of used colours and figure 5.4 for screenshots of the four types of saturated environments. Note that an additional (and intentional) difficulty for critters evolving in the later experiments is caused by the increased similarity of the colours used to the grey background colour.

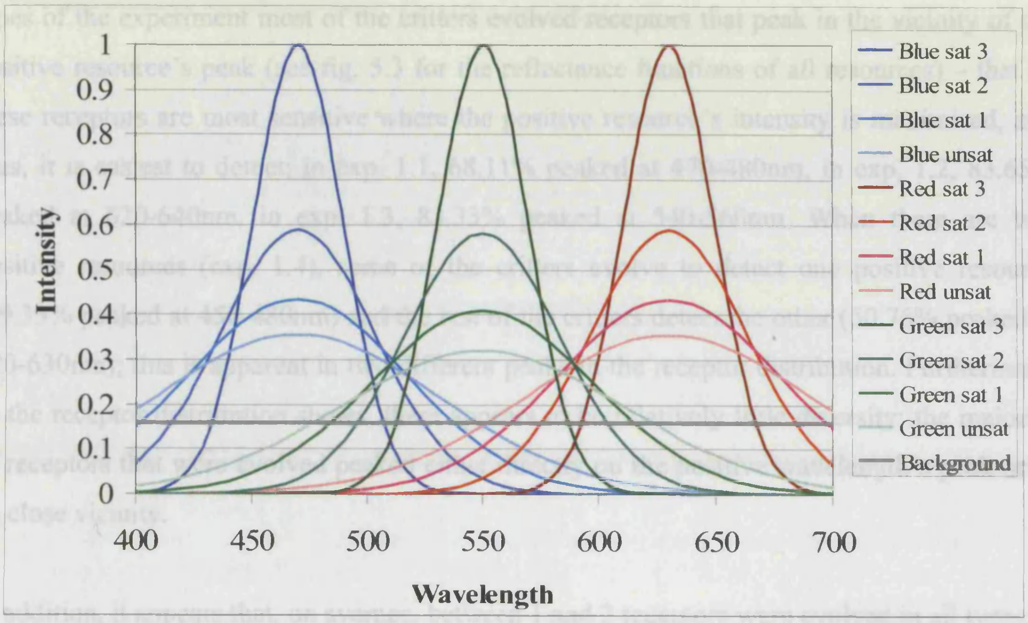


Fig. 5.3. The reflectance functions of the four colours in four different levels of saturation that were used in the experiments. There is a greater overlap of reflectance functions of unsaturated colours, thus, they are harder to tell apart. Note that the most unsaturated colours are also the most similar to the grey background colour.

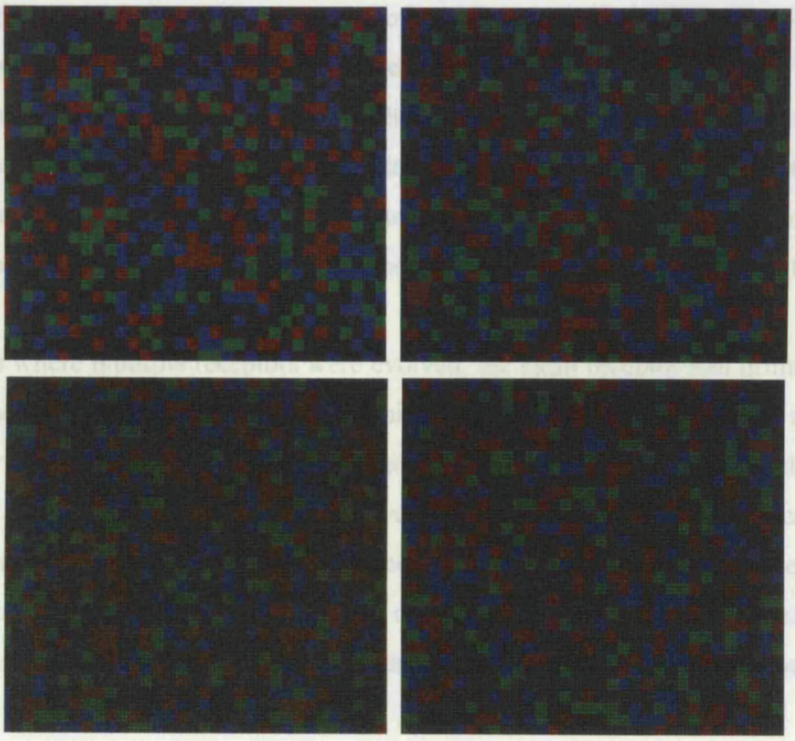


Fig 5.4. The four levels of saturation in clockwise order (from top left).

5.3.4 Results of experiment 1

The results of exp. 1 are shown in fig. 5.5 and 5.6, and in table 5.3. After analysing these results, several conclusions are immediately obvious. First, as fig. 5.5 and 5.6 show, in all run types of the experiment most of the critters evolved receptors that peak in the vicinity of the positive resource's peak (see fig. 5.3 for the reflectance functions of all resources) – that is, these receptors are most sensitive where the positive resource's intensity is maximised, and thus, it is easiest to detect; in exp. 1.1, 68.11% peaked at 470-480nm, in exp. 1.2, 83.65% peaked at 620-640nm, in exp. 1.3, 83.33% peaked at 540-560nm. When there are two positive resources (exp. 1.4), some of the critters evolve to detect one positive resource (39.33% peaked at 450-480nm) and the rest of the critters detect the other (50.76% peaked at 620-630nm); this is apparent in two different peaks in the receptor distribution. Furthermore, as the receptor distribution shows, there appears to be relatively little diversity: the majority of receptors that were evolved peaked either directly on the positive wavelength's peak or in its close vicinity.

In addition, it appears that, on average, between 1 and 2 receptors were evolved in all types of run (see table 5.3). When analysing where these receptors are placed, it appears one structure is consistently evolved: there is *always* a receptor placed to detect stimulus from the critter's current location (distance = 0); this receptor's peak is always very close to the peak of the positive resource of the environment (in exp. 1.4, the average peak is actually close to the average of the two positive resources; this demonstrates that some critters detect one of the positive resources and the rest detect the other). Interestingly, this evolved receptor is primarily very highly tuned, that is, it is very sensitive and covers a small area of the spectrum; the average and median coverage show that it covers between 26-34nm. Note that the median statistic was obtained and used in table 5.3 as well, because an exceptionally high coverage caused by a very wide tuning function can skew the average of the entire experiment and the median statistic thus may be more appropriately used for this type of data.

In those runs where multiple receptors were evolved, the extra receptor still primarily peaked around the positive resource; however, the tuning function of these receptors is much wider, that is, their coverage was significantly higher – these receptors predominantly cover the entire visual spectrum. The extra receptors were not placed in a consistent location across runs, so distance > 0 was picked to describe their location (e.g., in some runs these receptors detect stimuli from one surface to the left and one surface above the critter's location, and in other these receptors detect stimuli from one surface to the right of the critter's location).

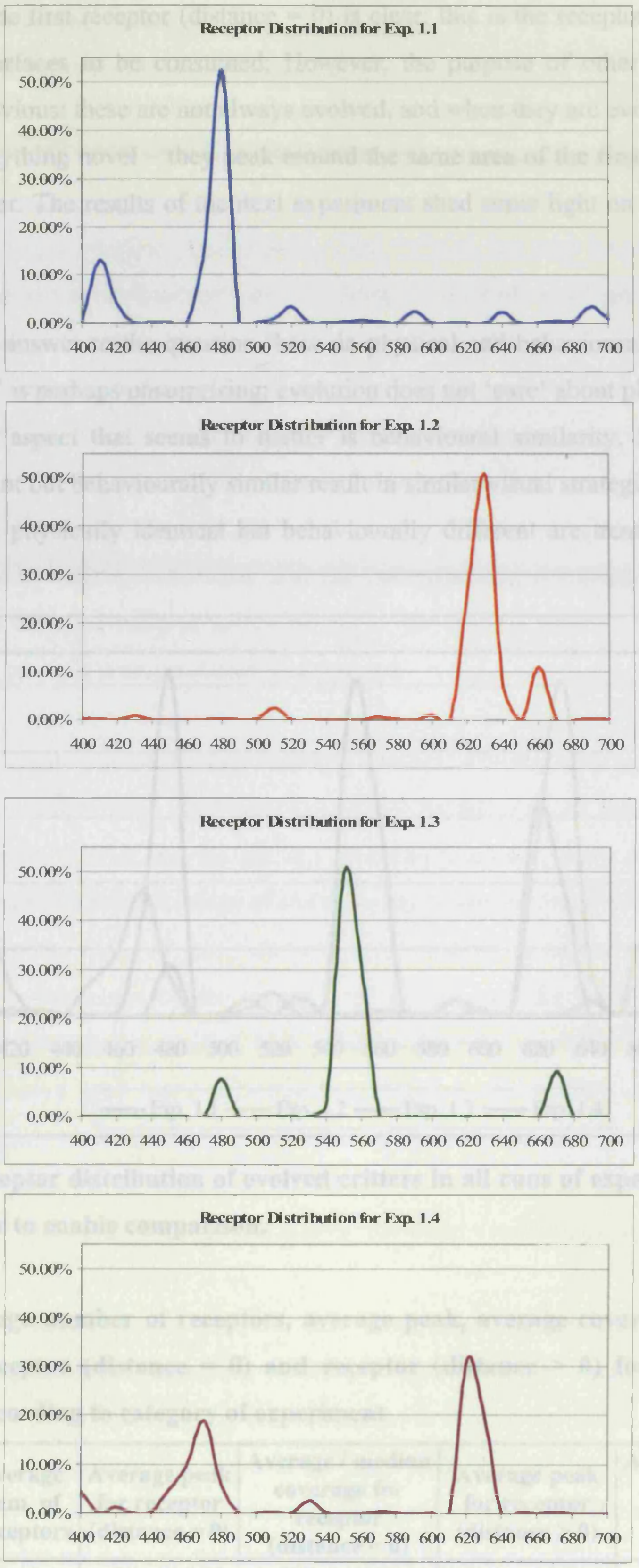


Fig. 5.5. The receptor distribution of evolved critters in all runs of experiment 1

The purpose of the first receptor (distance = 0) is clear: this is the receptor that enables the recognition of surfaces to be consumed. However, the purpose of other receptors, when present, is less obvious: these are not always evolved, and when they are evolved, they do not seem to detect anything novel – they peak around the same area of the first receptor, but are considerably wider. The results of the next experiment shed some light on the usefulness of these receptors.

To conclude, the answer to the question ‘how do physical and behavioural similarity affect visual evolution?’ is perhaps unsurprising: evolution does not ‘care’ about physical similarity. Indeed, the only aspect that seems to matter is behavioural similarity. Surfaces that are physically different but behaviourally similar result in similar visual strategies being evolved. Surfaces that are physically identical but behaviourally different are treated differently by evolution.

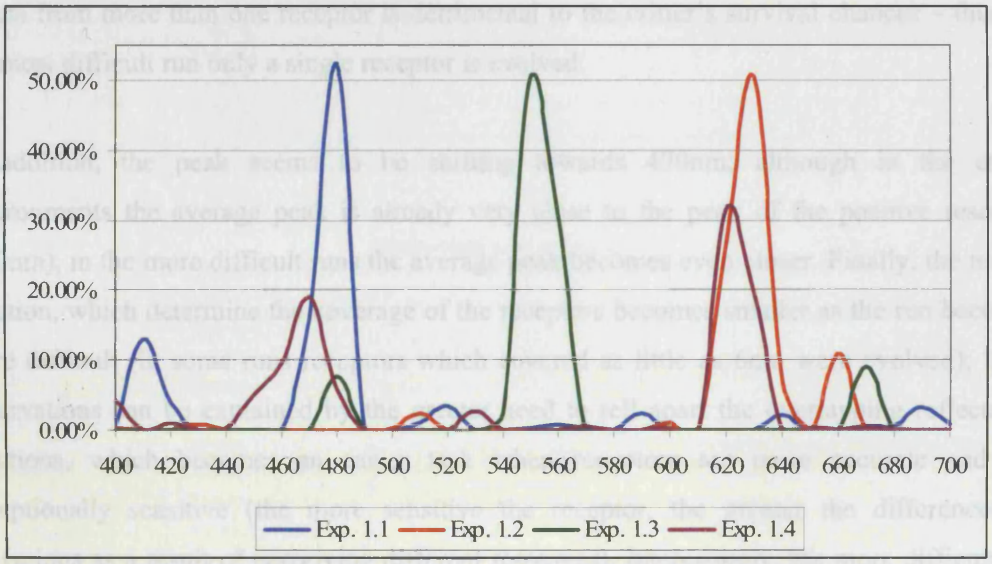


Fig. 5.6. The receptor distribution of evolved critters in all runs of experiment 1, shown together in order to enable comparison.

Table 5.3. Average number of receptors, average peak, average coverage and median coverage for receptor (distance = 0) and receptor (distance > 0) for experiment 1; broken down according to category of experiment

Experiment	Average num. of Receptors	Average peak for receptor (distance = 0)	Average / median coverage for receptor (distance = 0)	Average peak for receptor (distance > 0)	Average / median coverage for receptor (distance > 0)
1.1	2.00	476.66 nm	26 / 28 nm	491.50 nm	300 / 300 nm
1.2	2.00	625.00 nm	30 / 34 nm	622.00 nm	250 / 250 nm
1.3	1.34	552.66 nm	30 / 30 nm	N/A	N/A
1.4	1.61	559.00 nm	32 / 34 nm	490.00 nm	300 / 300 nm

5.3.5 Results of experiment 2

As can be seen in fig. 5.7 and 5.8 which show the receptor distribution in experiment 2, evolved receptors peak around the positive's resource peak as they did in experiment 1. However, the more difficult the run is, the less diverse the receptor distribution; in fact, in the most difficult environment (exp. 2.4), 99.3% of all receptors in all runs peaked at 470nm – receptor diversity was negligible. Additionally, table 5.4 indicates that the average number of receptors drops when the environment becomes harder. These observations can be explained in the following way: one receptor, which detects stimuli in the critter's immediate location (distance = 0), is sufficient and provides all the required information for survival in this type of environment. The additional information provided by extra receptors is simply not needed – it is possible that in the easier environment, the selection pressure is simply not strong enough to remove this extra receptor. In fact, because the extra receptor is not kept in the more difficult environments, it is likely that the computational overhead of managing the inputs from more than one receptor is detrimental to the critter's survival chances – thus, in the most difficult run only a single receptor is evolved.

In addition, the peak seems to be shifting towards 470nm; although in the easier environments the average peak is already very close to the peak of the positive resource (470nm), in the more difficult runs the average peak becomes even closer. Finally, the tuning function, which determine the coverage of the receptors becomes smaller as the run becomes more difficult (in some runs receptors which covered as little as 6nm were evolved); these observations can be explained by the greater need to tell apart the overlapping reflectance functions, which becomes an easier task when receptors are more accurate and are exceptionally sensitive (the more sensitive the receptor, the greater the differences in activations as a result of perceiving different resources). Interestingly, the more difficult the run type, the harder it was to evolve: in the hardest environment the population repeatedly perished and many attempts were required in order to obtain a number of successful runs.

To conclude, the answer to the question 'how does increased similarity affect receptor evolution' is straightforward: increased similarity requires greater visual specialisation in order to be able to correctly recognise the various types of resources; this is evident by the smaller coverage of receptors and the average peak drifting closer to the good resource's peak. Furthermore, because the increased similarity of resources makes the environment more challenging, in order to survive, the margin of error becomes smaller, thus, virtually all evolved receptors in the difficult runs have the same characteristics – both in terms of the visual structure (peak and coverage) and also by the fact that only a single receptor is used in the most difficult environment.

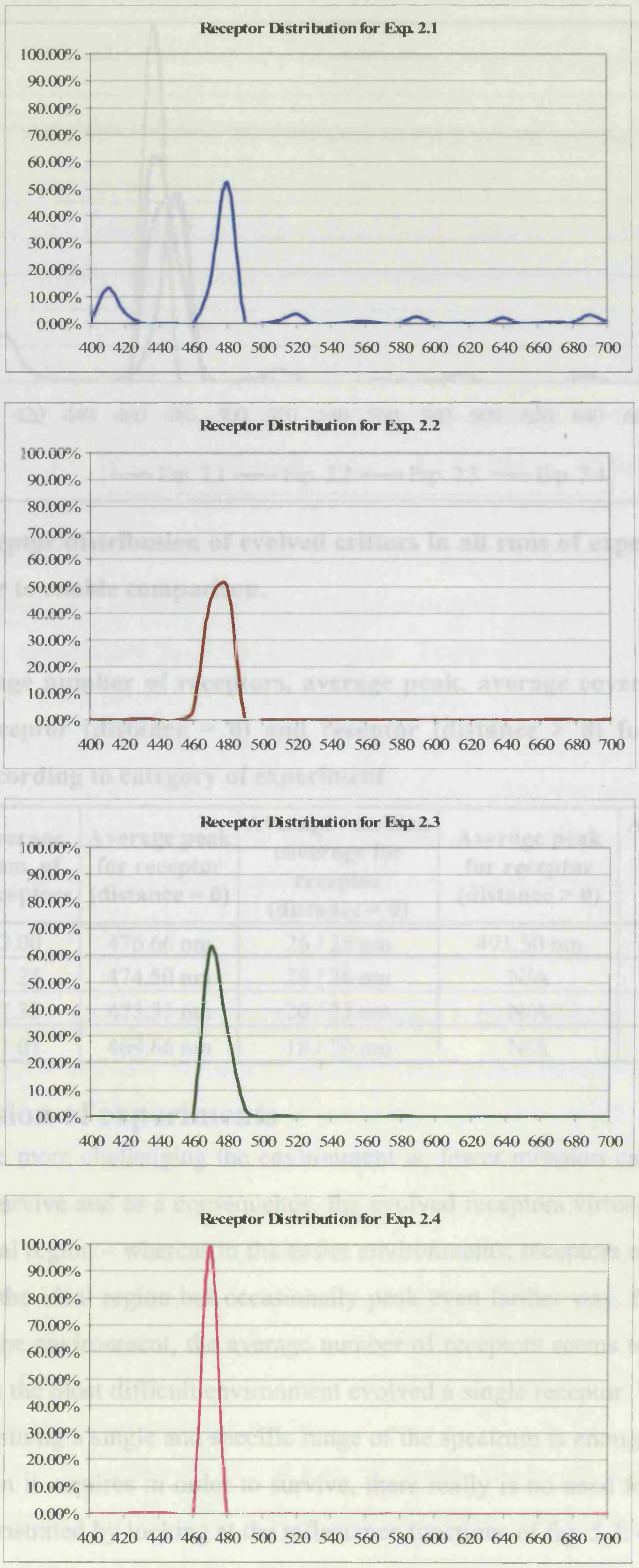


Fig. 5.7. The receptor distribution of evolved critters in all runs of experiment 2

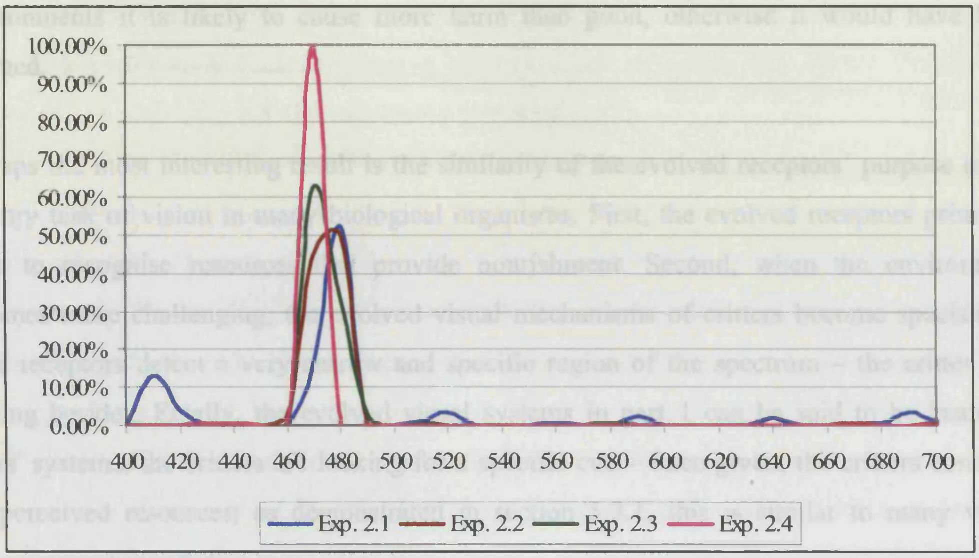


Fig 5.8. The receptor distribution of evolved critters in all runs of experiment 2, shown together in order to enable comparison.

Table 5.4. Average number of receptors, average peak, average coverage and median coverage for receptor (distance = 0) and receptor (distance > 0) for experiment 2; broken down according to category of experiment

Experiment	Average num. of Receptors	Average peak for receptor (distance = 0)	Average / median coverage for receptor (distance = 0)	Average peak for receptor (distance > 0)	Average / median coverage for receptor (distance > 0)
2.1	2.00	476.66 nm	26 / 28 nm	491.50 nm	300 / 300 nm
2.2	1.25	474.50 nm	28 / 26 nm	N/A	N/A
2.3	1.33	473.33 nm	20 / 22 nm	N/A	N/A
2.4	1.01	469.66 nm	18 / 20 nm	N/A	N/A

5.3.6 Discussion of experiments

It is clear that the more challenging the environment is, fewer mistakes can be made or the critters will not survive and as a consequence, the evolved receptors virtually always evolve to peak in the ideal region – whereas in the easier environments, receptors mostly peak in the close vicinity of the ideal region but occasionally peak even farther way. Moreover, as was seen, the harder the environment, the average number of receptors seems to be going down; in fact, all runs in the most difficult environment evolved a single receptor. This has a simple explanation: examining a single and specific range of the spectrum is enough to give a critter all the information it requires in order to survive, there really is no need for other receptors (this can be demonstrated by looking at the reflectance functions of fig. 5.3: certain intensities at some peaks can indicate exactly one type of resource, e.g., intensity of 1 at 470nm has to be 'blue'). Thus, even if the evolved extra receptor provides some usefulness (a conclusion which has not been demonstrated so far), it can be said that in the more difficult environments it is likely to cause more harm than good, otherwise it would have been retained.

Perhaps the most interesting result is the similarity of the evolved receptors' purpose to the primary task of vision in many biological organisms. First, the evolved receptors primarily learn to recognise resources that provide nourishment. Second, when the environment becomes more challenging, the evolved visual mechanisms of critters become specialised: these receptors detect a very narrow and specific region of the spectrum – the critter sees nothing besides. Finally, the evolved visual systems in part 1 can be said to be 'matched filters' systems; the critters are looking for a specific cue – once given, the critters consume the perceived resources; as demonstrated in section 5.3.1, this is similar to many visual strategies seen in nature.

These results indicate that certain universal guiding principles shape the evolution of visual systems, both in nature and in artificial systems. These principles work through the interaction of the environment and the visual system, which in Mosaic World are environment→receptor interactions, and result in the visual system becoming increasingly better adapted to performing its task: to provide useful information that assists the organism's survival, and *not* to create a full portrayal of the environment. In the experiments described here, these interactions resulted in the evolution of simple 'matched filters' visual systems of various levels of specialisation.

5.4 Part II: ambiguity and visual evolution

In this part, the hypothesis that the need to deal with ambiguous environments is a possible reason for the evolution of colour vision is examined. Therefore, a set of experiments is conducted in which a population of critters is exposed to environments of various types of ambiguity. It is anticipated that the environment→receptor interactions that take place will result in the visual system of the critters becoming better adapted to the environment in the course of evolution; the experiments are conducted in order to confirm this and assess whether these adaptations can be referred to as 'colour vision'.

5.4.1 The evolution of colour vision

The selection pressures underlying the origins of colour vision are still unknown [50], however, it is known that colour vision evolved several distinct times during evolution [232]. One theory suggests that the original appearance of colour vision in vertebrates was a result of the need to maintain lightness constancy [44, 137] – the ability to filter the differences between sunny and shaded regions. In other words, colour vision originally evolved in order to deal with ambiguity of the visual environment, and not necessarily to tell different colours apart. This could have been the case in shallow water environments, where illumination flickers pose a serious constraint on visual processing [137].

Ecological forces have been shown to be a major element in directing the evolution of visual systems [90, 134]. There is a great diversity in the number and the spectral sensitivities of the cone types in different mammals. This is not only the case for mammals; for example, insects that occupy entirely different ecological niches occasionally possess very similar sets of receptor cone types [37]. It is widely assumed that these variations represent adaptations for specific visual needs that are linked to specific habitats or lifestyles; however, in many cases the adaptive usefulness of the examined system is not identified [172]. A possible explanation is that these organisms have inherited these systems from a common ancestor, and constraints (e.g. molecular) have kept them from optimally adapting to their environment [37]. Other constraints, such as those imposed on the processing of receptor signals, may explain why some animals (e.g. non-primate mammals) have not evolved trichromacy [137].

5.4.2 Experiments

In order to examine the relationship between ambiguous environments and the evolution of colour vision, a set of experiments was conducted. All experiments required a random population of 2,200 evolving individual critters to be placed in a test world and ended after 550,000 time steps (roughly 20-24 hours). Once finished, the critter population was stored and analysed. Each experiment was repeated at least 8 times – reported results were averaged across runs. All runs used the same randomly generated environment.

This set of experiments consisted of four types of runs. The dynamic value function (see section 3.4.1) was used in all runs except where stated otherwise; the parameters of the value function assigned positive value to the short wavelength and negative value to the long wavelength. Consequently, surfaces which are rich in short wavelength (and tend to look 'bluish') provide the most potent nourishment and surfaces that are rich in long wavelength (and tend to look 'reddish') provide the most damaging 'poison' (green, grey, and purple surfaces would – on average – offer no reward as they would add as much to the health of a critter as they take away).

(1) No ambiguity: uniform illumination. In this run type, a uniform static illuminant illuminates the surface matrix (a constant 0.6 across all wavelengths). Consequently, there is a one-to-one relationship between stimuli and their behavioural significance, meaning, a perceived surface may only have one behavioural meaning: it could

potentially be generated by only one reflectance (which would have a value that could be reliably predicted).

(2) Ambiguity type I: multiple illuminants. In this run type, multiple light sources illuminate the surface matrix (see sections 3.4.2 and 3.5). Thus, there is a one-to-many relationship between stimuli and their behavioural significance; meaning, a perceived surface may have many different behavioural meanings because it could have been potentially created by a lot of different reflectances (thus, its perceived value is ambiguous – more difficult to predict).

(3) Ambiguity type II: ambiguous value function. In this run type, a uniform static illuminant illuminates the surface matrix, and the ambiguous value function (section 5.2.2) is used. As a result, there is a one-to-many relationship between stimuli and their behavioural significance – thus, a perceived surface may have different underlying values at different points in time.

(4) Ambiguity type III: ambiguous perceived stimuli. In this run type, a uniform static illuminant illuminates the surface matrix, yet the perceived stimuli are ambiguous as described in section 5.2.3. As a result, there is a one-to-many relationship between stimuli and their behavioural significance. Potentially, the same surface could have been generated by many different reflectances (thus, its perceived value is ambiguous – more difficult to predict).

Note that some of these ambiguities are quite different from each other, in particular ambiguity type II which differs from the rest. The aim behind incorporating such diverse ambiguities was to see whether the type of ambiguity makes a difference with regards to the evolved results, and if so, what sort of difference.

5.4.3 Results

An analysis of results for the different run types (see table 5.5) clearly shows that ambiguous environments, regardless of the way the ambiguity is generated, result in a greater average number of receptors evolving per critter (see fig. 5.9 for an illustration of the receptors of three evolved critters). When compared with the control (the 'no ambiguity' runs), it appears these results are statistically significant (a t-Test with a one-tailed distribution was used). A more detailed analysis of the results shows that when there is no ambiguity in the environment, the vast majority of critters (92.41%) possess only a single receptor. However, when there is any type of ambiguity in the environment, there is a definite effect on the evolution of multiple receptors: for some types of ambiguity, most critters evolve multiple receptors (e.g. in ambiguity type III, 99.01% of the critters evolved multiple receptors), for others the effect is weaker (e.g., in ambiguity type II, 35.19% of the critters evolved multiple receptors); regardless, the percentage of critters that evolve multiple receptors is considerably higher in all of these than when there is no ambiguity present (only 7.52% of the critters evolved multiple receptors).

Yet the presence of multiple receptors does not mean that an organism possesses colour vision – to truly possess colour vision, an organism must (i) perform a comparison of activations from two receptors (or more) that (ii) differ in spectral sensitivity [134, 225]. Without integrating receptor activation in post-receptor processing, it is impossible to differentiate a change in colour from a change in stimulus intensity.

Since it is now known that in the run types with ambiguous environments, the critters frequently, and in some run types mostly, possess two receptors or more, an additional analysis was performed in order to discover the kind of spectral sensitivities the receptors possess. This analysis will enable the determination of whether the receptors the critters evolved possess different spectral sensitivities which is a requirement for colour vision. The results of this analysis (see table 5.6) show the percentage of critters that have certain receptor types and receptor combinations. Receptors were broken to three categories: short wavelengths (peaking between 400-490nm), medium wavelengths (peaking between 500-600nm) and long wavelengths (peaking between 610-700nm).

Table 5.5. The average number of receptors in the population and the statistical significance in comparison to the control (no ambiguity), the percentage of critters in all runs that evolved a single receptor and multiple receptors (2 or more); broken down according to the type of runs. Note: a very small number of critters in the 'no ambiguity' category have no receptors, thus, the total percentage of critters in the row is less than 100%)

Run type	Average number of receptors	P_{value} (Comparison with 'No ambiguity' runs)	% of critters with a single receptor	% of critters with multiple (2+) receptors
No ambiguity	1.31	-	92.41%	7.52%
Ambiguity type I	2.11	0.0045	29.44%	70.56%
Ambiguity type II	2.29	0.028	64.81%	35.19%
Ambiguity type III	2.87	0.000095	0.99%	99.01%

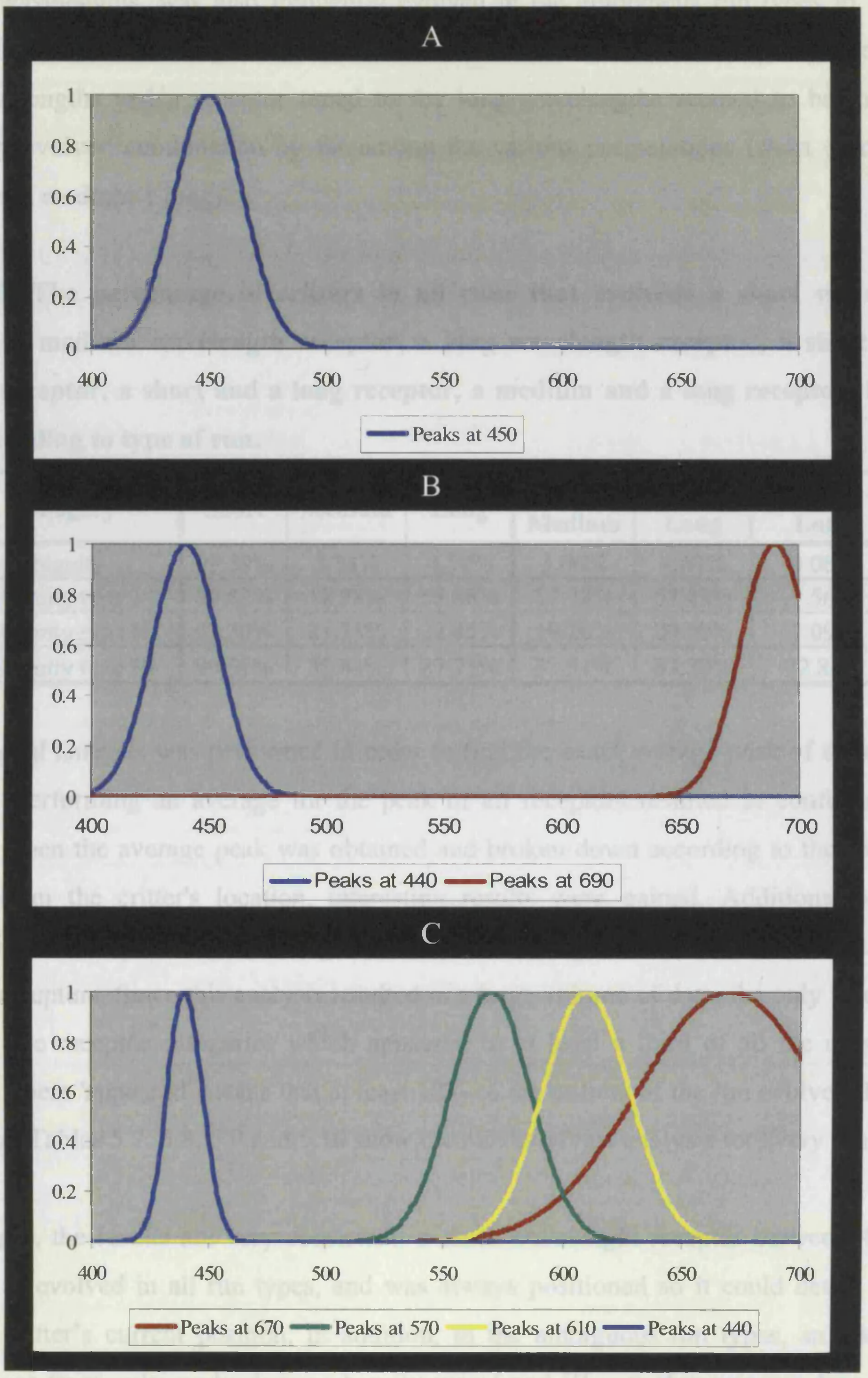


Fig. 5.9. Evolved receptors for three sample critters: (A) evolved in the unambiguous environment, has a single receptor (B) evolved in ambiguous environment I, has two receptors (C) evolved in ambiguous environment III, has four receptors.

It appears that the vast majority of critters in all run types evolved a receptor tuned to the short wavelengths – thus, it may be assumed that a short receptor is mandatory for survival, as this short receptor can detect the presence of wavelengths that provide positive resources (according to the dynamic value function which was used). An additional receptor, tuned to the long wavelengths, was also frequently evolved in the ambiguous run types to various degrees. In fact, in all ambiguous environments, the combination of a receptor tuned to the short wavelengths and a receptor tuned to the long wavelengths seemed to be the most commonly evolved combination by far among the various permutations (short + medium, short + long, medium + long).

Table 5.6. The percentage of critters in all runs that evolved: a short wavelength receptor, a medium wavelength receptor, a long wavelength receptor, a short and a medium receptor, a short and a long receptor, a medium and a long receptor; broken down according to type of run.

Category	Short	Medium	Long	Short + Medium	Short + Long	Medium + Long
No ambiguity	99.59%	3.34%	4.59%	3.06%	4.54%	0.08%
Ambiguity type I	99.52%	17.98%	53.88%	17.72%	53.43%	2.56%
Ambiguity type II	97.30%	21.33%	22.45%	19.24%	20.99%	7.09%
Ambiguity type III	99.51%	33.84%	87.71%	33.51%	87.30%	22.88%

An additional analysis was performed in order to find the exact average peak of the evolved receptors. Performing an average for the peak of all receptors resulted in confusing data; however, when the average peak was obtained and broken down according to the receptor's distance from the critter's location, interesting results were gained. Additional statistics obtained in this analysis are the average and median coverage (based on the tuning function) for these receptors. Since this analysis resulted in a large volume of data, the only results that are given are receptor categories which appeared in at least a third of all the runs in the category, where 'appeared' means that at least 10% of the critters of the run evolved this type of receptor. Tables 5.7, 5.8, 5.9 and 5.10 show the results of this analysis for every run type.

Interestingly, the results are very consistent: a short wavelength receptor between 435 and 451nm was evolved in all run types, and was always positioned so it could detect stimuli from the critter's current position. In addition, in the ambiguous run types, an additional receptor was frequently evolved; in ambiguity type I and III runs this receptor detects light from one surface away from the critter's centre, and is sensitive to long wavelengths: between 628nm and 657nm. Intriguingly, the extra receptor for ambiguity type II was sensitive to medium wavelengths (peaks in 545nm), and was also consistently placed to perceive stimuli farther away from the critter's centre (distance = 4). This receptor is also considerably less sensitive than all other receptors, according to the median statistic, normally covering most or all of the modelled spectrum, unlike the 74 to 118nm, far more sensitive receptors utilised by all other run types.

Table 5.7. The percentage of runs, average peak, and average and median coverage for the 'no ambiguity' runs.

Category of run	Receptors of distance	% of runs	Average peak	Median coverage	Average coverage
No ambiguity	0	100.00%	444.67nm	74nm	76nm

Table 5.8. The percentage of runs, average peak, and average and median coverage for the 'ambiguity type I' runs; broken according to the distance of receptors from critter centre.

Category of run	Receptors of distance	% of runs	Average peak	Median coverage	Average coverage
Ambiguity type I	0	100.00%	451nm	102nm	104nm
Ambiguity type I	1	54.54%	628.27nm	106nm	300nm

Table 5.9. The percentage of runs, average peak, and average and median coverage for the 'ambiguity type II' runs; broken according to the distance of receptors from critter centre.

Category of run	Receptors of distance	% of runs	Average peak	Median coverage	Average coverage
Ambiguity type II	0	100.00%	435.77nm	130nm	118nm
Ambiguity type II	4	46.15%	545.67nm	272nm	300nm

Table 5.10. The percentage of runs, average peak, and average and median coverage for the 'ambiguity type III' runs; broken according to the distance of receptors from critter centre.

Category of run	Receptors of distance	% of runs	Average peak	Median coverage	Average coverage
Ambiguity type III	0	100.00%	441.5nm	118nm	212nm
Ambiguity type III	1	62.50%	657.8nm	102nm	98nm
Ambiguity type III	2	37.50%	604.33nm	118nm	300nm

The results of this analysis show that the evolved critters for all ambiguous environments possess two or more receptors, where one is sensitive to the short wavelengths and the other is sensitive to the long wavelengths (or much less frequently, the medium wavelengths), thus, they fulfil the 'different spectral sensitivities' criteria required for true colour vision.

The last remaining requirement for colour vision is the comparison of activations from different receptors. In Mosaic World critters, this type of comparison may occur when a hidden unit receives stimulus from one receptor and subtracts it from the stimulus received from another receptor (R1 – R2 or R2 – R1), and both receptors differ in spectral sensitivities. A network examination showed that the networks that comprise the critter brains often contain many such connections. However, since statistically it is likely to frequently get such connections randomly, an analysis was performed in order to determine which of these connections were functional, that is, discover whether their presence makes any difference with regards to critter behaviour. Interestingly, these types of connections are somewhat reminiscent of colour opponent processing in mammals that are used for comparing activations from different photoreceptors [182].

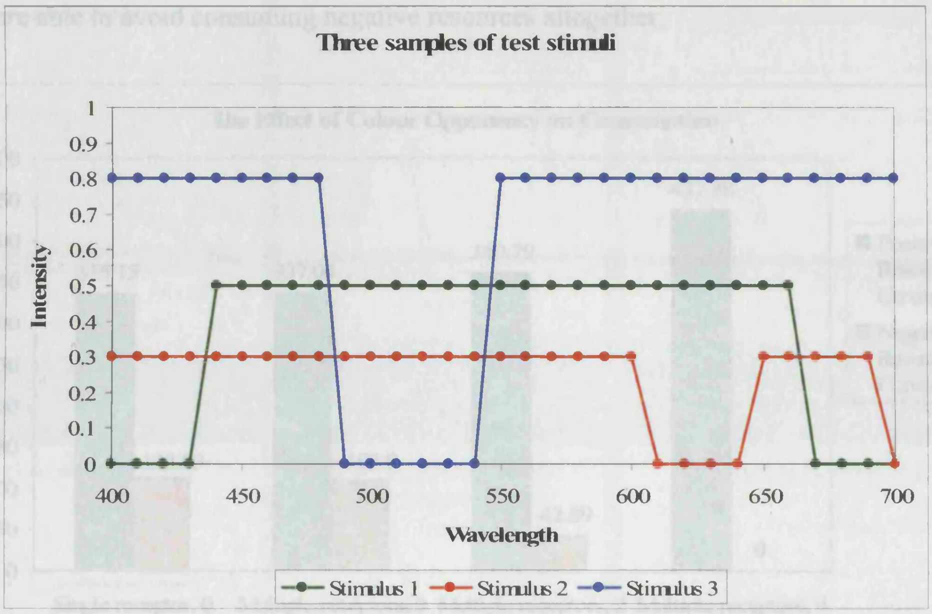


Fig. 5.10. Three samples of the test stimuli used in the opponency analysis

Therefore, a selection of 25 representative critters that possess two or more receptors from all runs was presented with 71 hand-made stimuli (see fig. 5.10 for three sample stimuli) and the behaviour of every critter – specifically, the amount of positive and negative resources consumed – was recorded. These stimuli were created to be challenging for the critters that evolved in Mosaic World, e.g. stimulus 3 in fig. 5.10, which is a negative resource, would look like a positive resource to any critter which possesses only a single receptor in the short wavelengths.

Afterwards, this analysis was repeated multiple times for every critter: in each repetition, a different connection between a receptor and hidden unit was lesioned (disabled); the purpose of this analysis was to discover which 'opponent' connections have an effect on critter consumption. The opponent connections that altered behaviour were termed 'true opponent' connections. An additional goal was to examine whether the presence of true opponent connections was conductive towards more successful behaviour of the critter, that is, whether these types of critters tended to consume more positive resources and less negative resources.

The results of the analysis showed that the number of true opponent connections varied from 0 to 4 per network (with 27.3% of critters have 0 connections, 63.7% with 2, and 9% with 4; the number of connections is even since every comparison requires exactly two connections, one from each receptor). Furthermore, the more 'true opponent' connections a critter possessed, the more efficient was its behaviour towards consuming positive resources and avoiding negative resources, which is shown in figure 5.11. Thus, critters with a maximum number of 'true opponent' connections consumed the highest amount of positive resources and were able to avoid consuming negative resources altogether.

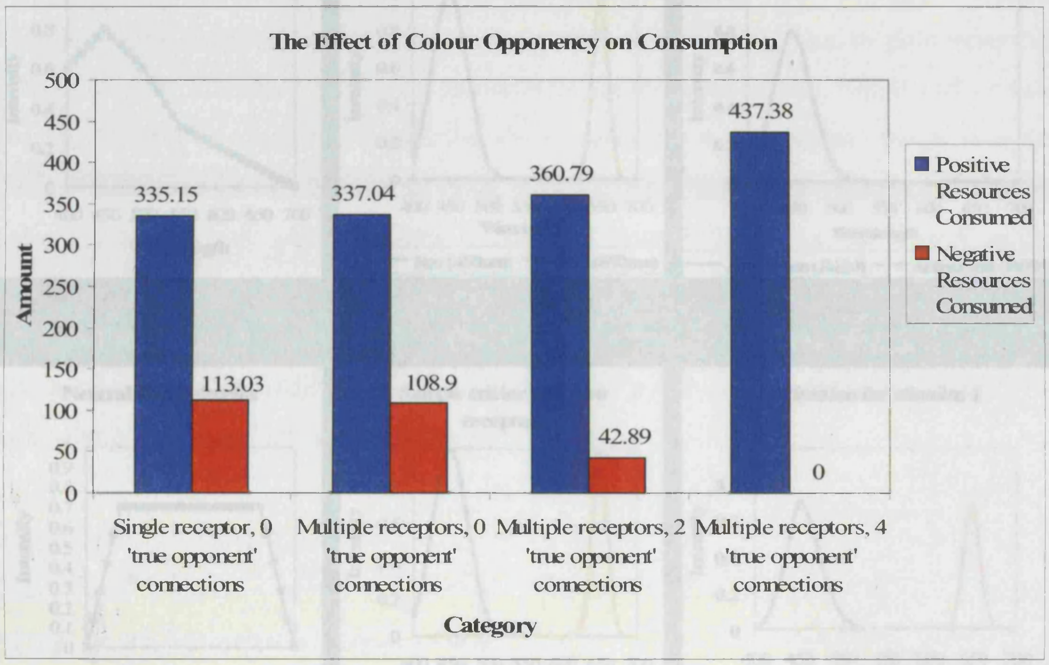


Fig. 5.11. The average consumption of positive and negative resources per critter; broken down according to number of 'true opponent' connections.

Three additional questions remain: first, why do critters that evolve in ambiguous environments require two receptors and not a single receptor? Second, why is the most common combination a short and a long receptor rather than another combination, such as a short and a medium receptor? Finally, why does the short wavelength receptor peak around 430-450nm and not at 400nm, where the value of every wavelength is at maximum value?

It is possible to answer the first question by considering the criteria for colour vision. By having at least two receptors, each sensitive to different regions of the spectrum, and comparing their activations, it is possible to discern the overall value of the resources; using a single receptor would not give enough information to determine the quality of the resource. For example, fig. 5.12 demonstrates this principle by taking a test critter with two receptors (the first peaks at 450nm and the second peaks at 650nm) and displaying three test stimuli to it: a positive resource (rich in short wavelengths), a neutral resource and a negative resource (rich in long wavelengths). By comparing the activations for each resource, it is possible to estimate whether the resource should be consumed or not, specifically, the resource should be consumed when the activation for the short wavelength receptor is stronger than the activation for the long wavelength receptor.

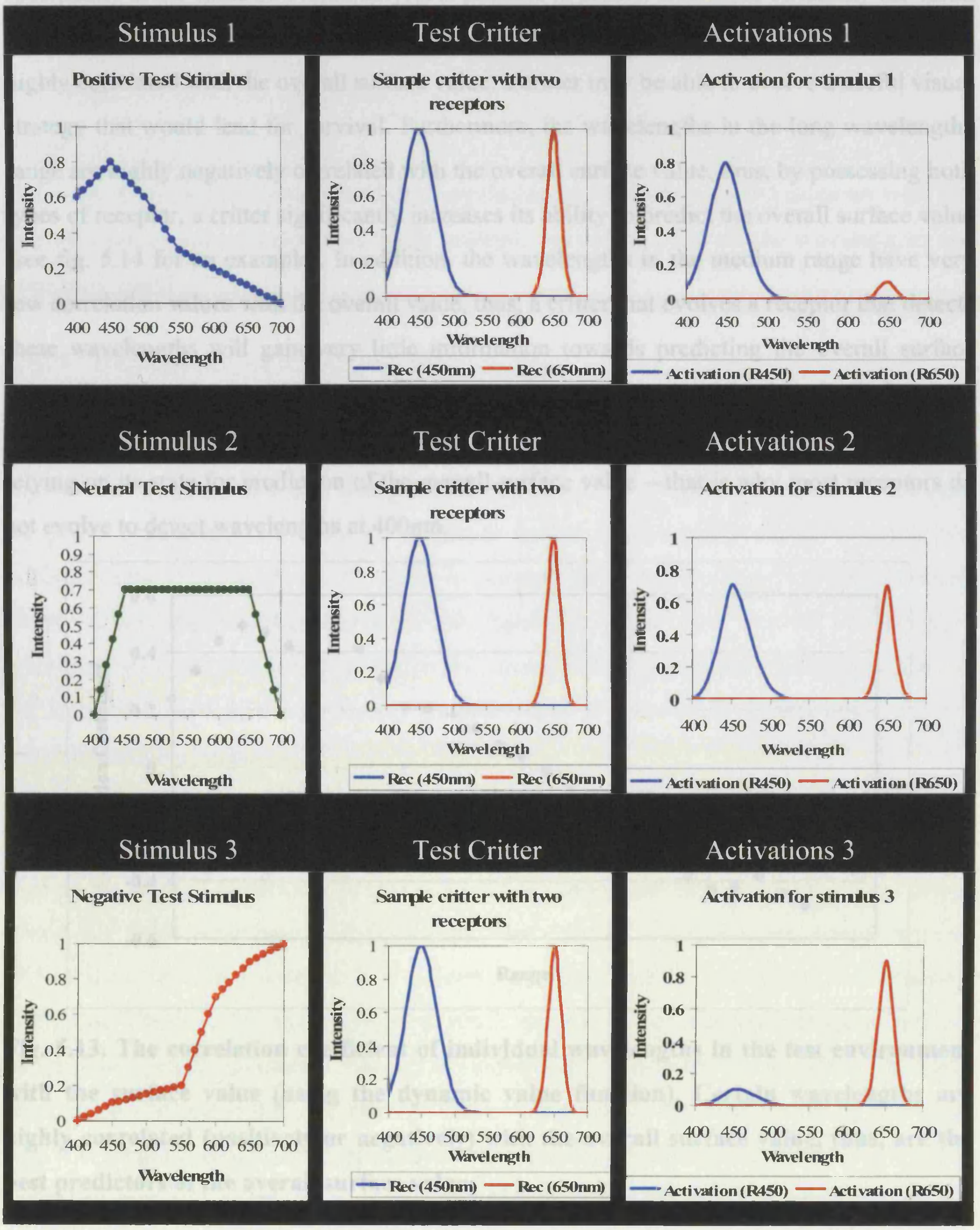


Fig. 5.12. Three sample stimuli and the activations they elicit from a sample critter: the first column is the stimuli, the second is the critter (the same always), and the last column is the activation

The answers to the second and third questions can be gained by looking at fig. 5.13, which explains why – in statistical terms – the majority of critters evolved receptors tuned to the short and long wavelengths, specifically, the values that were evolved. The figure describes the correlation coefficient value of every individual wavelength with the surface value; for example, 440nm is highly positively correlated with the surface value, and so, by looking specifically at the value of 440nm only, it is possible to predict with some reliability the value the surface will have. Therefore, by evolving a receptor that examines a wavelength that is highly correlated with the overall surface value, a critter may be able to evolve a useful visual strategy that would lead for survival. Furthermore, the wavelengths in the long wavelengths range are highly negatively correlated with the overall surface value, thus, by possessing both types of receptor, a critter significantly increases its ability to predict the overall surface value (see fig. 5.14 for an example). In addition, the wavelengths in the medium range have very low correlation values with the overall value, thus, a critter that evolves a receptor that detects these wavelengths will gain very little information towards predicting the overall surface value. Finally, although 400nm provides the most potent positive wavelengths, it is not as correlated with the overall surface value as 430 and 440nm, thus, it is less useful to a critter relying on its state for prediction of the overall surface value – that is why most receptors do not evolve to detect wavelengths at 400nm.

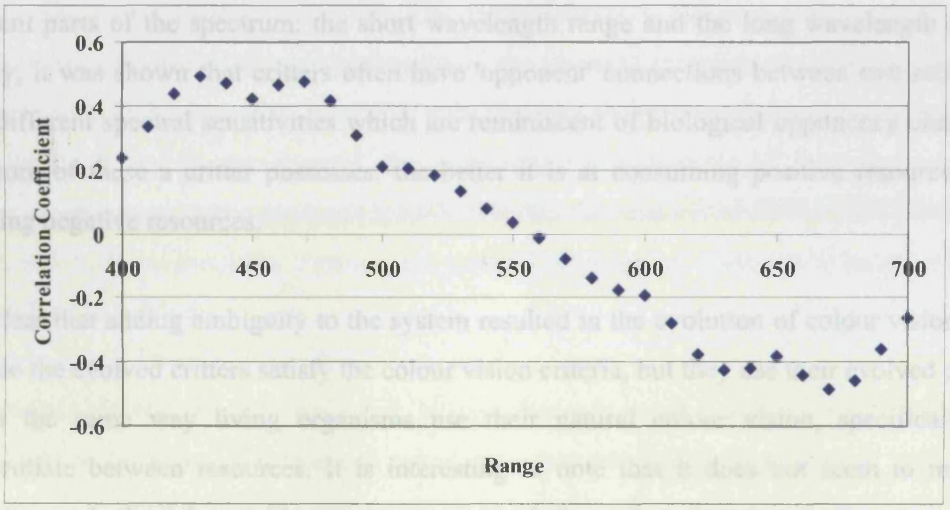


Fig. 5.13. The correlation coefficient of individual wavelengths in the test environment with the surface value (using the dynamic value function). Certain wavelengths are highly correlated (positively or negatively) with the overall surface value, thus, are the best predictors of the overall surface value.

Note that the 'bumpy' shape of the graph in fig. 5.13, where 430nm and 670nm are the wavelengths most highly correlated with the overall surface value is a result of the way reflectance functions are generated in the system, specifically, the use of 7 major wavelengths (described in section 3.3.1). Although this resulted in very interesting (and surprising) effects, this particular element is unique to this system and does not correspond to anything specific in nature.

Critter 1 **has a single receptor which peaks at 450nm and covers 420-480nm.**
Uses: 420, 430, 440, 450, 460, 470, 480nm as predictors.
R = 0.537

Critter 2 **has two receptors; receptor 1 peaks at 650nm and covers 630-670nm, receptor 2 peaks at 430nm and covers 400-470nm.**
Uses: 400, 410, 420, 430, 440, 450, 460, 470, 630, 640, 650, 660, 670nm as predictors.
R = 1

Fig. 5.14. Two sample critters and the correlation coefficient of their receptors with the overall surface value (calculated using multiple correlation for all the wavelengths the receptors span)

5.4.4 Discussion of experiments

The experiments and analysis described in this part of the chapter provide evidence supporting the hypothesis that colour vision is the result of ambiguous environments. These experiments demonstrated that ambiguous environments result in the evolution of multiple receptors. In addition, it was shown that these receptors consistently evolve to detect two different parts of the spectrum: the short wavelength range and the long wavelength range. Finally, it was shown that critters often have 'opponent' connections between two receptors with different spectral sensitivities which are reminiscent of biological opponency channels; the more of these a critter possesses, the better it is at consuming positive resources and avoiding negative resources.

It is clear that adding ambiguity to the system resulted in the evolution of colour vision. Not only do the evolved critters satisfy the colour vision criteria, but they use their evolved colour vision the same way living organisms use their natural colour vision, specifically, to differentiate between resources. It is interesting to note that it does not seem to make a difference whether the ambiguity is a result of the value function having a random component, perceived stimuli having an ambiguous component or simulated multiple illuminants – all these result in evolved colour vision. However, runs involving ambiguity type II seemed to possess different characteristics; this may be a result of the different type of ambiguity involved: where the random component is affects the resource value, and not the perceived stimuli (like the other two types of ambiguity).

One possible criticism of the evolved vision may be that the two different receptors do not detect stimuli from the same surface, but instead detect neighbouring surfaces. Although technically correct, one of the premises of environments used in Mosaic World is that neighbouring surfaces are likely to be identical or very similar (see section 3.5) – which is the reason the environment evolves various types of clusters of colour. Thus, it can be reliably stated that although these receptors detect neighbouring surfaces, the comparison of signals that takes place would frequently be identical to the one that took place if the detection took place from the same surface. However, in this case, what is the advantage of 'looking ahead' using receptors that do not perceive the current location of the critter? There are two possible answers. The first possibility is that the 'look ahead' mechanism is indeed unutilised most of the time, however, the few instances it is used – for example, for edge and hole detection (only occasionally perceiving the darkness as a cue to turn around) – are important enough for evolving this mechanism. The second possibility is that looking ahead does not confer any compelling advantages but is used in the process of colour vision simply because it is impossible to evolve two receptors that view the same location, thus, viewing a nearby surface is as close as the critter can get to viewing the same surface.

It is also interesting to note the visual structures used by evolution; although some critters survived in the ambiguous environments with a single receptor, possessing multiple receptors appears to be a major advantage (and in fact, were occasionally – but not often – evolved in the unambiguous environment as well). The receptor tuned to the short wavelengths is used to detect the presence of short wavelengths in the resource (positive components), and the receptor tuned to the long wavelengths is used to detect the presence of long wavelengths in the resource (negative components). By comparing the activations of these two types of sensors, a critter can determine quite reliably whether the resource is likely to be positive or not, thus, whether it should be consumed or avoided. This is also shown to be the case from a statistical point of view.

To conclude, colour vision is evolved in Mosaic World in order to gain a more reliable way of discerning the value of a resource, which becomes particularly important in ambiguous environments. Critters that evolved in an unambiguous environment tend to 'settle' for a single receptor simply because the perceived stimuli are more reliable and multiple receptors require a greater computational overhead, whereas in the ambiguous environment, multiple receptors were evolved more often because the perceived stimuli is less reliable, thus, the increase in overhead is deemed to be worthwhile. This illustrates very well how the interactions between the environment and the visual system (environment→receptor interactions) cause the visual system to become increasingly more adapted to the environment. This is a recurring process: the ability of the receptors to perceive the environment influences the critter's overall behaviour and likelihood of survival and this enables such critters to be selected for reproduction. Finally, these experiments support the hypothesis that the original evolution of colour vision in nature occurred as a result of ambiguous changing light sources [40, 189].

5.5 Complex interactions analysis

The work described in this chapter primarily deals with the interaction of the visual system and the environment through environment→receptor interactions. In both parts of the chapter, a population of critters is presented with different environments which incorporate several different principles and the effect on the evolved visual systems is examined:

- In part 1, experiment 1: several combinations of physical similarity/dissimilarity and behavioural similarity/dissimilarity are incorporated into the design of the environment.
- In part 1, experiment 2: increasing levels of physical similarity are incorporated into the design of the environment.
- In part 2: an unambiguous environment and three types of ambiguous environments are used.

These environments present various types of challenges for the critters; the primary way which the critters overcome these challenges occurs through alterations to the visual system, by evolving specific adaptations that enable perceiving elements of the environment that are crucial towards survival and disregarding elements that are not. Therefore, the environment→receptor interactions are crucial towards accomplishing the challenge. It is important to emphasise that although these specific interactions take place in one level of the system, the level of the receptors, their effects reach all levels in the critter phenotype: both higher (neuron, network) and lower (genes), and because the critters interact, through competition on resources and reproduction, these affect the population level as well (population, species):

The interaction(s) that takes place are in parenthesis at the end of each sentence.

1) Every critter attempts to survive – several different behaviours are required:
    (a) **Perception**: the environment is perceived by the critter's receptors (environment→receptor), thus, the receptors are in charge of filtering the information that reaches them and relaying the 'right' information to the network. The more adapted to the environment the visual system of the critter is, the better it will be at extracting the relevant and useful information from the environment and passing it on and disregarding information that is of no use. Thus, the difficulty of this task depends on the nature of environment.

  - Although the environments used in exp. 1, part 1, are different from each other, the visual systems required for each follow similar principles, specifically, the need to perceive the peak of a positive resource within the environment; all 4 environments are quite simple and are roughly the same level of difficulty.
  - Several environments of varying levels of difficulty are used in exp. 2, part 1. The more unsaturated the resource types, the more challenging the task faced by the visual system of the critters, and the greater the difficulty in adapting the receptors so that they relay useful information from the environment.
  - All environments used in part 2 are complex, and so, the visual systems of critters must labour to determine which information is relevant and which is not. That said, the three ambiguous environments all have one-to-many relationship between stimuli and their behavioural significance, thus, offer a considerable challenge to the visual systems of the critters by requiring them to compare activations from multiple receptors in order to reliably determine the nature of the perceived stimuli. These environments are more challenging than the unambiguous environment.

(b) **Communication**: the receptors relay this information to the network through neurons (receptor→neuron, neuron→network).

(c) **Control**: the networks control the critter's behaviour (network→critter).

(d) **Consumption**: the critter may consume surfaces (critter→environment); and in this case, positive or negative energy is transferred from the environment to the consuming critters (environment→critter). The ability to recognise positive and negative resources is directly affected by the receptors' ability of perceiving/interacting with the environment.

(e) **Movement**: the critter may choose to move (forage for good, avoid edges and holes) (environment→critter). This behaviour is also affected by the receptors' ability of perceiving the environment.

(f) **Reproduction**: the critter may choose to reproduce (critter→critter). This decision, in case of sexual reproduction, may be affected by the receptors' ability of perceiving other critters.

2) **Selection (to evolve appropriate visual system and behaviour)**: many critters die during stages 1-d to 1-f, either by consuming negative surfaces, or by falling from the edges/into a hole, or by running out of energy, or by reproducing when not possessing enough energy. Because critters that possess appropriate behaviours are more likely to survive, and thus, pass on genes that define them, the advantages these behaviours confer directly affect the selection of these genes (network→genes). Furthermore, because

critters that have a visual system that is better adapted to the environment are more likely to identify good resources for consumption and avoid consuming bad resources, they are more likely to survive, thus, the advantages these visual systems confer directly affect the selection of the genes that define them (receptor→genes).

3) **Selection (to better compete)**: the critters that survive compete on resources (critter→critter). Consequently, critters that are fitter are more likely to out-compete others, thus, features which increase fitness (both evolved behaviours and other aspects of the critter) affect the selection of genes which define these features (network→genes, critter→genes). Critters that have a visual system that is better adapted to the environment are more likely to out-compete other critters on resources (receptor→genes).
4) **Reproduction:** continuing (1-f), the critters that survive past steps (2)-(3) and are now able to reproduce are fitter than those that died (genes→genes). Their offspring's phenotype is likely to be fit as well, as affected by the selection pressure in (2) and (3). These changes to genes affect the phenotype of the critters across all levels (genes→receptor, genes→neuron, genes→network, genes→critter) and eventually the overall population (genes→population).
5) Steps (1) to (4) are repeated until the run ends. The critters with visual systems that are better adapted to the environment are those that survive. Depending on the experiment, the critters that survive at the end of the runs have these types of visual systems:
   - In exp. 1, part 1, critters that survive have a single receptor that receives stimuli from the critter's current location (distance = 0) and peaks in the vicinity of the positive resource's peak. Occasionally these critters evolve more receptors that perceive stimuli from various distances from the critter's current location (distance > 0) whose function is not clear – but appear not to be crucial for survival.
   - In exp. 2, part 1, critters that survive have a single receptor at (distance = 0) that peaks on the positive resource's peak or very close, and is extremely sensitive.
   - In the experiments of part 2:
     - In the unambiguous environment, critters mostly evolve a single receptor at (distance = 0) that peaks around 440nm (a wavelength likely to enable good prediction of the surface value).
     - In all ambiguous environments, most critters evolve one receptor that receives stimuli from the critter's location and peaks between 435 and 451nm (wavelengths that enable very good prediction of the surface value). In ambiguous environment I, most critters evolve an extra receptor that peaks around 630nm and receives stimuli from one surface away from the critter's location. In ambiguous environment II many critters (46%) evolve an extra receptor that peaks around 550nm and receives stimuli from 4 surfaces away

from the critter's location. In ambiguous environment III most critters evolve an extra receptor that peaks around 650nm and receives stimuli from one surface away from the critter's location, and about a third of the critters evolve a receptor that peaks around 600nm and receive stimuli from two surfaces away from the critter's location. The long wavelengths enable very good prediction of the surface value (through negative correlation).

As indicated, the evolved visual systems assist survival by:

(a) In part 1, the evolved visual system enables the critter to survive by identifying only what it should eat (and of course, how to avoid other pitfalls of Mosaic World, such as the holes and edges). Only a single receptor is necessary and is used to detect a specific region of the spectrum which indicates whether the resource is good or not. This information flows from the receptor to the critter's network, and leads to the critter behaving in the appropriate manner.

(b) In part 2, the evolved visual system enables the critter to survive by identifying resources that are most likely to increase the critter's health (and avoid the other pitfalls of Mosaic World). In both unambiguous and ambiguous environments, two (or more) receptors are useful: by comparing activations from a receptor which detects short wavelengths in the resource and a receptor that detects long wavelengths, it is possible for the critter to compare the activations and quite reliably determine the quality of the resource it perceives. However, in the ambiguous environments possessing such a visual system is more crucial because the perceived visual stimuli is less reliable, so critters are more likely to evolve this type of visual mechanisms there than they are in unambiguous environments.

5.6 Conclusions

The aim of the work presented in this chapter was to investigate the environment→receptor interactions that take place in the system by setting a challenge to Mosaic World that required potentially several different types of visual adaptations to be evolved. By picking different environments, it was interesting to see the similarities and the differences between various adaptations that were evolved in the two parts of the chapter.

On one hand, very similar mechanisms were evolved by critters in both parts: one receptor is evolved, which is positioned to detect stimuli from the surface the critter is currently above, and tuned towards the peak of the positive resource of the environment. On the other hand, some differences were apparent as well: first, it appears that the first receptor is used in different ways; in part 1, it is used as a 'matched filter' – as a cue to be used when a resource can be reliably determined to be positive or not, thus, should be consumed, whereas in part 2, it is often used as a part of a colour vision system – comparing its activation with another activation is crucial. Consequently, it appears that the nature of the extra receptor that is evolved in both types of environments is very different. In part 1, the extra receptors are not very different from the first receptor (except for location), whereas in part 2, the extra receptors are mostly tuned to detect long wavelengths in order to accomplish their role in the colour vision mechanism; thus, the extra receptors are very different from the first receptor.

Another difference is that in part 1, multiple receptors were a liability that should be optimised when dealing with difficult environments, whereas in the part 2, multiple receptors were a significant advantage when dealing with difficult environments. The reason for this potentially conflicting information is fairly straightforward. In the environments used in part 1, there is nothing to be gained by possessing multiple receptors: the environment is simple enough that all the necessary information can be obtained using a single receptor, for example, a perceived intensity of 1 at 470nm can mean only one thing: the viewed resource is blue. However, as demonstrated by fig. 5.13, in part 2, multiple receptors of certain types provide useful information that can considerably increase a critter's likelihood of recognition of the surface type.

Why, then, were two receptors occasionally evolved in part 1? The usefulness of these receptors was never established, however, it is possible that these extra receptors help create neutral networks – allowing the phenotype of the critter to be changed without affecting its fitness (see section 4.2). If this is the case, then these extra receptors could have been used as a way to make the critters more evolvable, and would have been discarded when the critter reached its optimal state. In order to test this hypothesis, further work would have to be done.

Interestingly, the fact that at times the critters' receptors aimed to extract as much information as possible from the environment, and other times aimed to extract only a limited amount of information from the environment is suggested by Polani et al to depend on the information that is *relevant* – in the sense that it is useful – in the environment to the agent; in their work, they attempt to provide a framework for quantification of this relevant information [178].

To conclude: all experiments indicate that visual systems adapt to the environment they are placed in through their interaction with it. When it is useful to extract more information from the environment for survival, a visual mechanism evolves that achieves this. When it is useful to filter existing information and only use some of it, the evolved visual systems will do that instead.

Chapter 6

Challenge: behaviour

In the previous chapter, the interactions that occur between the receptors and the environment were investigated, as expressed by the evolution of structural adaptations to the visual system that facilitated survival in various environments. This chapter continues the investigation of Mosaic World and moves to a higher level in the model: the network level. In order to achieve this, a set of experiments was conducted to investigate the complex interactions that occur between the behaviour of the critter and the environment it is situated in: whereas previously the environment's effect on structural adaptations was examined, in this chapter, the environment's effect on behavioural adaptations is examined. The challenge posed for Mosaic World in this chapter is:

Can behaviours suitable for specific environments evolve in a population of critters, and if so, how do the characteristics of environments of various levels of difficulty affect the resultant behaviour?

In order to achieve this, a set of experiments was conducted to study the effect of three different types of environment on the behaviour of evolved critters under seven different health levels.

6.1 Introduction

Even though some of the Earth's environments are characterised by extreme conditions – for example, the cold at the icy shelves of Antarctica or the heat at the Saharan desert during midday – these are the habitats of many animals [23]. A species that wishes to survive in such environments – or any environment – must obtain a way of adapting to its conditions. A species can adapt to an environment by evolving certain structural adaptations. In addition, a species can adapt to an environment by evolving behavioural adaptations [139]. For this purpose, the behaviour of an entity, both natural (such as an animal) and artificial (such as a robot), can be defined as the dynamic interaction that takes place between itself and the environment it is situated in [143]. If a behaviour is genetically based rather one that has been learned in an individual animal's lifetime then it can be referred to an evolutionary strategy [139].

Even with appropriate structural adaptations, an animal's survival is critically dependent on its behaviour [139]. For example, in nature, dark moths are more difficult to spot when placed on a dark background and light moths are more difficult to spot when placed on a light background. However, to benefit from this type of camouflage, a moth must behave in an appropriate manner, by actively seeking backgrounds that are better suited for its colouring [103]. Consequently, the process of evolution results in animals that are very efficient at survival; this includes behaviours such as foraging, reproduction, hunting prey and avoidance of predators [139].

All behaviours an animal may perform cost energy; this energy must be replaced by the animal in various ways, all of which may be referred to as foraging. Yet the rate at which an animal is able to restore its lost energy also depends on the availability and accessibility of food. Furthermore, there may be occasions where an animal has only a limited amount of energy or time it can spend on foraging; this constrains the behaviour of the foraging animal. An animal can prepare for such a situation by saving energy (e.g. storing fat). Under natural selection, efficient foragers have an advantage; thus, most animals are very efficient at searching and obtaining food [139].

The best way to search for food depends on numerous factors, including the distribution of food (or prey) and whether it is static or moves [188]. Naturally, the physical structure of the habitat (e.g. the structure of the vegetation) also plays an important part at determining the search methods that can be used [189]. Different species possess different foraging methods; some actively search for their food while others lie and wait for food. Consequently, some spend a lot of energy while foraging but forage only a short amount of time, while other spend little energy while foraging but forage for long amounts of time [139]. In general, the more actively a forager looks for food – by moving faster or dedicating more time to the process – the faster it will find it; however, the more active the search, the higher the energy cost the forager pays [9, 161, 189].

In nature, food is frequently distributed in patches (e.g. different bushes, different leaves); when this is the case, the forager has to determine which patch to pick and how much time to spend in it. The forager may be able to determine which patch is likely to have food based on perceptual cues or memory [79, 99]. Once a patch has been picked, the forager needs to do an 'area-restricted search' within it (also called 'local search' [79]) to locate the food source [23]. There are many recurring foraging strategies which are used by animals when food is distributed in patches. For example, after a food item has been obtained, some animals perform a local search which is characterised by a decreased rate of movement and an increased rate of turning – this appears as spiralling movement patterns; clearly, this behaviour is useful when food/prey is distributed in clumps/groups, and such movements increase the likelihood of finding more food items [23, 25].

The study of foraging in insects, animals and humans relates to several areas of research in biology, psychology, behavioural ecology and anthropology with a very large body of work.

Food abundance (spatial distribution) and foraging behaviour

One topic of study is the effect of the food abundance (or prey) within a patch, specifically the spatial distribution of the food within the region, on the foraging strategies of the forager. Often the animal's behaviour aims to increase its chances of obtaining food which may be affected by the food's distribution; thus, the abundance of food tends to be negatively correlated with the length of time or speed the forager pursues it [60]. In a study of the environment's effect on the movement patterns of Chacma baboons that live in two different areas: the slopes and the belt [81], it was discovered that the slopes baboons foraged in longer journeys while moving faster than the belt baboons because of the lower food availability present on the slopes. However, when food availability increased, the length of the journeys decreased. In another study, on Rana catesbeiana tadpoles, it was reported that when food levels were low, the tadpoles increased their foraging efforts by moving more frequently and faster [9]. A study on bumblebees demonstrated that a change in foraging strategy takes place as a result of nectar abundance; when there is more nectar per flower, the bumblebees search more for flowers in the area; thus, the bumblebees clearly aim to forage mainly in more rewarding areas [139]. Finally, it was shown that the foraging strategy of thrushes depends on the distribution of food; when food is placed in small clamps, the best foraging strategy is to move straight and turn once a food item has been obtained in order to find the rest of the nearby food, however, when the food is spaced out, after a food item has been obtained it is best to continue moving [210, 211].

Food abundance (availability of food) and food preferences

Similar research investigates the effect of the availability of different types of food or prey within a patch on the food preferences of the forager [23]. Normally, when food is abundant, animals prefer the higher quality food – but when food is scarce, animals are less choosy. It was shown that foraging bluegill sunfish show no preferences with regards to capturing small, medium or large water fleas when these were available at low densities; however, when there were plenty of fleas, the fish preferred to capture the largest fleas and ignored the rest [236]. Similarly, it was shown that the redshank, a type of bird that feeds on worms, tends to ignore smaller worms and catch only worms that are above a certain size; however, its size preference depends on the rate of encounter of larger worms [72]. Another study examined the effect of seasonality on Tai Chimpanzees and showed that in dry season – when food resources are scarce, the chimpanzees spend more time feeding and eat more frequently lower quality food items than when food resources are abundant [56].

Temperatures and foraging behaviour

Temperatures may also affect the foraging behaviour of animals which require thermoregulation [161]; for example, a bumblebee must spend energy to keep its flight mechanisms warm when it is cold, and increasingly more as it gets colder [139]. It was shown that bumblebees forage on rhododendron flowers, very rewarding flowers in terms of energy in a wide range of temperatures – but they do not forage on wild cherry at low temperatures because the energy gained from these flowers is less than the energy costs of keeping warm and foraging [80].

Starvation and foraging behaviour

Foraging behaviour has also been found to be dependent on parameters that are internal to the organism such as the presence of hunger; these studies are linked to the previously described studies on the effect of resource abundance, i.e. when resource levels are low, an animal may be hungry. Generally, when an organism is hungry, it increases its efforts of locating food in several ways. In a study of Rhynocoris marginatus, a type of predatory insect, it was shown that the hungrier the insect, the shorter the distance it travels in search of prey; on the other hand, the hungrier it gets, the faster its movement rate and the more turns it makes during this search [49]. Another study, on wolf spiders [229], demonstrated that Hogna helluo changes its movement patterns when starved: it travels farther, more frequently, and its maximum speed is higher than the satiated spider. This is believed to be the case because Hogna seeks new areas with better chances of finding prey; it 'assumes' it is hungry because its current area has low prey availability. A study of Drosophila flies reported that hungry flies are more active than satiated flies – their level of locomotion increases [108]; the authors suggested that the increase in speed is a part of altered search behaviour, and argued that if food had already been found during the experiment, the speed would not have increased despite the fly's hunger. Conversely, in a study of darkling beetles [140], it was shown that hungry beetles move slower and cover less ground than satiated beetles. Although this behaviour appears to contradict the previously described work, its purpose appears to be the same: the authors argue that hungry beetles move slower in order to do a more thorough search (area-restricted foraging). A different study reported similar effects of hunger on the behaviour of Coccinellid Larvae [45]; the hungrier the larva, the slower it searches for food and the more turns it makes. Here, too, the change in speed aims to achieve a more thorough search within a patch.

Risk sensitivity and foraging behaviour

A related area of research is risk-sensitive foraging, the study of the effect of uncertainty on foraging decisions [17]. Several theoretical models, and numerous studies suggest that animals tend to be risk-averse when the amount of reward is variable and unpredictable, that is, they will always prefer the constant alternative, and are mostly risk-prone when the variability is related to delay, that is, they will prefer the uncertain alternative when reward is delayed in a random amount of time [16, 17]. In addition, it was reported that positive and negative energy-budgets – defined according to whether the animal receives enough food to satisfy its energy needs including elements such as thermoregulation [16] – occasionally cause an animal to switch from one behaviour to the other (risk-averse to risk-prone and vice versa). It is important to emphasise that a lot of contradictory results have been reported in multiple studies, thus, many research questions are still unresolved. It appears that foraging decisions are very complex and may be affected by what appear to be trivial elements in the conducted experiment – no one theory explains all the reported behaviour [17].

Computational models that investigate foraging

There are numerous computational models that simulate the behaviour of real world animals (e.g. one simulation was used in order to investigate the movement patterns of confined pigs [220]). However, there are fewer models that attempt to investigate the foraging behaviour of animals. In an agent-based simulation model, the foraging strategies of the common Hippopotamus were investigated and compared with field results from wild Hippopotami [126]. In another model, four foraging strategies of animals harvesting renewable resources from isolated patches in competitive situations were investigated and compared using a simulation model [163]. In another agent-based simulation, a predictive model attempted to determine the patch choice of animals for simulated landscapes characterised by various spatially distributed resources [150]. Finally, in her PhD thesis, Favreau used an agent-based simulation to investigate the effects of food availability on animal movement [60].

It is commonly accepted that the evolutionary persistence of a trait an animal possesses is linked to its contribution towards its survival and reproduction in its natural environment; therefore, when an animal behaves in a certain way, it is possible to ask how every behaviour contributes to its survival in its natural environment [139]. Since it is difficult to determine the quality of the animal's adaptation to its environment, similar species that reside in different environments are compared instead. Thus, this can illustrate the aspects of behaviour that are important in the animal's adaptation to its environment [139]. This refers to both the behaviours that an animal exhibits in its natural environment (e.g. the behavioural strategies of an animal that resides in a tough environment with little food) as well as the adaptive behaviours the animal expresses when its environment changes (e.g. the behavioural strategies that an animal displays when food becomes scarce in its environment).

In this chapter, the foraging behaviour of evolved critters is analysed (including movement, turning, movement speed, type of consumed food) under several different types of environments (easy, standard, difficult) and internal conditions (7 different levels of starvation). It is examined whether certain environmental conditions result in different behavioural strategies, and more so, whether these behavioural strategies are sensible strategies in light of the challenges the critters face. Finally, the evolved behavioural strategies are compared with the foraging strategies of natural organisms that face comparable conditions.

6.2 Additions to Mosaic World

The experiments that were conducted in this chapter required no additions to the model. The version of the model that is used is the one described in chapter 3, with the exception that it uses the most evolvable structural mutation discovered in chapter 4 (mutation type 4).

6.2.1 The methodology behind the model

Although no additions were made to the model, it is used in a way that differs from the way it was used in the previous two chapters: the behaviour of the critters is now compared with the behaviour of animals or insects, thus, further justification for its design is provided here.

Biological relevance: the model is used to compare the foraging behaviour of evolved critters in an ecosystem with the behaviour of animals and insects. As the result and discussion sections show, the results are clearly similar and the evolved strategies are sensible. Thus, this usage of the model is biologically relevant.

Level: there is no change to this parameter.

Generality: the fact no additions were made to the model, yet it can still be used to ask general biological questions, further supports the notion that the model is general.

Abstraction: this usage of the model can be said to be abstract and does not emulate any specific feature of a real world phenomenon except for the overall concepts of food distribution, food availability, distance, movement and foraging in an ecosystem.

Accuracy: in the experiments, environments with various amounts and distributions of food are presented to the critter. This can be said to be directly comparable to biological experiments that examine the effect of varying distribution of food and varying availability of food sources on animal behaviour (for example, [9, 49, 56, 140]) both because there is less food in the environment and also because there is a greater distance between food sources. In addition, by setting predefined values to the health monitor unit, the critters are 'misled' to believe that they have different health levels: this can be compared to the biological notion of positive or negative energy budgets. Both these usages of the model can be said to be accurate.

In addition, as will be shown in later sections, the behaviour of the critters can be described at times as risk-averse and other times as risk-prone. Although it is clear that these descriptions do in fact apply to the critters (who attempt to minimise and maximise energy/variability), this metaphor is only somewhat equivalent to the biological version which refers more to behaviour towards uncertainty. However, with this caveat in mind, this comparison is still very interesting and only applies to the analysed results and does not apply to the validity of the experiments.

Match: as the results and discussion sections show, most of the evolved behaviours – but not all – are strikingly similar to the foraging behaviour expressed by animals and insects under comparable conditions.

6.3 Experiments

The experiments described in this chapter were conducted in order to examine the behaviour of critters under three different types of environments: easy (plenty of resources, relatively close to each other), standard, and difficult (few resources, far apart). Furthermore, the effects of starvation and satiation on the critters' behaviour were examined as well. It is anticipated that environment→network interactions that take place in the experiments will result in the behavioural strategies of the critters becoming better adapted to the environment in the course of evolution; these experiments are conducted to confirm that this is indeed the case, and examine the precise nature of the evolved adaptations.

A simple way of increasing the difficulty of the environment is to alter the value function used (section 3.4.1). By altering the numerical rewards that certain wavelengths provide to the critters, the overall worth of all surfaces can be made to increase or decrease. Thus, the overall environment can be made easier for the critters by making the wavelengths that provide positive rewards (400-540nm) more rewarding – or alternatively, it can be made harder by making the wavelengths that provide negative rewards (560-700nm) more damaging. These changes not only affect the availability of food, but also affect its distribution in the environment, as there would be more or less resources, thus, the distance between good resources would decrease or increase. For example, increasing the numerical worth of all the wavelengths between 400-450nm would cause all surfaces that have reflectance functions that include these wavelengths to be more positive; this would make some positive surfaces even more positive, some negative surfaces less negative, and some weak negative surfaces could become weak positive; however, the overall environment would unquestionably become more positive, and the average distance between positive resources would unquestionably decrease (as there would be more positive resources in the environment). Note that 550nm is ignored because in this type of value function it provides zero reward. Figure 6.1 demonstrates the three value functions used, which were picked after a period of experimentation with various values functions; even though the differences in the functions used are relatively small, they makes a big effect with regards to the difficulty of the environment.

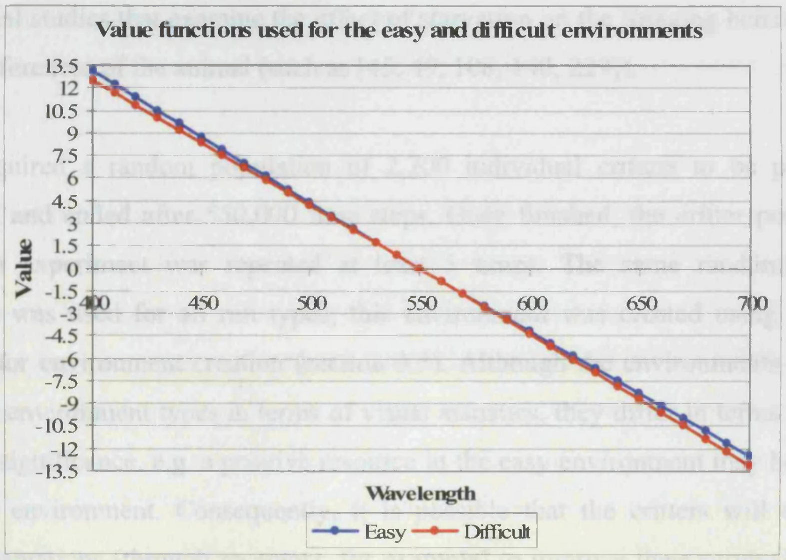


Fig. 6.1. The value functions used to describe the easy and the difficult environments. Note that the function for the standard environment overlaps with the difficult environment when wavelength<550 and overlaps with the easy environment when wavelength>550, so it is omitted for clarity.

Equations (6.1) and (6.2) are used as value functions (instead of equation (3.2)) as specified in table 6.1.

$$V(i) = -\frac{5}{6} * \frac{(i-400)}{10} + 12.5 \qquad (6.1)$$

$$V(i) = -\frac{21}{24} * \frac{(i-400)}{10} + 13.125 \qquad (6.2)$$

Where V(i) is the behavioural value of wavelength i using the value function.

Table 6.1. The three types of runs used in the experiment

Exp. #	Environment type	Value function for wavelengths between 400-540nm	Value function for wavelengths between 560-700nm
1.1	Easy	equation (6.2)	equation (6.1)
1.2	Standard	equation (6.1)	equation (6.1)
1.3	Difficult	equation (6.1)	equation (6.2)

As the three types of environments result in environments that have various amounts and distributions of resources, the results of these experiments can be compared to:

- Biological studies that examine the effect of the spatial distribution of food on the foraging behaviour of the animal (such as [9, 60, 81, 210, 211]).
- Biological studies that examine the effect of the availability of food on the food preferences of the animal (such as [56, 72, 111, 236]).
- Biological studies that examine the effect of starvation on the foraging behaviour and the food preferences of the animal (such as [45, 49, 108, 140, 229]).

All runs required a random population of 2,200 individual critters to be placed in the environment and ended after 550,000 time steps. Once finished, the critter population was stored. Each experiment was repeated at least 5 times. The same randomly generated environment was used for all run types; this environment was created using the standard mechanism for environment creation (section 3.5). Although the environments are identical for the three environment types in terms of visual statistics, they differ in terms of value and behavioural significance, e.g. a positive resource in the easy environment may be negative in the difficult environment. Consequently, it is possible that the critters will evolve some structural adaptations (through receptors, for example) to improve their survival. In order to minimise the likelihood of this occurrence, the same environment was used for all run types, thus, it is possible this will be a minor, if not negligible, element of these experiments. Only the behavioural adaptations are compared in this chapter.

In order to examine the behaviour of the evolved critters, five representative critters (the five longest lived critters of every run) were cloned five times and placed in a test world identical to the one they evolved in (in terms of environmental conditions) for 10,000 time steps. During this time, the behaviour of the critters was closely monitored including (among other statistics): the average number of accumulated bites per critter (the bite mechanism is explained in section 3.6.1) for a given interval defined as 100 time steps, the average value of resources consumed for the given interval, the number of positive and negative bites (meaning, the number of bites taken from positive resources and the number of bites taken from negative resources), average number of steps taken for the given interval, the average number of times a critter stood without moving for the given interval, and the average number of turns a critter made in the interval. In addition, after the run ended, the average survival age was measured. To be able to accurately quantify these behaviours and also reduce the effects of critters on each other, only a small number of critters was used in every run and these were prevented from reproducing (e.g. to avoid a situation where one critter reproduces very quickly and its offspring distort the results). Critters that survived until the end of the run were assumed to have died then.

Every test run was repeated 7 times with a small yet significant difference: in each test run, the critters' "perceived health" was fixed: the critters were instructed to believe that their health was at a predefined level regardless of its real value; this was accomplished by setting the value of the health monitor unit to a predefined value (0%, 10%, 30%, 50%, 70%, 90% and 100%). These runs enable comparing the behaviours of the same critters for different levels of health. After the test runs were complete, results were averaged across categories for every health level.

Because the test runs cannot give any information on the critters' reproduction, an additional analysis was performed. This required taking 500 random surfaces from the environment. Every chosen surface was taken twice in two levels of consumption (9%, 25% left of the surface – these values represent the two states of the surface: 'eaten' and 'full'), and fed to the five critters which were used in the test runs. By analysing the activations of the critter brain, it was possible to determine when the 'reproduction' output unit was active. This analysis was performed 7 times; in each, the value of the health monitor is set to the same values used in the test runs (0%, 10%, 30%, 50%, 70%, 90% and 100%). By averaging the results for all critters in the same environment type, it was possible to determine the average number of times that the random stimuli caused the critter to reproduce for every health level.

6.4 Results

Although the three types of environments that were used have the same visual characteristics, the different value functions which were used affect the percentage of positive and negative resources in each environment. An analysis was performed in order to quantify these differences. Table 6.2 shows the percentage of positive, negative and hole surfaces for every environment type (hole surfaces are surfaces that are a part of a hole). As can be seen, in the easy environment there are almost twice as many positive surfaces as there are negative surfaces, in the standard environment the number of positive surfaces is roughly equivalent to the number of negative surfaces, and in the difficult environment there are almost twice as many negative surfaces as there are positive surfaces. Logically, the fewer positive resources that are present in the environment, the greater on average the distance between positive resources.

Table 6.2. The percentage of positive, negative and hole surfaces in every environment type

Environment Type	Positive	Negative	Hole
Easy	64.45%	34.05%	1.50%
Standard	49.41%	49.09%	1.50%
Difficult	34.03%	64.47%	1.50%

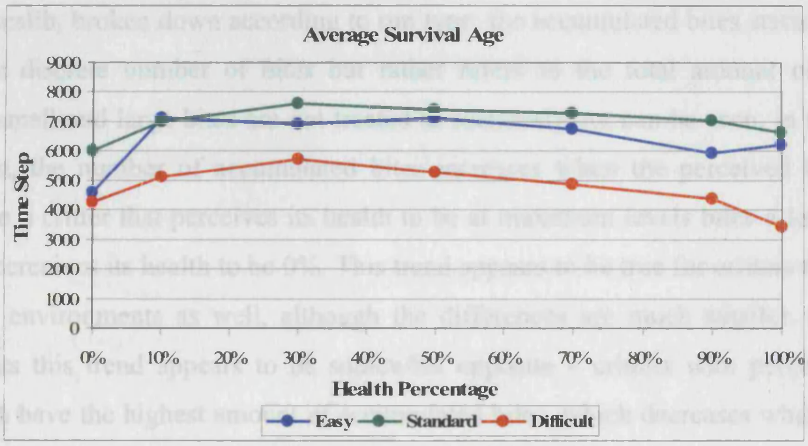


Fig. 6.2. Average survival age per health level for every run type

As can be seen in fig. 6.2 which shows the average survival age for every examined level of perceived health, broken down according to run type, critters appear to be best at survival when their perceived level of health is between 10% and 70%, and worst when their perceived level of health is 0% or 100% (depending on the run type). This is true for all environment types, but most noticeable – the differences in survival age are the largest – for critters that evolved in the difficult environment where these differences are very large (5734 time steps in 30% compared with 3435 in 100%). In addition, it appears that on average, critters that evolve in difficult environment tend to survive less than critters that evolved in easy or standard environments; this result is unsurprising considering the lower amount of resources. However, it also appears that critters that evolved in the standard environment tend to survive more than critters that survived in the easy environment; this result is surprising, but may be within statistical errors as the differences are quite small.

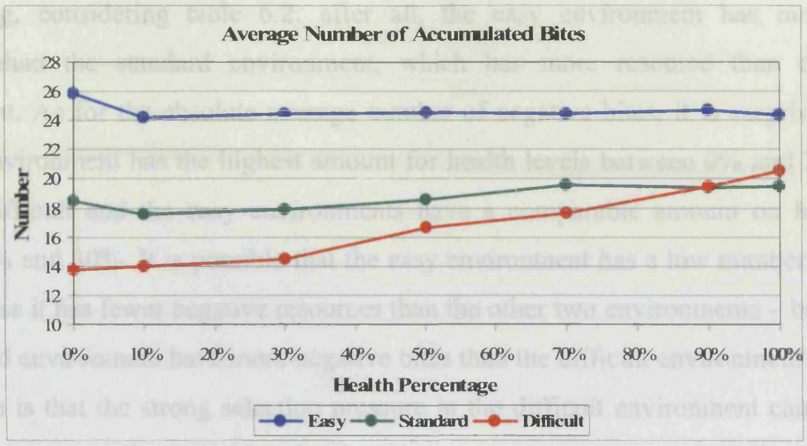


Fig. 6.3. Average number of accumulated bites per health level for every run type

Fig. 6.3 shows the average number of accumulated bites for every examined level of perceived health, broken down according to run type; the accumulated bites statistic does not refer to the discrete number of bites but rather refers to the total amount of bite sizes (therefore, small and large bites are not treated as identical). As can be seen, in the difficult environment, the number of accumulated bites increases when the perceived health level increases, so a critter that perceives its health to be at maximum levels bites a lot more than critter that perceives its health to be 0%. This trend appears to be true for critters that evolved in standard environments as well, although the differences are much smaller. In the easy environments this trend appears to be somewhat opposite – critters with perceived health levels of 0% have the highest amount of accumulated bites, which decreases when the health level drops to 10% and stabilises afterwards.

Fig. 6.4 and 6.5 which describe the average number of positive and negative bites respectively, indicate that for critters that evolved in difficult environments, as the perceived level of health goes up, so do the number of positive and negative bites. A similar, but much weakened, trend occurs for critters that evolve in the standard environments: the number of negative bites goes up with perceived health, and the number of positive bites goes up by a bit as well. In the easy environments this trend is partially opposite: as the critter's health goes up, its number of positive bites goes down, but its number of negative bites goes up by a very small amount. It is difficult to explain the differences in behaviour in the three types of environments – additional statistics below help shed light.

In terms of absolute values, in the easy environment on average, more positive bites were taken than in the standard environment, and more positive bites were taken in the standard environment than in the difficult environment, for all health levels. These results are unsurprising, considering table 6.2; after all, the easy environment has more positive resources than the standard environment, which has more resource than the difficult environment. As for the absolute average number of negative bites, it is surprising that the standard environment has the highest amount for health levels between 0% and 70%, and in fact, the difficult and the easy environments have a comparable amount on health levels between 0% and 30%. It is possible that the easy environment has a low number of negative bites because it has fewer negative resources than the other two environments – but why does the standard environment have more negative bites than the difficult environment? A possible explanation is that the strong selection pressure in the difficult environment causes evolved critters to be very discriminating in the resources they consume, and in the standard environment the selection pressure is not strong enough to cause this behaviour, but there are enough negative resources for the critters to consume.

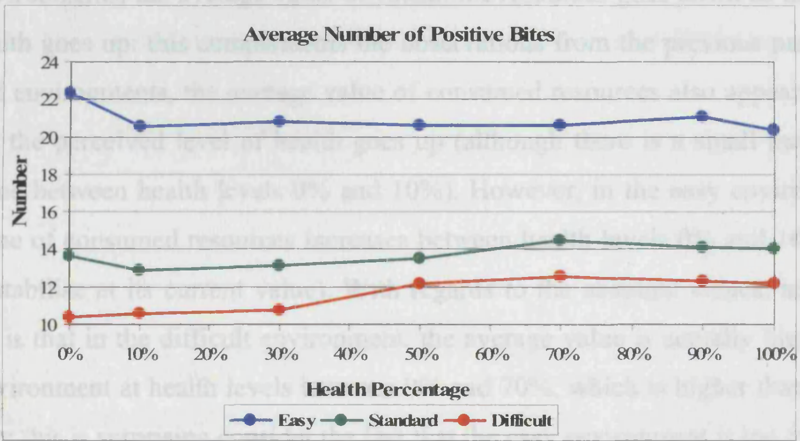


Fig. 6.4. Average number of positive bites per health level for every run type

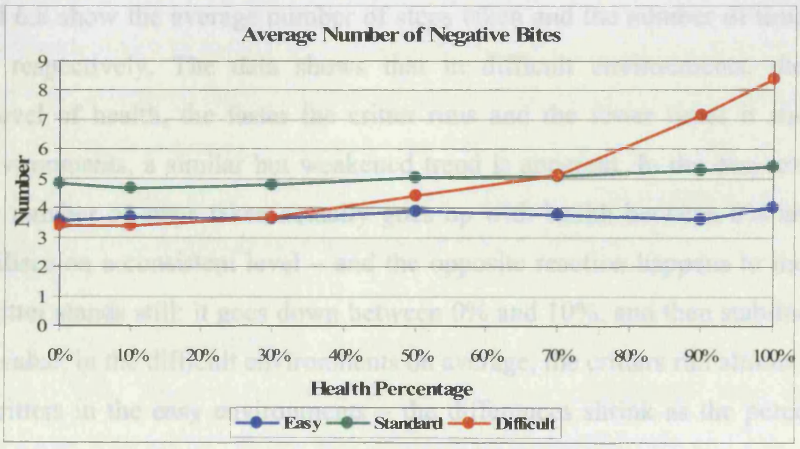


Fig. 6.5. Average number of negative bites per health level for every run type

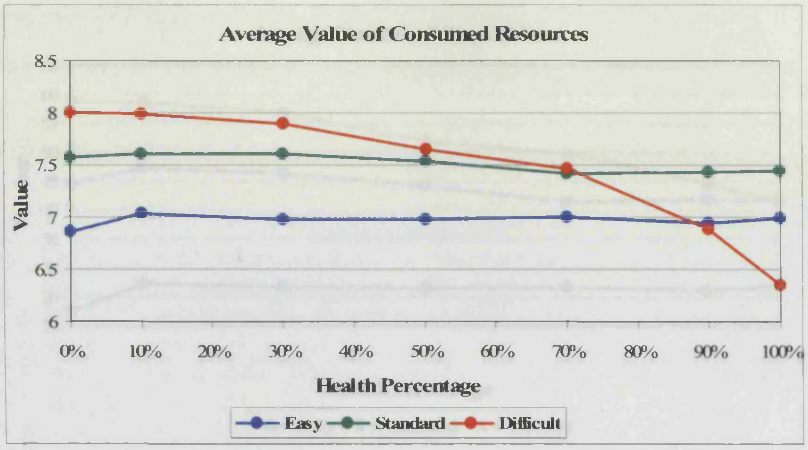


Fig. 6.6. Average value of consumed resources per health level for every run type

Fig. 6.6, which shows the average value of consumed resources, raises more questions; in the difficult environments, the average value of consumed resources goes down as the perceived level of health goes up: this complements the observations from the previous paragraphs. In the standard environments, the average value of consumed resources also appears to slightly go down as the perceived level of health goes up (although there is a small increase in the average value between health levels 0% and 10%). However, in the easy environments, the average value of consumed resources increases between health levels 0% and 10%, but then appears to stabilise at its current value). With regards to the absolute values, an interesting observation is that in the difficult environment, the average value is actually higher than the standard environment at health levels between 0% and 70%, which is higher than in the easy environment; this is surprising consider the fact that the easy environment is the most positive environment of the three, followed by the standard environment.

Fig. 6.7 and 6.8 show the average number of steps taken and the number of times the critter stood still, respectively. The data shows that in difficult environments, the lower the perceived level of health, the faster the critter runs and the fewer times it stands still. In standard environments, a similar but weakened trend is apparent. In the easy environments, the average number of steps taken actually goes up with health between 0% and 10%, but then it stabilises on a consistent level – and the opposite reaction happens to the number of times the critter stands still: it goes down between 0% and 10%, and then stabilises. In terms of absolute value, in the difficult environments on average, the critters run almost 2 to 3 times as fast as critters in the easy environments – the differences shrink as the perceived health increases.

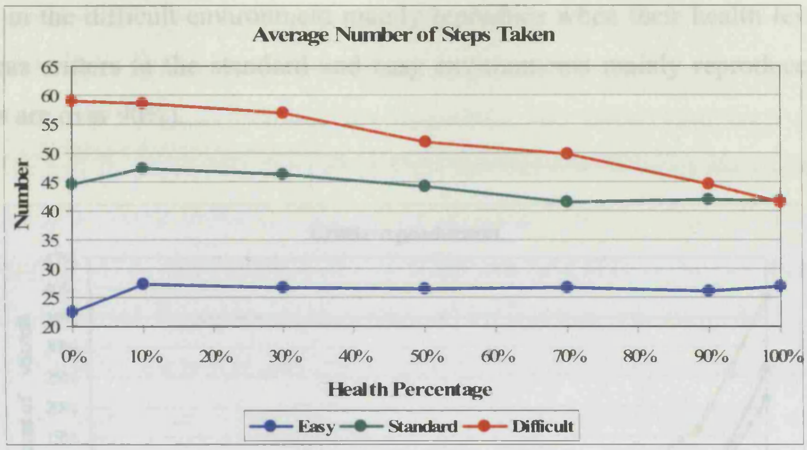


Fig. 6.7. Average number of steps taken per health level for every run type.

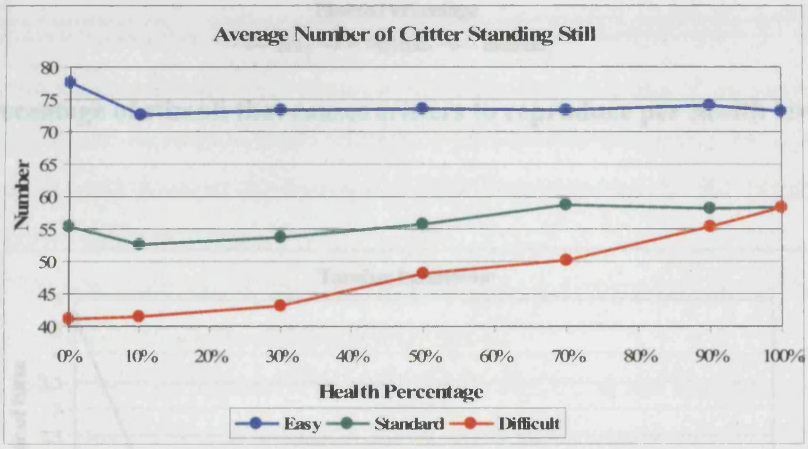


Fig. 6.8. Average number of times a critter stands still per health level for every run type

Fig. 6.9 shows the results of the analysis performed to discover when the critters reproduce, and shows the percentage of stimuli that causes the critters to reproduce at every health level for every run type. Although the reproductive behaviour of the critters was sampled only at 7 discrete different health intervals, it appears – as was also expected – that the behaviour of the critters in other health levels follows the same trends as the obtained values (e.g., the value at health level of 80% would be somewhere between 70% and 90%).

Interestingly, it appears that critters in all environments mainly reproduce when their health levels are over 70%. However, critters in the difficult environment tend to reproduce considerably more than critters in the easy and standard environments (1.47%, 16.05% and 38.28% of stimuli cause reproduction in health levels of 70%, 90% and 100% respectively in the difficult environment in comparison with 0.3%, 3.30% and 25.94% in the standard environment and 1.01%, 3.10% and 21.15% in the easy environment). Essentially, this means that critters in the difficult environment mainly reproduce when their health levels are over 70%, whereas critters in the standard and easy environments mainly reproduce when their health levels are over 90%).

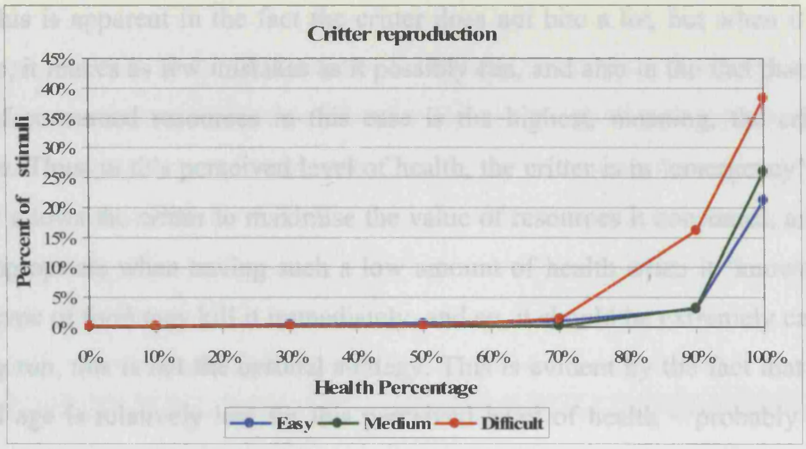


Fig. 6.9. Percentage of stimuli that causes critters to reproduce per health level for every run type.

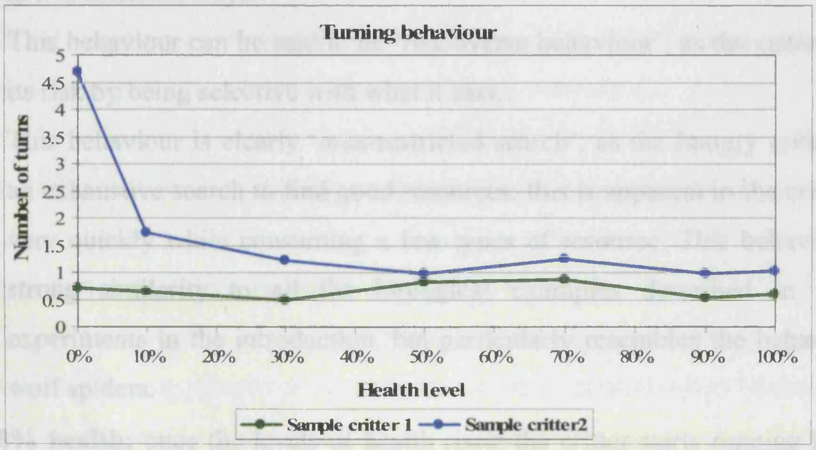


Fig. 6.10. The turning behaviour of two critters: one that exhibits turning behaviour, and one that does not.

Finally, fig. 6.10 shows an observation that occurs occasionally in evolved critters; increased turning at 0% health, which decreases as health goes up. This behaviour is clearly involved in the area-restricted search: once a critter finds a positive resource, it makes more turns with the hope that more positive resources will be found.

6.5 Discussion

Taking all the above results into consideration, it is possible to come up with several conclusions.

First, it is possible to state that in the difficult environments, a behavioural strategy is repeatedly evolved:

- **0%-10% health:** When the health levels are low, the critter runs very quickly, only rarely stopping to stand still; the critter does this because it looks for specific types of food. This is apparent in the fact the critter does not bite a lot, but when it does bite a resource, it makes as few mistakes as it possibly can, and also in the fact that the average value of consumed resources in this case is the highest, meaning, the critter is very selective. Thus, in this perceived level of health, the critter is in 'emergency' mode. This strategy allows the critter to maximise the value of resources it consumes, and it may be most appropriate when having such a low amount of health when it 'knows' eating the wrong type of food may kill it immediately, and so, it should be extremely careful; but in the long run, this is not the optimal strategy. This is evident by the fact that the average survival age is relatively low for this perceived level of health – probably because the costs for looking for specific resources are too high, both in terms of movement costs and also in terms of having a small selection of possible resources to consume. This behaviour is analogous to the biological behaviour reported in the beginning of the chapter in two different ways.
    (i) This behaviour can be said to be 'risk-averse behaviour', as the critter minimises its risk by being selective with what it eats.
    (ii) This behaviour is clearly 'area-restricted search', as the hungry critter performs an exhaustive search to find good resources: this is apparent in the critter running very quickly while consuming a few types of resource. This behaviour bears a strong similarity to all the biological examples described in the hunger experiments in the introduction, but particularly resembles the behaviour of the wolf spiders.
- **10%-70% health:** once the levels of health rises, the critter starts running less quickly and becomes less cautious with regards to what resources it consumes (and so, the average value of consumed resource decreases as well). It can be said that the critter's behaviour is balanced when the critter's health is between 10% and 70%. Afterwards, its number of negative bites skyrockets and its average survival plummets.
- **70%-100% health:** at these levels of health, the critter's behaviour can be said to be 'reckless' – it consumes plenty of negative resources and eats much of what it encounters: this is apparent in the high amount of standing still it does, in the lower average value of consumed resource, and in the low average survival ages. This behaviour does not seem to make any sense, *until* one looks at the reproduction analysis: since a large number of stimuli triggers reproduction, it appears the critter does not 'plan' on staying at this level of health: a successful asexual reproduction would remove 40% of

its maximum health (see section 3.6.4), so even in an ideal state, its health would be 60% – which is within the range of reasonable behaviour. This behaviour can be said to be 'risk-prone behaviour', as the critter maximises its risk (and number of resources consumed) by being unselective in what it eats.

Second, it appears that in the standard environments, a similar – but much weakened – behavioural strategy is seen. However, this behavioural strategy does not appear to be utilised in the easy environments, even though some behaviours are reminiscent of it (most notably, the behaviours at perceived level of 0%, and the identical shape of the average survival curve).

It is not obvious why there are such great differences between critters that evolve in the three environments: there appears to be a progression between the difficult and medium environments – a weakening of the same behavioural strategy – and a further progression between the medium and easy environments – a possible weakening to the point of non-existence of the same behavioural strategy. It is possible that in the difficult environment, the selection pressure is so strong that specialised behaviours are required, whereas in the easy environment it is very easy to survive, thus, no specialised behaviour is required; the standard environment is somewhere in between in terms of ideal behaviours.

There are also several interesting parallels with behaviours seen in nature:

Scarcity of resources (spatial distribution)

Scarcity of resources in terms of greater spatial distribution of resources causes critters to move faster while foraging. Clearly some of this behaviour occurs, both in Mosaic World and in nature, because the organism needs to look for food more actively because there are greater distances between the food sources. Therefore, in the difficult environments it is harder to find a good resource, so more running is required – whereas in the easy environments, a good resource is likely to be found closely at any given point, so less running is required. It is important to emphasise that this is not the only reason for running, as indicated by the higher average consumed resource in the difficult environments; this is explained in the next item.

Scarcity of resources (availability of food)

Fig. 6.6 revealed an interesting observation: the average value of consumed resources is actually higher for critters in the difficult environments than the other environments, despite the fact these environments contain the fewest amount of positive resources. Interestingly, these critters also bite the lowest number of positive and negative bites. Although the critters bite fewer negative and positive resources, the overall value of what they consume is higher – this means that either the positive resources they eat are very potent and/or the negative resources they eat are relatively mild. Most importantly, it is clear that these critters are far more efficient in their consumption habits – and that they attempt to minimise the risk and the bite cost. Thus, it can be said that scarcity of resources in terms of a lesser availability of positive resources causes critters to become choosier in what they eat by consuming more positive surfaces and/or less negative surface than they normally would.

Interestingly, this behaviour at first appears to conflict with behaviours normally seen in nature: as described in the introduction, when resources are scarce, animals tend to be less choosy in what they eat, which is not the result obtained here. Yet a simple explanation can resolve this mystery. In the real world, when food is scarce, animals become less choosy for a straightforward reason: the best resources, those resources they would prefer to eat are simply not available in the quantity they desire; otherwise they would continue only eating them. Thus, foraging bluegill sunfish eat whatever water fleas they find when food is scarce, but prefer to eat the largest fleas when food is abundant [236]. However, in Mosaic World, because the same environment is used both for the easy and the difficult environments with the only difference being the value function used to characterise the resources, the result is that resources that are the most positive in the easy environment continue being the most positive in the difficult environment – the only difference would be the absolute value of the resource. Therefore, the availability of food analogy is not mirrored here: the *best* food is available in all types of environments, in a suitable amount (the fact the critters survive is evidence of that), so there is no need to consume lesser alternatives; the positive food that is no longer positive is food that previously could be classified as 'mild'. But this only explains why the critters do not become *less* choosy and does not explain why the critters become *more* choosy. The critters become more choosy for the obvious reason: there is a greater selection pressure present because of the harsher conditions that forces them to become better foragers, thus, learn to recognise better food; this is equivalent to the increasing specialisation of the visual systems of critters in challenging environments in chapter 5.

That being said, this evolved behaviour is reminiscent of the bumblebee behaviour described in the introduction – in cold environment, bumblebees only forage from flowers they know will restore the energy costs for both foraging and thermoregulation – here the critters only consume resources that they 'know' will sustain their survival.

Starvation

Starvation causes critters to increase their search effort by moving faster. Clearly this behaviour occurs, both in Mosaic World and in nature, because the hungry organism increases its search efforts to find nourishment before it weakens and eventually dies.

Area restricted search

Occasionally, critters evolved a search strategy that is comparable to biological search strategies that require many turns once a resource has been found.

Risk sensitivity

The fact that the behaviour seen in the difficult environment at 0% health is risk-averse behaviour which gradually changes to risk-prone behaviour at 100% is very interesting, specifically because the 'switch' from these two extreme behaviours is also seen in biological organisms, as described in the introduction.

These results further support the results from the previous chapter that indicate that certain universal guiding principles affect the behaviour of both biological and artificial organisms. These principles operate through the interaction of the environment and the critter, and result in the critter's behaviour becoming better adapted to the environment it is placed in. Similar to natural organisms, the critter's survival is directly dependent on its behaviour: its ability to determine what resources it should and should not consume, when it should invest the extra energy in moving faster, and when it should reproduce. This conclusion is supported by the fact that most behavioural strategies that were evolved in this chapter bear a striking resemblance to behavioural strategies seen in nature.

6.6 Complex interactions analysis

The work described in this chapter primarily deals with the interaction of the environment and the critter through its behaviour (environment→critter interactions, e.g. consumption of a resource). In the described experiments, a population of critters was presented with three different types of environments that possess different amounts and distributions of resources, and their effect on the evolved behaviour was examined. By setting the critters' health monitor unit to 7 different values, it became possible to examine the range of different behaviours that critters exhibit at the various health levels.

The environments presented various types of challenges to the critters: the primary way which the critters overcame these challenges occurred through behavioural strategies, by evolving behaviours that are appropriate for the prevailing conditions in the environment, and passing them on to future generations. Therefore, the critter→environment and environment→critter interactions are critical towards accomplishing the challenge that was set in this chapter. Although these specific interactions take place in one level of the system, their effect reaches every other level: network, neuron, receptor and gene; these are essential in order to enable behavioural changes, and to enable that these are passed on to the critter's offspring. Furthermore, because the critters interact through competition on resources and reproduction, the interactions between the critter and the environment reach and affect the population and species levels as well.

The interaction(s) that takes place are in parenthesis at the end of each sentence.

1) Every critter attempts to survive – this requires several different behaviours:
    (a) **Perception**: the environment is perceived by the critter's receptors (environment→receptor). Obviously, it is important that the receptors relay useful and relevant information to the controlling network. Furthermore, although the visual environments are identical in all run types, there are behavioural differences between the run types: a resource that is positive in the easy environment may be negative in the difficult environment; thus, it is possible that some visual adaptations are evolved. However, these are disregarded in this analysis.
    (b) **Communication**: the receptors relay this information to the network through neurons (receptor→neuron, neuron→network).
    (c) **Control**: the networks control the critter's behaviour (network→critter). Obviously, this interaction is very important as it enables the effect of the environment to eventually reach and affect the critter's behaviour.
    (d) **Consumption**: the critter may consume surfaces (critter→environment); and in this case, positive or negative energy is transferred from the environment to the consuming critters (environment→critter). This critter→environment interaction is one of the critical interactions, as the critter's behaviour and likelihood of survival directly depend on its ability to consume resources selectively. Nonetheless, this interaction matters more in some environments than other:
        - Difficult environment: in this environment this interaction is most important, as the critter exhibits different consumption patterns under different health levels. Presumably, were the critter to be less selective, they would not survive (or could not survive as well) in such an environment. As was explained in the results section, as the critter's health becomes lower, it becomes increasingly more selective with regards to the resources it consumes: both positive and negative resources. Because of this selectiveness, the average consumed value of what it eats becomes increasingly higher, thus, enabling survival.

  - Standard environment: in this environment this interaction is important, but less so than the difficult environment for the same reason described in the last item.
  - Easy environment: it appears that because there are abundant resources in the environment, the critter can survive without evolving a specific behavioural strategy of consumption. However, just like in any other environment, in this environment, the critter's consumption is critical: obviously, if the critter did not consume anything, it would perish quickly.

(e) **Movement**: the critter may choose to move (forage for food, avoid the edges and holes) (environment→critter). Similar to the previous interaction, this environment→critter interaction is one of the critical interactions as the critter's behaviour and ability to survive directly depend on its ability to move appropriately. As before, in some environments this interaction matters more than others:

  - Difficult environment: in this environment this interaction is most important, as the critter displays different movement patterns under different health levels. Clearly, in order for the critter to be selective in what it consumes, it must be able to *find* these resources. For this purpose, as the critter's health becomes lower and it becomes more selective in what it eats, it also moves increasingly faster in search of nourishment. If the critter did not have this ability to vary its movement rates, it would not be able to consume the resource of its choice, and as a result, would not be able to survive in such an environment.
  - Standard environment: this interaction is less important than in the difficult environment, but still vital for the same reasons described in the last item.
  - Easy environment: because there are abundant resources in the environment, the critter can survive without evolving a specific movement strategy. However, just like in any other environment, here too the critter's movement is critical: obviously, if the critter could not move, it would die.
  - All environments: as indicated, occasionally the critters evolve the Mosaic World equivalent of restricted-area searching, by making many turns once a resource has been located. Just like in nature, this strategy is likely to convey advantages on critters that possess it, although it does not appear to be crucial for survival (otherwise it would appear on most or all critters).

(f) **Reproduction**: the critter may choose to reproduce (critter→critter). This decision also appears to be related to the critter's health (as fig. 6.9 indicates), thus, it can be assumed that the decision to reproduce in certain health levels, and in certain amounts, is necessary for the critter's survival, particularly in the difficult environment. Presumably, if the critter were less cautious with this strategy (e.g. reproduce when its health is low), it would not survive (or not survive as well).

2) **Selection (to evolve appropriate behaviours)**: many critters die during stages 1-d to 1-f, either by consuming negative surfaces, or by falling from the edges/into a hole, or by moving too quickly (and running out of energy), or by reproducing when not possessing enough energy. Critters that behave appropriately are better adapted to their environment, and consequently, are more likely to overcome its challenges and survive. Therefore, the advantages these genetically encoded behaviours confer directly affect the selection of the genes that define them (network→genes).
3) **Selection (to better compete)**: the critters that survive compete on resources. Critters that have evolved behavioural strategies appropriate for their environment are more likely to out-compete critters that did not evolve any behavioural strategies on resources, thus, are more likely to survive and pass on their genes (network→genes). Similarly, additional aspects (e.g. critter transmittance) that enable critters to out-compete other critters also affect the selection of genes that define them (critter→genes).
4) **Reproduction:** continuing (1-f), the critters that survive past steps (2)-(3) and are now able to reproduce are fitter than those that died *(genes→genes)*. Their offspring's phenotype is likely to be fit as well, as affected by the selection pressure in (2) and (3). These changes to genes affect the critter's behaviour, which affects its genes at all levels (genes→receptor, genes→neuron, genes→network, genes→critter) and the population (genes→population). Because of the nature of experiments in this chapter, this selection pressure is likely to be expressed in the evolved behavioural strategies which result in the critter becoming better adapted to its environment (although, admittedly, it is possible that some structural adaptations have occurred as well as the previous item indicated).
5) Steps (1) to (4) are repeated until the run ends. The critters that evolved appropriate genetically encoded behavioural strategies are better adapted to the environment and are those that survive.

6.7 Conclusions

It is very interesting to note the parallels between behaviours seen in the real world and behaviours evolved in the experiments in this chapter, particularly in the difficult environment. It can be said that within this environment:

- Scarcity of resources in terms of greater spatial distribution causes critters to move faster and forage in longer trips. This is very similar to the behaviour of Chacma baboons [81] and Rana catesbeiana tadpoles [9].
- Starvation causes critters to increase their search effort by moving faster. This is very similar to the behaviour of Rhynocoris marginatus (a predatory insect) [49], wolf spiders [229] and Drosophila flies [108]. Additionally, although other animals move more slowly when hungry, their behaviour is also explained by an increase in search effectiveness, thus, this too resembles – in intent – the evolved behaviour.
- Some critters evolved a search strategy that mirror their biological counterparts in the fact that many turns are taken once a food has been located. This is very similar to the behaviour of thrushes [210, 211].
- The critter's evolved behaviour is risk sensitive (rather than risk indifferent). At times the critters behave in a risk-averse manner, and other times they behave in a risk-prone manner. The fact that these behaviours depend on the critter's hunger level is also significant and has been reported to occur in some animals as well [16, 17].

To conclude, critters in Mosaic World evolve behavioural strategies that vary when the environment varies. This indicates that the interaction of the environment and critter has an enormous effect on the evolved behaviour: as anticipated, the environment acts as a selective force that determines the behaviour of the critter. In addition, the evolved behaviours are sensible – there is a sound reason underlying their usage. Finally, most of the evolved behaviours strongly resemble behaviours used by animals and insects in comparable natural situations; this further supports the conclusion from ch. 5 that certain universal guiding principles similarly affect the evolution – in this case, the evolution of behaviour – of both biological and artificial organisms.

Chapter 7

Challenge: modular specialisation

In this chapter, the hierarchical nature of the system is expanded through the addition of a new level to the model, by replacing the standard network used to control a critter's behaviour with a new control mechanism: the modular neural network. The modular neural network encompasses a control network and up to eight modules. This new level is the focus of this chapter's investigation of complex interactions.

Similarly to chapter 4 where the interactions that occur between genes that could lead to more effective evolution of the critter brain were investigated, in this chapter, the interactions within a modular network, in particular, the interactions between the control network and its subordinate modules are investigated for the purpose of improving critter fitness and exploration of modular specialisation. The challenge posed for Mosaic World in this chapter is:

Can appropriate control network→module interactions occur that improve the fitness of critters that adapt to an environment which changes in time? If so, will modular specialisation be responsible for this improvement?

In order to achieve this, a set of experiments that presents several populations of critters with modular brains and non-modular brains to a changing environment was conducted and additional behavioural analyses were performed.

7.1 Introduction

It is commonly believed that solving multiple simple subtasks is easier than solving a single complex task. For this reason, decomposing a complex problem into several simpler problems may be a potent way to approach a problem. Unsurprisingly, this seems to be a frequently used strategy in nature as well; it is a well known fact that the human brain works in a modular manner [207]. A neural network that exploits this principle by utilising multiple specialised modules, each trained to solve a specific subtask, should be better than a single large network. Another advantage attributed to this architecture is that it reduces the presence of crosstalk (conflicting training messages that occur as a result of a network trying to learn two tasks [95]).

Several approaches have been taken to achieve this goal. One computational approach literally decomposes the task to several subtasks. This method is referred to as a 'mixtures-of-experts' architecture, and is mostly used for supervised learning tasks [96]. Under this scheme, a gating network is connected to several expert networks. Both the gating network and the expert networks are concurrently trained. By the time that the process is complete, the gating network learns to break the task into useful subtasks enabling each expert network to solve an aspect of the larger task. It has been shown that this approach is faster than using a single network [95]. Interestingly, the way the task is decomposed matters greatly; it has been shown that different ways of decomposing a task affect the quality of the result – some ways are superior to others [7]. Therefore, by understanding how the gating network decomposes the task, interesting insights about the nature of the problem faced can be gained.

The principles behind 'mixtures-of-experts' can be utilised in many ways. Koza added architecture-altering operators to a genetic programming simulation that were inspired by gene duplication and gene deletion mechanisms [110]. These additions enabled a main program to create subprograms to deal with subtasks dynamically, effectively decomposing a larger problem into smaller subproblems. The effect of adding these operators was an improvement in the performance of the system. The parallels are clear: the main program is equivalent to the gating network, and the subprograms are equivalent to the modules.

Similar principles underlie Brooks' subsumption architecture, which is used for controlling robots [38]. This architecture decomposes the overall robot control task into several simpler behaviourally oriented subtasks (e.g. avoiding objects, moving, exploring). Each of the subtasks is explicitly solved; combining these solutions enables successful robot control.

Modular neural networks are another type of methods that exploit the same principles. Using this approach, a network that is comprised of several subcomponents is used to solve a task. The structures of these subcomponents can vary greatly, and their number can be dynamic (grow or shrink as needed). Consequently, every component of the neural network has the potential of specialising in a subtask; thus, this architecture is more powerful than a 'standard' architecture. In support of this notion, Rueckl et al demonstrated that a neural network with a modular architecture is better at solving the "what" and "where" vision tasks than a non-modular neural network [193]. In another study, five different architectures were used to control a robot for a garbage collection task [159]. The one that performed best was named 'emergent modular architecture' and had modules competing for control of output units in a control network.

Ensembles are another category of methods. Normally, when evolving neural networks, the best individual is picked from the population. However, there is a lot of information in other members of the population that is not used; ensembles try to use this extra information. An ensemble works by combining outputs of several individuals from the population (using a few different mechanisms), and ideally generalises better than any individual network [246]. A good ensemble is likely to comprise individuals that specialise in different aspects of the overall problem, and thus, it can be argued that this method is related to the other previously mentioned approaches.

In addition, hybrids of the various approaches mentioned have been created, e.g. a method of evolving a population of modules, which are synthesised into modular neural networks [104].

A study of the interactions that take place within a modular neural network used to control critters is useful for two reasons. First, according to the relevant literature, it is likely that incorporating modularity into the critter brains will result in an improvement in the efficacy of evolution in the system, which is naturally a very desirable goal. Second, by understanding how and when modular specialisation occurs in the system, valuable insights into critter functionality and dynamics in general may be obtained. This is accomplished by expanding the existing framework to include a unique hybrid of the approaches described.

In the version of the model described in this chapter, the critters start with a control network that is linked to one module. The number of modules may grow up to eight, and individual modules as well as the control network itself, are concurrently evolved. As was previously described, every aspect of these networks is subject to evolution: number, attributes, topology, weights; allowing the system to evolve both the number and the structure of the modules is a big advantage which most existing systems do not have. This allows evolution to fit the appropriate structure to the subtask, which increases the likelihood it will work well with the overall task [94]. Furthermore, allowing modularity to work at the level of the network is said to have significant advantages [95]. In this sense, it can be said that the new mechanism described here is a hybrid between 'mixture-of-experts' and modular neural networks. The work described here has been published in [199].

7.2 Additions to Mosaic World

The investigations described in this chapter required that Mosaic World be expanded in several ways. The most significant change is the addition of a new level to the model, which now comprises the following levels of abstraction: genes, neurons, receptors, modules, control networks, critters, population and species; figure 7.1 illustrates the differences between the object models of the standard and the modular critter brains. Figure 7.2, which is an expansion of fig. 3.2, shows the interactions map for all objects in Mosaic World.

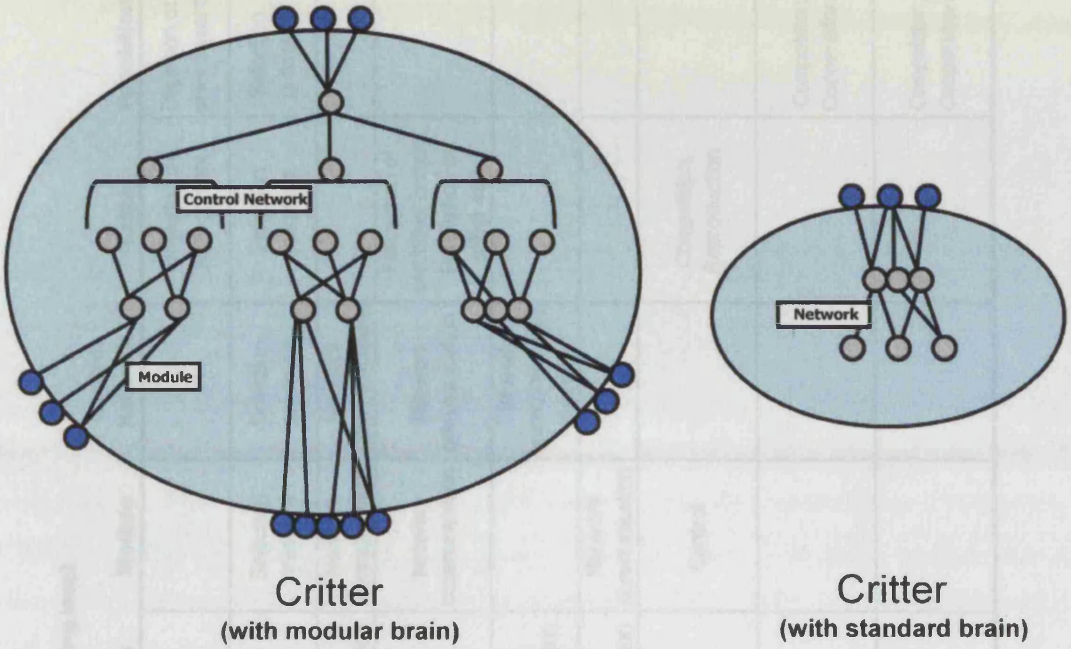


Fig. 7.1: The object model of the standard and the modular critter brains: the network object is replaced by a control network that activates modules. Note that both critters are the same size within the environment.

7.2.1 Neighbour indicator unit

The standard critter brain was expanded by adding a neighbour indicator unit in addition to the existing health monitor unit. The neighbour indicator unit receives a signal if another critter is present at the critter's location. Neighbour recognition is important because in order for a critter to reproduce sexually, it must have a neighbour in its present location – more importantly, if *no* critter is present its current location, the critter pays an energy penalty (this was added to encourage critter recognition, as explained in section 3.6.4). This feature was added to decrease the difficulty of recognition of other critters, as recognition that is purely based on transmittance, that is, being able to extract the critter's transmittance from the perceived stimuli (see section 3.6.5 for the full explanation), appeared to be too difficult to evolve.

Affected level \ Affecting level	Environment	Genes	Neuron	Receptor	Module	Control Network	Critter	Population	Species
Environment	External effect						Depletion of environment	Depletion of environment	Depletion of environment
Genes	Selection pressure	Epistasis, Evolution/Reproduction, Selection pressure	Selection pressure	Selection pressure	Selection pressure	Selection pressure	Selection pressure	Selection pressure	Selection pressure
Neuron		Phenotype	Network communication	Network communication	Network communication	Network communication			
Receptor	Perception of the environment	Phenotype			Network communication	Network communication	Perception of self/other critters, Perception of critter state		
Module		Phenotype	Network communication	Network communication		Network communication, Activate			
Control Network		Phenotype	Network communication	Network communication	Network communication				
Critter	Consumption of environment, Movement in environment	Phenotype			Control		Competition, Reproduction		
Population	Consumption of environment, Movement in environment	Extended phenotype						Competition Cooperation	Competition, Cooperation
Species	Consumption of environment, Movement in environment	Extended phenotype						Competition, Cooperation	Competition, Cooperation

Fig. 7.2: Major interactions within this chapter's version of Mosaic World

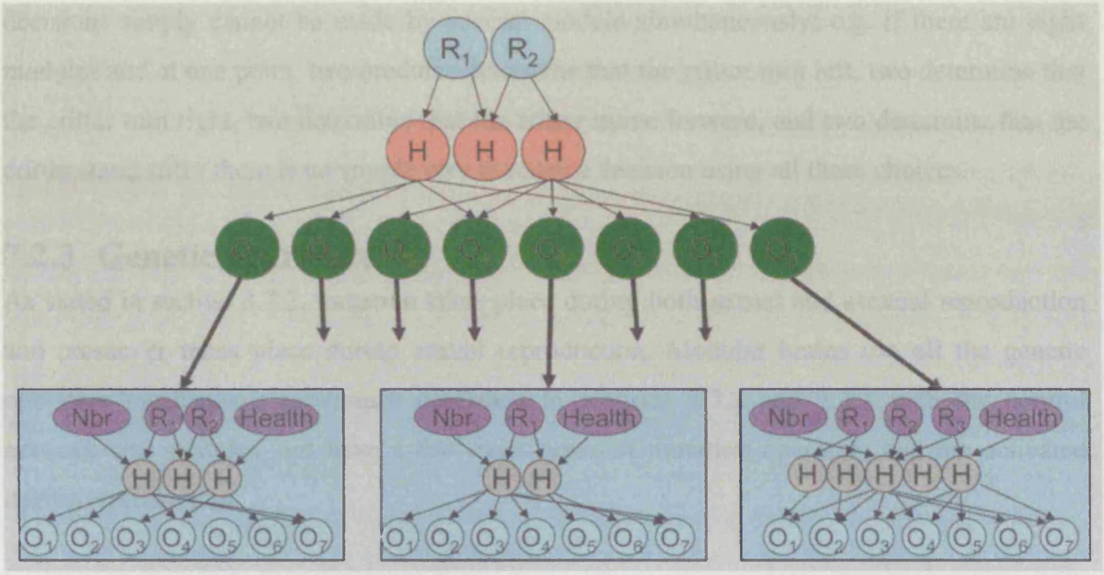


Fig. 7.3: An illustration of a modular critter brain comprised of a control network (2 receptors, 3 hidden units), that connects to 3 modules. The first module has 2 receptors, 3 hidden units. The module has 1 receptor, 2 hidden units. The third module has 3 receptors, 5 hidden units. All modules possess the neighbour indicator and health units. This figure disregards the 3D coordinate scheme

7.2.2 Modular brains

The modular visual brain is comprised of a control (gating) network and one to eight modules; see fig. 7.3 for an illustration. The control network is roughly identical to a standard non-modular critter brain described in section 3.7 with two exceptions; the first is that it does not have a health monitor unit or a neighbour indicator unit. The second is that it has eight output units. The control network is evolvable in the same way a standard non-modular brain is (topology, weights, attributes); it receives stimuli from the environment and determines which module to activate at any given time step. The module activated is the one that connects to the output unit that returns the highest activation. When there is only one module, it is automatically active all the time.

The number of modules is evolvable; a critter starts with one module connected to its control network and new modules can be added and removed up to a total of eight modules. Each module is identical to a standard non-modular critter brain in all respects. With this scheme, every action requires two layers of decisions: first, the control network has to decide which module to activate; then, the activated module determines what action the critter should perform.

It is important to emphasise that only one module can be active at any given moment. Some decisions simply cannot be made by several module simultaneously: e.g. if there are eight modules and at one point, two modules determine that the critter turn left, two determine that the critter turn right, two determine that the critter move forward, and two determine that the critter stand still - there is no simple way to reach a decision using all these choices.

7.2.3 Genetic operators

As stated in section 3.7.2, mutation takes place during both sexual and asexual reproduction and crossover takes place during sexual reproduction. Modular brains use all the genetic operators mechanisms previously described in sections 3.7.2 and 3.7.3 with the control network and modules, but have a few more types of mutation operators that are activated during reproduction.

Crossover of Modular Brains

The control network undergoes crossover the same way a standard non-modular brain does. In addition, a number between 1 and 8 is randomly picked. All modules from 1 to the picked number are cloned from one parent, and the remainder are cloned from the other parent. If as a result of this process a brain is created with no modules, the process is repeated.

Mutation of Modular Brains

The control network undergoes mutation the same way a non-modular brain does. The currently active module (the last module that has been active) is mutated normally. The other modules are not mutated (otherwise very quickly they will not be usable at all). In addition, there are four new types of mutations:

- *'Add Module'*: the currently active module is cloned at a given probability (2%). The new module is randomly placed in an empty slot. If there are already eight modules, this mutation is disabled.
- *'Delete Module'*: one module is randomly deleted (2%). This module cannot be currently active. If only one module is left, this mutation is disabled.
- *'Duplicate Module'*: the active module is randomly (2% to 35%) duplicated and overwrites the least used module.
- *'Discard Module'*: if a module has not been active for a given amount of time steps, it is deleted. The exact number is evolvable.

All percentages were determined empirically and were modified in experiments described below.

7.2.4 Modular duplication

In the experiments described below, a 'Duplicate Module' operator was utilised that acts similarly to gene duplication in nature. Multiple experiments were performed with various probabilities assigned to this operator since the literature stated that this makes a big difference with regards to functional specialisation. One theory suggests that gene duplication facilitates modular specialisation by first relaxing the selection pressure (as the same module exists twice) and then altering the regulation of this module which causes it to be utilised in a different functional context [43]. This allows the new module to accumulate mutations and specialise [164, 248]. An alternative theory suggests that in nature, the gene being duplicated mostly already has two functions and that gene duplication simply allows the two daughter genes to specialise in one of the original tasks [88]. Indeed, Nolfi demonstrated how hardwired modularity without gene duplication resulted in unspecialised modules in his system [159]. In addition, Calabretta et al [43] showed that the duplication rate linearly affects performance, with greater values leading to better performance in a robot control task.

7.2.5 Changing environments

When this setting is active, every predefined amount of time a new environment is generated using the same algorithm and the same environmental statistics. The current environment is continually and gradually replaced with the new environment – this change can be made to occur instantaneously, or it can be made to occur extremely slowly.

This setting presents a challenge to the critters not only because they cannot memorise the location of resources, but also because the actual process of changing is greatly ‘confusing’; during a significant percentage of the time, there are effectively no good resources as all surfaces constantly shift. A critter may start consuming a positive resource (a process which takes time), only to find out that the resource became a negative resource by the time it finished.

7.2.6 The methodology behind these additions

Biological relevance: the additions to the model presented in this chapter, which explicitly incorporate modularity into the design of neural networks (though evolution can choose to ignore these modular aspects), represent conceptual principles rather than specific biological metaphors. Specifically, the modular brain feature does not aim to correctly represent biological brains but rather to investigate the effect of modularity on agent fitness and behaviour. That said, as the next few sections show the results are biologically relevant as they increase our understanding of biology (in terms of the effect of gene duplication and the usefulness of modular specialisation), and are computationally relevant because they demonstrate how useful modular designs are, both in terms of capabilities (indicated by critter fitness) and in terms of analysis of the problem (indicated by the strategies evolved by the control network which are shown to be appropriate for this setting).

Level: the version of the model described in this chapter contains of a new level and consists now of: genes (level 1), neurons and receptors (level 2), modules (level 3), control networks and critters (level 4), population and species (level 5). Because the model now comprises a larger hierarchical complex system, this addition increases the range of complex interactions that can be explored. In addition, the expanded model enables to demonstrate that incorporating hierarchical complexity into the model can provide an improvement in the understanding of the modelled phenomena. For example, in this chapter:

- The effects of internal interactions within a modular brain on critter fitness are examined.
- The effect of environment on modular specialisation is examined:
    - in terms of the number of modules and the behavioural strategies evolved.
    - in terms of visual structures and strategies evolved for each module within the modular brain and type of task it is allocated for.

Generality: the changes to the model do not affect this parameter: the model can still be said to be a general model despite the fact it is used in this chapter to examine specific hypotheses.

Abstraction: all the additions to the model can be said to be very abstract – the notion of modular complex brains has been abstracted to the approach used in this chapter.

Accuracy: the additions to the model implement modular designs accurately; however, unlike modular designs in nature, the usage of modularity here is limited – only up to 8 modules can be evolved, and creation of explicit sub-modules is not possible. Thus, these additions do not mirror the real world principle completely. That said, this level of accuracy is sufficient to enable the investigations conducted in this chapter.

Match: as the results sections of the chapter show, the additions to the model produce behaviours that are very similar to their real world counterparts, specifically:

- Modular specialisation occurs in terms of behaviours.
- Modular specialisation occurs in terms of visual systems.
- Control networks learn to break a task in a meaningful way.
- 'Module duplication', the model's genetic operator that is equivalent to biological gene duplication, is shown to affect the fitness of evolved critters since the utilisation of modularity in the critter brains appears to be linked to the probability of mutation – which is what theory suggests gene duplication does in nature.

Therefore, it can be said that the model matches the real world behaviours that it aims to capture because its generated behaviours are similar to the real world behaviour of the target phenomena.

7.3 Experiments

In order to investigate the interactions within a modular network, specifically, discover whether appropriate control network→module interactions can occur that lead to an increase in the critter fitness, and understand the nature of these interactions, two sets of experiments were performed. In setting the experiments, the goals were threefold. First, it was aimed to determine whether the novel mechanism introduced in this chapter would enable critters with modular brains to perform better than critters with the standard, non-modular brains. Second, if this proved to be the case, it was aimed to discover how modularity improved the fitness of the critters: does specialisation take place, and if so, what sort of specialisation it is. Finally, it was aimed to discover how the control network operated: by discovering when modules were activated, it was hoped interesting insights about critter behaviour and the conducted experiments would be gained.

To be able to answer these questions, a task was chosen that critters with non-modular brains had difficulties with: survival in a changing environment. It was anticipated that critters with modular brains would perform better in this task, and that the predicted improvement in fitness would be the result of control network→module interactions within the modular brain. However, in order to be certain that the results do not depend on the task itself, a limited set of runs were performed when the environment is static (non-changing).

The purpose of both experiments was comparing the fitness and functionality of critters with modular brains and critters with non-modular brains. Both experiments required a population of evolving critters to be placed in a training world, and ended after 550,000 time steps. Once finished, the critter population was stored and analysed.

The criterion used to measure the fitness of the evolved critters was survivability: the average survival ages of critters across runs. Though somewhat arbitrary, this criterion is strongly correlated with fitness as survival requires possessing many important skills (see section 4.4 for a more thorough discussion of critter fitness). This was done by placing 15 copies of the 5 oldest critters of every run in a survival test world (the attributes of which varied depending on the experiment); the critters were expected to survive as long as they could – reproduction was disabled during these runs. The test runs were stopped after 10,000 time steps.

7.3.1 Experiment 1: changing environments

The goal of this experiment was to measure the fitness of evolved critters in a changing environment. In this experiment, the changing environment operated as follows: after a run started, every 1300 time steps the world changed randomly, a process which took 300 time steps (meaning, at time step 1000 the world gradually started 'morphing' to its new configuration, a process which completed at time step 1300). This process was repeated until the run ended. Fitness was measured using the survival test world, however, unlike training conditions, this environment changed at a faster rate: every 800 time steps there was a 300 time step period of changing. This was done to increase the selection pressure on critters that are not good at dealing with the change period. Six types of runs were conducted; each was repeated at least 16 times. As stated, different mutation probabilities were picked for 'Duplicate Module' in order to probe the influence this has on the fitness of evolved critters and the specialisations that emerge.

(1) **Critters with non-modular brains:** all critters started with the same characteristics (3 receptors, 3 hidden units, fully connected).
(2) **Critters with modular brains:** all critters started with one control network (3 receptors, 1 hidden unit, fully connected) and a single module (same structure as the non-modular critters). The probability of the 'Duplicate Module' mutation is 2%.
(3) Same as (2), but the probability of 'Duplicate Module' is 12%.
(4) Same as (2), but the probability of 'Duplicate Module' is 18%.
(5) Same as (2), but the probability of 'Duplicate Module' is 25%.
(6) Same as (2), but the probability of 'Duplicate Module' is 35%.

7.3.2 Experiment 2: static environments

The goal behind this experiment was to measure the fitness of evolved critters in a static environment. This experiment investigated whether the results of exp. 1 are different for an easier problem: a static environment. This experiment effectively repeated exp. 1, run type 1 (non-modular brains) and run type 5 (modular brains, 'Duplicate Module' value is 25%), but the environment is static – it does not change (note: the 'Duplicate Module' value of 25% was used because it was found to produce the most effective results in exp. 1, see section 7.5). Fitness was measured using the test world. The test world environment does not change.

7.4 Results

Table 7.1, columns 1-2, shows the results of experiment 1: the average survival ages of the critters, broken down according to category of run. As can be seen, the average survival age for the critters with non-modular brains was lower than the average survival age of most critters with modular brains. Furthermore, the value of the 'Duplicate Module' mutation strongly affected the average survival age: when 'Duplicate Module' was set to 25%, the average survival age was highest (3831.23 – 63% higher than the average survival age of critters with non-modular brains, 2341.13), when set to 35%, the average survival age was lowest (2051.44), in fact, even lower than the average survival age of critters with non-modular brains.

Table 7.1. Average survival age, average number of total modules, average number of functional modules and percentage of modular critter brains for critters in test worlds; broken down according to category (critters with non-modular brains, critters with modular brains with 2%, 12%, 18%, 25%, 35% probability of 'Duplicate Module')

Category of Critter Brain	Average Survival Age	Average # of Modules	Average # of Functional Modules	% of Modules
Non-modular	2341.13	1	1	N/A
Modular (Duplicate Module 2%)	2375.70	3.52	1.58	50.00%
Modular (Duplicate Module 12%)	3021.41	3.98	1.85	68.75%
Modular (Duplicate Module 18%)	2513.76	4.81	1.46	43.75%
Modular (Duplicate Module 25%)	3831.23	4.02	1.78	66.67%
Modular (Duplicate Module 35%)	2051.44	4.85	1.56	38.89%

Table 7.2, rows 1-2, shows the results of experiment 2, the average survival age for critters with modular and non-modular brains in a static environment. Evidently, in this setting too the critters with modular brains survived longer on average than critters with non-modular brains, although the differences were not as extreme.

Table 7.2. Average survival age for critters with modular and non-modular brains in a static (non-changing) environment

Category of Critter Brain	Average Survival Age
Static environment, non-modular	4279.77
Static environment, modular (all)	5472.04
Static environment, modular (most critters utilised modularity)	5537.19
Static environment, modular (most critters did not utilise modularity)	5363.45

7.5 Analysis

It is clear, then, that incorporating modularity into the brains increased fitness as indicated by critter survivability. However, it is still unknown why this was the case. In addition, it is still unknown whether functional specialisation took place, and if it did, what was the manner of specialisation. To obtain this information, two types of analyses were performed.

For this purpose, it is necessary to know the number of modules: the number of evolved modules is readily available; however, the number of functional modules, modules that are actually used is unknown. Thus, the first type of analysis studies the control network and attempts to discover the number of functional modules and what causes the control network to activate them. This is obtained using an analysis similar to the one used in chapter 6, by creating five sample environments and taking 500 random surfaces from each. Every chosen surface is taken five times, in two levels of consumption (9%, 25% left of the surface – these values represent the two states of the surface: 'eaten' and 'full'), and fed to the five oldest critters of all runs. By analysing the activation of the control network, it is possible to discover the modules that are actually used. Moreover, by examining the stimulus that activated every module, it is possible to understand when the control network activates the various modules.

Table 7.1, columns 3-5, show the average number of modules and functional modules evolved, as well as the percentage of critters with functional modularity (defined as the percentage of runs where most critters utilised modularity) for critters in the test world in every category of run. In general, the greater the value of the 'Duplicate Module' mutation, the more modules were evolved, though this number does not seem to correlate with the average survival age. However, the number of functional modules was correlated with the ability to survive; the longest surviving runs (12%, 25%) had the most functional modules. Interestingly, the percentage and number of functional modules appeared to be influenced by the mutation value: a higher percentage of functional modules was evolved when the mutation value was in a certain range (12% to 25%). This may be the cause of the higher survival age.

By breaking down the results of exp. 1 according to category and according to whether functional modularity evolved, a new average survival age figure was created (fig. 7.4). Evidently, critters with modular brains that utilised modularity were *always* better than critters with modular brains that did not utilise modularity (and used a single module). Interestingly, when evolution had the ability of evolving modular brains, and yet did not utilise this mechanism, the results tended to be worse on average than when evolution could not evolve modular brains. Table 7.2, rows 3-4, shows the results of the same analysis for critters evolved in a static environment. Under a static environment modularity played a role as well, albeit smaller than under changing environments.

To understand the differences between critters of varying qualities, several representative critters were picked for the next analyses. Each selected critter was the oldest critter in a run with modular brains where most critters utilised modularity, thus, the critters used were: 9

very good critters (survived more than 5,100 time steps on average), 6 good critters (survived between 2,100 and 3,300 time steps), and 5 poor critters (survived less than 1,100 time steps).

Table 7.3 shows the results of the analysis of the control network activations for the selected critters. First, all critters evolved two functional modules (occasionally there were more, but modules that were utilised less than 2% of the time were disregarded). Second, the operation of the control network was very consistent: one module was activated under all conditions (surfaces appeared as full or empty), and the second module was only activated when the surface appeared as full. Thus, it appears that one module acts as the primary module (appropriate for all stimuli) and the other acts as the secondary module (used only in some situations).

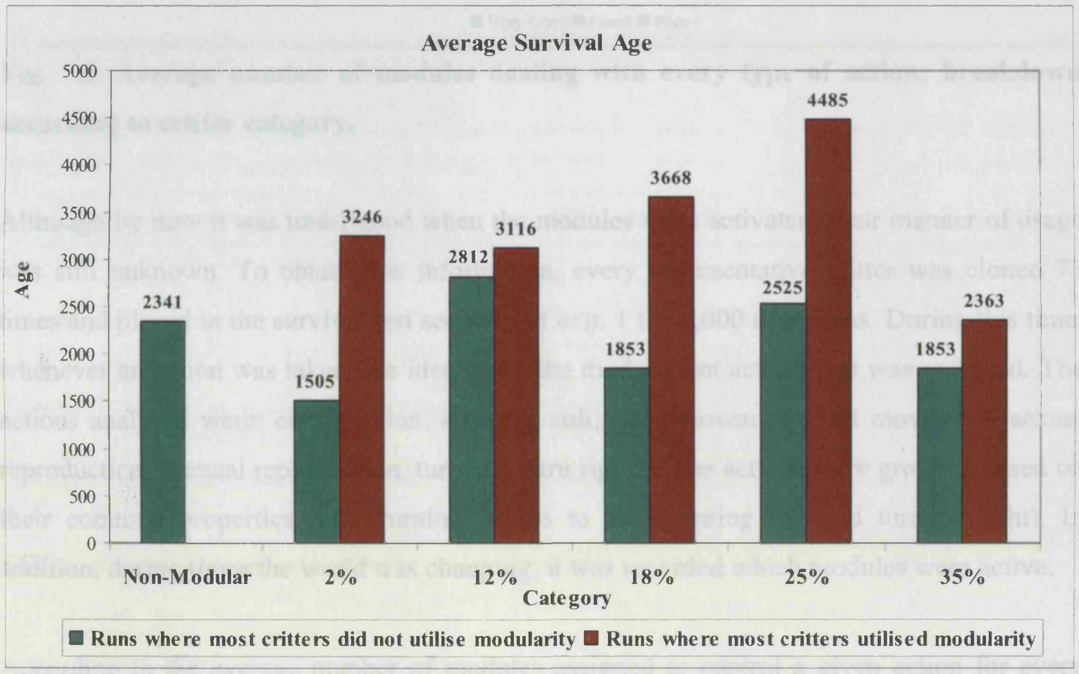


Fig. 7.4. Average survival age for critters; breakdown according to category (non-modular critters, percentage of ‘Duplicate Module’), and according to whether modularity was utilised by most critters in run.

Table 7.3. Control network activation for the tested critters; break down according to critter quality

Critter Quality	Average Active Modules	Module 1 active under all conditions	Module 2 active under all conditions
Very Good	2	33.33%	66.66%
Good	2	33.33%	66.66%
Poor	2	60.00%	40.00%

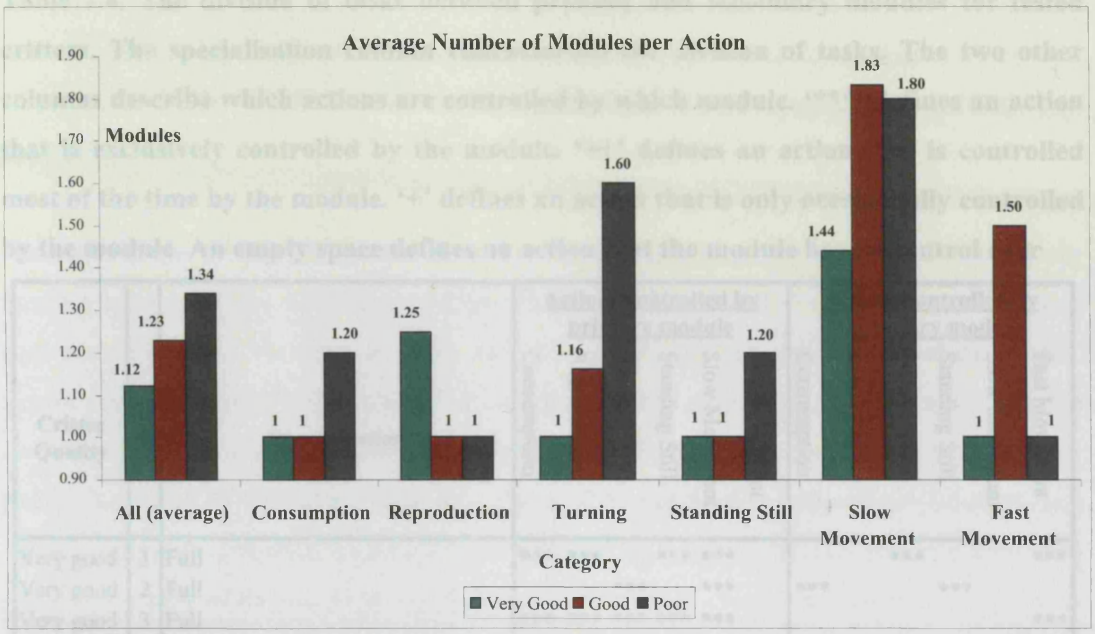


Fig. 7.5. Average number of modules dealing with every type of action; breakdown according to critter category.

Although by now it was understood when the modules were activated, their manner of usage was still unknown. To obtain this information, every representative critter was cloned 75 times and placed in the survival test scenario of exp. 1 for 3,000 time steps. During this time, whenever an action was taken, the identity of the module that activated it was recorded. The actions analysed were: consumption, standing still, slow movement, fast movement, sexual reproduction, asexual reproduction, turn left, turn right (some actions were grouped based on their common properties, e.g. ‘turning’ refers to both turning left and turning right). In addition, during times the world was changing, it was recorded which modules were active.

According to the average number of modules assigned to control a given action for every category (fig. 7.5), the better the critter, the more specialised it was: on average, fewer modules controlled any given action. When looking at the module analysis of the individual critters, specifically, the division of tasks between the primary and secondary modules (table 7.4), more conclusions are apparent. First, it is clear that the fitter the critter, the more specialised it tended to be: 33.33% of the very good critters were fully specialised, where every action was controlled by a single module, contrary to 16.66% of the good critters and none of the poor critters. As for the other critters, almost all were partially specialised, meaning, most actions were controlled by a single module but there were one or more actions which were controlled by both modules; this overlap was often in reproduction or slow movement. Finally, 20% of the poor critters (and no critters in the other categories) had no specialisation at all – both modules controlled all actions.

Table 7.4. The division of tasks between primary and secondary modules for tested critters. The specialisation column characterises the division of tasks. The two other columns describe which actions are controlled by which module. '**' defines an action that is exclusively controlled by the module. '++' defines an action that is controlled most of the time by the module. '+' defines an action that is only occasionally controlled by the module. An empty space defines an action that the module has no control over**

Critter Quality	#	Specialisation	Actions controlled by primary module						Actions controlled by secondary module					
			Consumption	Reproduction	Turning	Standing Still	Slow Movement	Fast Movement	Consumption	Reproduction	Turning	Standing Still	Slow Movement	Fast Movement
Very good	1	Full	***	***		***	***				***			***
Very good	2	Full			***		***		***			***		
Very good	3	Full	***	***	***	***	***							***
Very good	4	Partial: overlap in reproduction		+	***		***		***	++		***		
Very good	5	Partial: overlap in reproduction		+	***		***		***	++		***		
Very good	6	Partial: overlap in slow movement	***	***	***	***	+						++	
Very good	7	Partial: overlap in slow movement	***	***	***	***	+						+	
Very good	8	Partial: overlap in slow movement	***	***	***	***	++						+	***
Very good	9	Partial: overlap in slow movement	***	***	***	***	+						++	***
Good	1	Partial: overlap in slow & fast movements	***	***		***	+	+			***		++	++
Good	2	Partial: overlap in slow movement	***	***	***	***	++						+	
Good	3	Partial: overlap in slow movement	***	***		***	++				***		+	***
Good	4	Full	***		***	***	***			***				***
Good	5	Partial: overlap in slow & fast movements	***	***	++	***	++	+			+		+	++
Good	6	Partial: overlap in slow movement	***	***	***	***	+						++	
Poor	1	Partial: overlap in slow movement	***	***		***	+				***		++	***
Poor	2	No specialisation - complete overlap	+		+	+	+		++	***	++	++	++	
Poor	3	Partial: overlap in slow movement	***	***		***	+				***		+	***
Poor	4	Partial: overlap in turning and slow movement	***	***	+	***	+				++		++	
Poor	5	Partial: overlap in turning	***	***	++	***	***				+			***

Interestingly, when examining the 'Duplicate Module' value of the runs the critters were taken from, it appears it had no effect on module specialisation. Another surprising discovery was that no specific module was allocated for the times the world was changing – both modules were used regularly during these times.

7.6 Discussion

The results lead to several interesting conclusions. First, enabling the ability to evolve modular brains increased the fitness of the evolved critters on average, a difference that is exaggerated further when only critters that used more than one module are considered. This finding was true for both static and changing environments, though bigger differences were observed in changing environments. Interestingly, critters that did not utilise modularity despite having structurally modular brains occasionally performed worse than critters with non-modular brains – this seemed to be linked to the utilised probability of 'Duplicate Module'.

The value of the 'Duplicate Module' mutation had a large effect on evolution of critters with modular brains: too low (2%) or too high (35%), and the overall average survival age was equivalent or worse than the average survival age for critters with non-modular brains. According to the analysis, the modular critters that utilised modularity still did better than the modular critters that did not, however, there appeared to be fewer of the former. In other words, the value of 'Duplicate Module' affected the emergence of functional modules, and consequently, affected overall critter fitness. Interestingly, once functional specialisation does occur (regardless of the mutation value), it occurs normally – modular specialisation patterns are very consistent. Therefore, it can be argued that when the value of 'Duplicate Module' is too low, evolution is unable to successfully utilise the modules for specialisation (as indicated by the gene duplication literature). When it is too high, it becomes disruptive to the evolutionary process. The ideal value is somewhere in between.

Specialisation played a key factor in critter fitness; the more specialised the critters' modules, the fitter the critters were. The very good critters tended to be more specialised, whereas the poor critters often had a large overlap in specialisations, and at times no specialisation at all (complete overlap). As table 7.4 shows, the specialisations became less distinct the worse the critters were, and the division of tasks became less logical (e.g. a 'poor' critter #4 divided control of 'turning' and 'slow movement' and as a result did not do very well: if a critter turns while consuming a resource or attempting to reproduce, the action is negated. Therefore, limiting the number of modules that can control this activity appears to be a smart strategy).

Looking at the analysis of the control network, it is clear the network uses the state of a viewed surface as a cue for switching between modules. Thus, it always breaks the stimuli into two groups ('full surface' and 'eaten surface'), and assigns one module to deal with all surfaces (the primary module) and another to deal with only the eaten surfaces (the secondary module). This breakdown is probably why two modules were mostly used – it is possible that a different problem may require a different number of modules. When correlating this with the analysis of the modules, two dominant behavioural strategies emerge:

- **Strategy one**: use the primary module for most actions. When reaching an eaten surface, activate secondary module which specialises in movement and occasionally in turning as well. This strategy works by minimising the danger of consuming a negative resource; if a surface is already eaten, better to assign a module that can never eat. Furthermore, in some critters this module specialised in fast movement, which can be a very appropriate behaviour when running out of energy and scanning quickly for a good surface (as seen in the previous chapter). This strategy is very common, and was utilised by most critters.

- **Strategy two**: use the primary module for movement and turning. When reaching a full surface, activate secondary module which specialises in consumption and reproduction. This strategy works by allowing one module to specialise in tasks that require standing still (consumption and reproduction). Given that identifying the right surface is the most difficult task in Mosaic World, creating a specialised module for consumption appears to be a good strategy. This strategy was less frequently used and only a third of the very good critters utilised it ('very good' critters #2, #4 and #5 in fig. 6).

The above conclusions are consistent with the findings of Calabretta et al [43] which reported that modular networks performed better than non-modular networks. However, in the system described in this chapter, specialisation is the reason behind the increased fitness, whereas in their system specialised modules were not fitter than non-specialised ones. Conversely, in a study by Anderson and Hong [7], modular networks were not fitter than non-modular ones. It is possible that the differences are a result of the nature of the problems that were addressed.

To conclude, the results described in this chapter indicate that modularity does indeed improve the fitness of critters that utilise it. This is a direct result of the interactions between the control network and the subordinate modules. The reason fitness is improved is (a) because the control network learns to break down the task in a meaningful way and (b) because each module specialises in some tasks. Thus, this type of network is frequently superior to a standard, non-modular network in solving the tasks described in this chapter (and probably others as well). Consequently, it is unsurprising modular designs are frequently seen in nature.

7.7 Modularity and the visual system

In this chapter it was shown that critters with modular brains improved their fitness by dividing tasks between modules and by learning to activate the appropriate module in every situation. It is logical to assume that the visual systems of every module and the control network are similarly affected – the only question is: in what way? For this purpose, two different critters (described in table 7.5) which were used in the previous analysis were picked, their control network was analysed to discover which modules are used and when are they active, and most importantly, the visual systems of these modules and the control network were studied.

Table 7.5. Description of the two critters used in the analysis: the number of modules and functional modules, the conditions which cause modules 1 and 2 to activate, and the task breakdown for modules 1 and 2

Critter #	# of modules	# of functional modules	Module 1 active for:	Module 2 active for:	Tasks performed by module 1	Tasks performed by module 2
1	8	2	All surfaces	Only full surfaces	Consumption, reproduction, some movement, turning	Most movement
2	3	2	All surfaces	Only full surfaces	Most movement	Consumption, reproduction, some movement, turning

Figures 7.6 and 7.7 illustrate the evolved visual system for the control network and the two functional modules of critters 1 and 2 respectively. An analysis of the two critters suggests that there are many similarities between their evolved visual systems. Both critters have a module which is exclusively used for consumption and reproduction, and in both this module utilises a sophisticated visual system, clearly very useful for the recognition of surfaces. In addition, both critters have a module which is primarily responsible for movement, and in both this module utilises a simple visual system that is colour blind (indicated by the presence of a single receptor which is insufficient for colour vision); these visual systems appear to be indifferent to useful wavelengths, evident by the fact that critter 1's single receptor is very insensitive and critter 2's receptor is attuned to a rather useless wavelength. A possible explanation is that in both critters, the module only 'cares' about moving properly: avoiding the holes and edges. Since these are dark, a visual system that only detects brightness is sufficient, and colour vision is not necessary.

Interestingly, the visual systems of the control networks of both critters are somewhat similar as well. Both systems are relatively sophisticated and have the potential for possessing colour vision (2+ receptors). In fact, critter 1's control network's visual system has two receptors of nearly ideal peaks and tuning for colour vision in Mosaic World (one in the short wavelengths and one in the long wavelengths). It is possible – even likely – that these sophisticated visual systems of the control networks improve the critters' capabilities by operating in sync with the two modules' visual systems. This can be accomplished, for example, by using the visual system of the control network to redirect potentially dangerous surfaces to a module which cannot consume surfaces, or alternatively, to a module which possesses a superior visual system that can reliably determine whether the surface should be consumed.

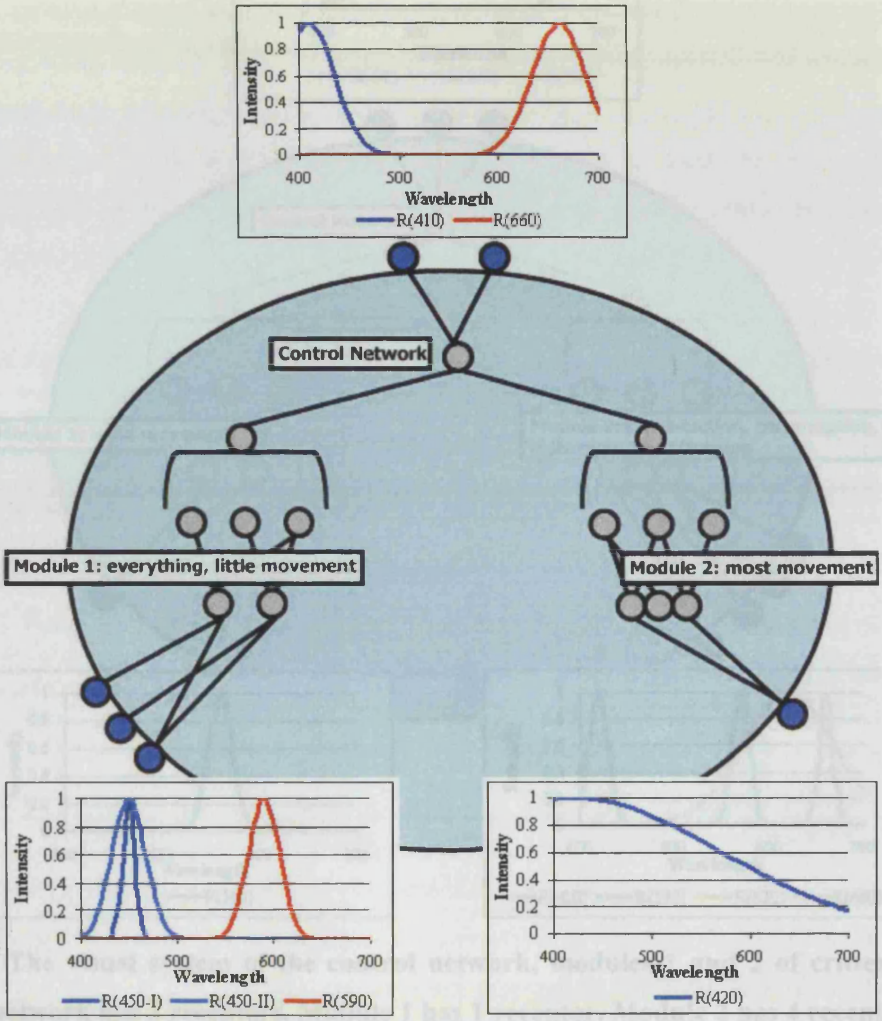


Fig. 7.6. The visual system of the control network, modules 1 and 2 of critter 1. The control network has 2 receptors. Module 1 has 3 receptors. Module 2 has 1 receptor.

In order to obtain a conclusive answer for this puzzle – discover whether the visual systems of the control network and the modules work in sync – an additional analysis was performed. Thus, each critter was exposed to 500 different surfaces under three different conditions and the behaviour of its control network and activated modules was noted. The conditions were: (i) full (uneaten) surfaces, randomly picked from the test world (ii) very positive surfaces, randomly picked from the available potent surfaces in the test world (resource value>30) (iii) very negative surfaces, randomly picked from the available lethal surfaces in the test world (resource value<-30).

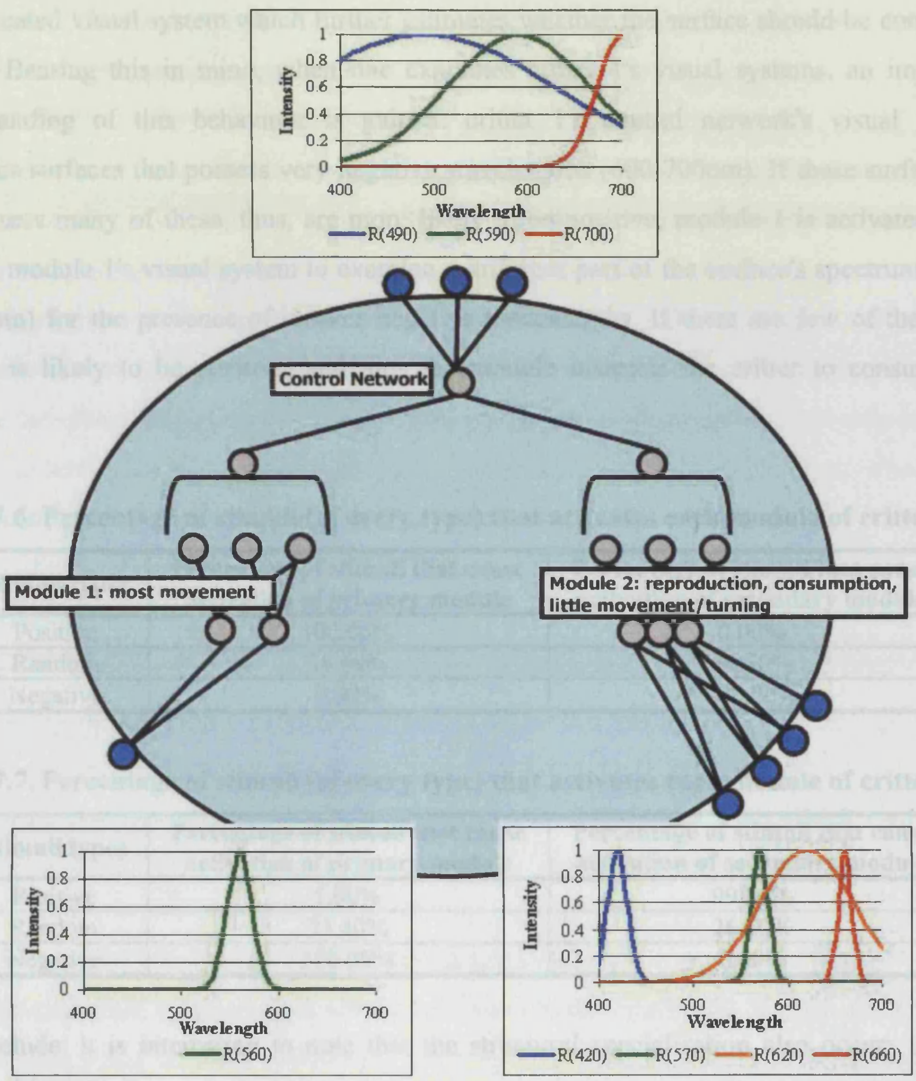


Fig. 7.7. The visual system of the control network, modules 1 and 2 of critter 2. The control network has 3 receptors. Module 1 has 1 receptor. Module 2 has 4 receptors.

Tables 7.6 and 7.7 show the results of this analysis, specifically, the percentage of stimuli of every type that activates every module for critters 1 and 2 respectively. It appears that when the surfaces are very positive, module 1 of critter 1 – which controls consumption – is *always* activated, whereas when the surfaces are very negative, module 2 – which only controls movement – is always activated. Critter 2 behaves in a similar way: when surfaces are very positive, module 2, which controls consumption, is (almost) always activated, and when surfaces are very negative, module 1 is activated.

Therefore, it appears that in both cases, the visual system of the control network improves fitness by acting as an additional filter: when it estimates the surfaces are likely to be negative, it activates a module which cannot consume (and possesses a simple visual system); however, when it estimates the surfaces might be positive, it activates a module with a sophisticated visual system which further estimates whether the surface should be consumed or not. Bearing this in mind, when one examines critter 1's visual systems, an improved understanding of this behaviour is gained: critter 1's control network's visual system examines surfaces that possess very negative wavelengths (600-700nm). If these surfaces do not possess many of these, thus, are more likely to be positive, module 1 is activated. This enables module 1's visual system to examine a different part of the surface's spectrum (~540 to 600nm) for the presence of weaker negative wavelengths. If there are few of these, the surface is likely to be positive, and thus the module instructs the critter to consume the surface.

Table 7.6. Percentage of stimuli (of every type) that activates each module of critter 1

Stimuli types	Percentage of stimuli that cause activation of primary module	Percentage of stimuli that cause activation of secondary module
Positive	100.00%	0.00%
Random	35.60%	64.50%
Negative	0.00%	100.00%

Table 7.7. Percentage of stimuli (of every type) that activates each module of critter 2

Stimuli types	Percentage of stimuli that cause activation of primary module	Percentage of stimuli that cause activation of secondary module
Positive	1.00%	99.00%
Random	73.40%	26.60%
Negative	100.00%	0.00%

To conclude: it is interesting to note that the structural specialisation also occurs in other areas of the critter brain, such as the visual system within every module. In particular, the fact that different parts of the modular critter brain respond to different aspects of the visual stimuli bears a resemblance to biological visual systems. In both analysed critters, one module reacts to the colour information in the visual stimulus and thus is in charge of the critter's consumption and reproduction behaviours, and another reacts to the brightness information in the stimuli and thus is in charge of the critter's movement behaviours. This is analogous to many visual strategies which can be seen in nature, for example, in monkeys, different aspect of the perceived stimuli are analysed in different pathways of the brain [225]; these can normally be classified into two general categories: 'what' and 'where'. The 'what' pathways process the features of stimuli (e.g. shape, colour), whereas the 'where' pathways process the spatial elements of the stimuli (e.g. motion, form).

An interesting additional observation is the fact that the visual systems of certain modules *filter* some of the visual information. For example, a module which only controls movement is colour blind. This further supports the observation reported in chapter 5, that when appropriate, the visual system only relays relevant information to the brain and disregards information that is unnecessary.

The analysis described in this section, which examined the effect of incorporating modularity on the evolved visual systems, is particularly important because it supports part of the premise underlying this thesis, specifically, that incorporating hierarchical complexity into models is necessary in order to gain a more comprehensive understanding of the modelled phenomena. Indeed, the greater number of levels of this model enabled discovering that:

(1) Specialisation takes place at more than one level of the model. Not only modular specialisation took place within the critter brain, but each module had specialised visual systems as well. This specialisation is directly linked to the environment.
(2) Visual specialisation for artificial agents can occur for a *specific* task (like movement) and not just for the general survival task.
(3) The evolved visual strategies for subtasks are consistent with known visual principles, for instance, that filtering irrelevant information is at times beneficial.

In a simpler, non hierarchical (or less hierarchical) model, these observations are likely not to be available.

7.8 Complex interactions analysis

The work described in this chapter primarily deals with the interaction of the control network with its subordinate modules (control network→module interactions) as a way of increasing critter fitness through modular specialisation. In order to be able to examine these interactions, a set of experiments which presented two types of critter populations (critters with modular brains, and critters with non-modular brains) to two different types of environments (changing environment and static environment) was conducted.

The results of the experiments showed that critter fitness is indeed higher for critters with modular brains, and this was determined to be the result of the interactions within the modular brain: the control network specialised in breaking the task to two (or more) different subtasks, and several modules specialised in performing their assigned subtasks. Therefore, the control network→module interactions were critical towards accomplishing the challenge that was set in this chapter. These interactions took place within the modular brain, however, their effect reached lower levels: neuron, gene, and as was demonstrated, receptor. And also higher levels: critter (as it is controlled by the network), population and species, (through the behavioural effects on competition and reproduction).

The interaction(s) that takes place are in parenthesis at the end of each sentence.

1) Every critter attempts to survive – this requires several different behaviours:
    (a) **Perception**: the environment is perceived by the critter's control network's receptors (environment→receptor). It is crucial that these receptors relay the relevant information to the control network: specifically, information that will enable it to do an appropriate breakdown of the task. The two critters analysed in section 7.7 possessed visual systems that were sophisticated enough for the purpose of assisting modules in the survival task; that said, it is possible that other types of control strategies may require different types of visual systems. In addition, it does not appear that the changing environment problem required any specialised visual adaptations (as none were found).
    (b) **Communication**: the receptors relay this information to the control network through neurons (receptor→neuron, neuron→control network).
    (c) **Activation**: the control network determines, based on the stimuli it receives, which module to activate (control network→module). This is possibly the most important interaction, as the control network must be able to properly break down the stimuli into meaningful tasks. For critters that evolved in the conducted experiments, it appears that the control network needs to be able to break the task to at least two distinct parts: the primary part includes – potentially – all visual stimuli, and the secondary part includes only stimuli that come from eaten surfaces. This interaction is also important because through the interaction of the control network and the module, the critter brain may be able to achieve additional capabilities (for example, as exhibited by the critters in section 7.7).
    (d) **Perception**: the environment is perceived by the activated module's receptors (environment→receptor). It is crucial that the receptors relay the relevant information to the activated module: the better adapted the visual system of the module to the task it is supposed to perform, the better the critter will be. As was shown, different modules have specialised visual systems according to the task they are supposed to perform. It is possible that different critters have different specialisations; however, according to the analyses performed:
        - Consumption: it appears that tasks that demand colour perception (such as consumption) require the visual system to be able to differentiate between visual stimuli, presumably using colour vision.
        - Movement, turning: tasks that only demand brightness perception require the visual system be able to differentiate only between light and dark stimuli. In this case, a simple visual system is sufficient.
    (e) **Control**: the activated module controls the critter's behaviour (module→critter).

Clearly, this interaction is important as it enables the environment to exert selection pressure and eventually determine the task breakdown (of the control network) and specialisations of every module.

  (f) **Consumption**: the critter may consume surfaces (critter→environment); and in this case, positive or negative energy is transferred from the environment to the consuming critters (environment→critter). This behaviour appears to be linked to the evolutionary strategy evolved. There are two strategies; in the first, consumption is controlled by the primary module (deals with all surfaces). In the second, consumption is controlled by the secondary module (deals only with full surfaces). In both cases, the module specialises in recognition of positive surfaces. Obviously, it is also possible that the evolved critter does not have specialised modules, and in this case, all modules may attempt to control consumption (the critter fitness is likely to be mediocre at best).
  (g) **Movement**: the critter may choose to move (forage for food, avoid edges and holes) (environment→critter). Similarly to the previous item, the identity/task of the controlling module appears to be dependent on the strategy taken: according to one strategy, movement and turning are performed by the primary module and in the other, movement and turning are performed by the secondary module, which is activated when the critter reaches eaten surfaces.
  (h) **Reproduction**: the critter may choose to reproduce (critter→critter). This decision is also dependent on the evolutionary strategy taken: in one scenario, the primary module controls reproduction, and in the other, the secondary module controls reproduction, and is activated when the critter reaches a full surface.

2) **Selection (to better break down the task)**: many critters die during stages 1-f to 1-h, either by consuming negative surfaces, or by falling from the edges/into a hole, running out of energy, or by reproducing when not possessing enough energy. Critters whose control networks have learned to break the task ideally (for these experiments, breaking the task to two subtasks appears to be ideal) are far more likely to survive than critters whose control networks break the task incorrectly or do not break the task at all, and only utilise a single module. Therefore, the advantages these control networks grant directly affect the selection of the genes that define them (control network→genes).
3) **Selection (to evolve appropriate behaviours and structures)**: the critters that survive are likely to have appropriate structures for their modules, and are more likely to exhibit the appropriate behaviour in every situation. Therefore, the advantage of possessing appropriate behaviours and structures (which are now expressed in individual modules) affects the selection of genes that define them (module→genes).
4) **Selection (to better compete)**: the critters that survive compete on resources

(critter→critter). Critters that evolved a good breakdown of tasks, and have evolved specialised modules (suitable structures and behaviours) are more likely to out-compete critters that have not evolved either, thus, are more likely to survive and pass on their genes (control network→genes, module→genes). Other aspects that enhance the critters' ability to compete also affect the selection of the genes that define them (critter→genes).

5) **Reproduction**: continuing (1-h), the critters that survive past steps (2)-(4) and are now able to reproduce are fitter than those that died (genes→genes). Their offspring's phenotype is likely to be fit as well, as affected by the selection pressures in (2), (3) and (4). These changes to genes affect the critter's task breakdown to modules, modular specialisation and overall behaviour which affects it across all levels (genes→receptor, genes→neuron, genes→module, genes→control network, genes→critter) and eventually the population as well (genes→population). As was shown in this chapter, the critters do not exhibit any specific strategy in order to deal with changing environments, but instead simply become better at all tasks, thanks to modular specialisation.
6) Steps (1) to (5) are repeated until the run ends. The critters that evolved a good task breakdown between modules, appropriate structures for every task, and consequently, appropriate behaviours for every situation are those that survive.

7.9 Conclusions

The aim of the work presented in this chapter was to investigate the premise that control network→module interactions can enable critter fitness to increase through modular specialisation by setting a challenge to Mosaic World that seemed to be very demanding, thus, will require specialised adaptations or behaviours. The results confirm this hypothesis: incorporating modularity into brains used for critter control can greatly improve their capabilities, as critters that evolved modular brains survived much longer on average than critters with non-modular brains. Although critters faced a challenging problem (changing environments), the enhanced survival ability appeared to be derived from the improved capabilities of the modular brains, rather than any specific adaptation to this problem. This improvement in fitness was achieved by dividing the tasks between two modules. Furthermore, the way the tasks were divided was important, the more distinct the division of tasks, the better the overall result.

To conclude: this chapter demonstrated the way in which modular specialisation can greatly improve fitness. Furthermore, and perhaps, more interestingly, it showed that when the evolving structure is hierarchical, this improvement occurs by evolving appropriate specialisations for the various levels of the structure (i.e. each of the specialised modules evolved visual systems appropriate for the module's role).

Chapter 8

Challenge: aggregation

In this chapter, the hierarchical structure of the system is expanded once again through the addition of a new level to the model, by enabling individual critters to aggregate and form Mosaic World's equivalent of multicellular organisms. An aggregate may consist of up to 25 critters, and is controlled by its constituent members. This new level is the focus of this chapter's investigation of complex interactions. Specifically, this chapter focuses on the interactions that take place between individual critters and aggregates, as well as interactions that take place within an aggregate. These interactions include aggregation: the forces that cause individual critters to interact and form new aggregates, differentiation: the interactions of critters within an aggregate that enable it become an appealing evolutionary alternative to critters, and predation: the effects of predation by aggregates on critters and smaller aggregates.

Naturally, the study of theses types of interactions bears a strong similarity to investigations conducted by biologists in the attempt to understand the evolutionary transition from single cells to multicellular organisms. This chapter complements these studies by exploring the factors that may have provided an advantage for multicellular life when it first appeared in nature. The challenge posed for Mosaic World in this chapter is:

Can stable species of aggregates evolve in Mosaic World, and if so, what is the nature of the critter→aggregate and critter→critter interactions that are necessary for this to occur?

In order to investigate this challenge, a set of experiments examines the effect of several different conditions on the formation of aggregates within a population, and these are compared with biological equivalents.

A second study described in this chapter examines the effect of environmental change on aggregates capable of altering their shape and growing protective structures around themselves, by adding a new type of environment to Mosaic World that offers new benefits but new dangers as well. This study also investigates the origin of development, specifically, morphogenesis, as exhibited by aggregates that evolve specific shapes and shell structures that increase their chances of survival.

Finally, as this chapter presents the full version of Mosaic World, a thorough analysis of one evolved aggregate is provided and demonstrates how complex interactions across all levels are integral for a broader understanding of the modelled phenomenon.

The work described in the first part of the chapter has been published in [198].

8.1 Part I: the transition to multicellularity

Explaining the transition from single cells to multicellular organisms is one of the key challenges faced by evolutionary theory [145]. A multicellular organism is comprised of more than one cell that are in physical contact; these cells are specialised (or differentiated) to perform specialised tasks – and their activities are coordinated, at least with regards to some key functions. Multicellular life, which is believed to have independently arisen multiple times in the different kingdoms [33], is evident even in the most ancient fossils dating some 3.5 billion years (these microfossils are of filamentous cyanobacteria, which are considered the Earth's oldest known multicellular organisms) [98, 200]. Multicellularity can be achieved in two ways: through aggregation and through cell division accompanied by adhesion [242].

Although it is accepted that for this transition to repeatedly take place it must offer some advantages, no one knows for certain the conditions that led to the original emergence of multicellularity, nor how it emerged. One view is that the transition to multicellularity occurred by accident, caused by a mutation that prevented offspring cells from separating [33], and that at first there were no advantages [173]. In this scenario, the benefits came later, thus causing the selection of the organism. Another theory suggests that predation pressure was one of the causes leading to the emergence of multicellularity, as multicellular organisms would be more resistant to phagotrophy (ingestion of whole prey) [217]. This theory was tested by exposing a unicellular organism, Chlorela vylgas, to a predator. Within few generations the multicellular version of the organism, a rare mutant, evolved and was nearly immune to predation [35].

The possible advantages associated with multicellularity are numerous. One is the enhanced efficiency of dividing labour between cells [138]. This can provide advantages in feeding (e.g. efficient feeding through cooperation) and dispersion (e.g. a larger fruiting body improves spore dispersion) [33]. The larger size may improve protection from environmental disturbances [24] and enable greater storage capacity of inorganic nutrients [105]. It also enables a greater division of labour – more cell types that offer greater specialisation [34]. Perhaps, most importantly, sheer size itself can be advantageous with regards to predation: the prey may be too large for the predators to eat and organisms may be able to move faster so could better catch prey or escape predation (e.g., in water environments [32]).

It is important to emphasise that a group of individual cells is not a multicellular organism. The first necessary step for this transition is that the individual cells stop competing and start cooperating; in other words, the individual cells start sacrificing their fitness for the fitness of the group [144]. Only then can cell differentiation begin and the organism becomes multicellular [106]. It is crucial that functions that limit internal conflict emerge [146]. According to some, successful complex multicellular organisms must be comprised of genetically identical members [242].

Computational models that investigate the transition to multicellularity

It is difficult to study events such as the emergence of multicellularity for obvious practical reasons. This is where artificial life models can greatly help. Indeed, several researchers have modelled aspects of the emergence of multicellular life: for example, Rothermich and Miller investigated the emergence of multicellularity by modelling cells using Cartesian genetic programming [192]. Bull used versions of the abstract NKC model to examine the conditions under which multicellularity is likely to occur [40]. Furusawa and Kaneko studied the origin of multicellularity using artificial chemistry [63]. Bryden modelled the macrocyst stage in slime mould in order to understand why an organism might decide to aggregate [39].

8.2 Additions to Mosaic World

The investigations described in this chapter required that Mosaic World be expanded in several ways. The most significant change is the addition of a new level to the model, which now comprises the following levels of abstraction: genes, neurons, receptors, modules, control networks, critters, aggregates, population and species; figure 8.1 illustrates a sample model of an aggregate which comprises 4 critters (each possessing a modular brain, described in the previous chapter). Figure 8.2, which is an expansion of fig. 3.2, shows the interactions map for all objects in Mosaic World.

8.2.1 Action capacities and metabolism

In all versions of Mosaic World used until this chapter, a critter loses a certain amount of energy every time step (explained in 3.6.1). The critter can also perform all actions: reproduction, consumption, movement, turning. In this version of Mosaic World, these two elements are linked: the aim is to model the notion that in nature, different types of cells have different energy costs (e.g. [190]). Thus, every critter has a metabolic rate which determines the rate of energy it loses over time.

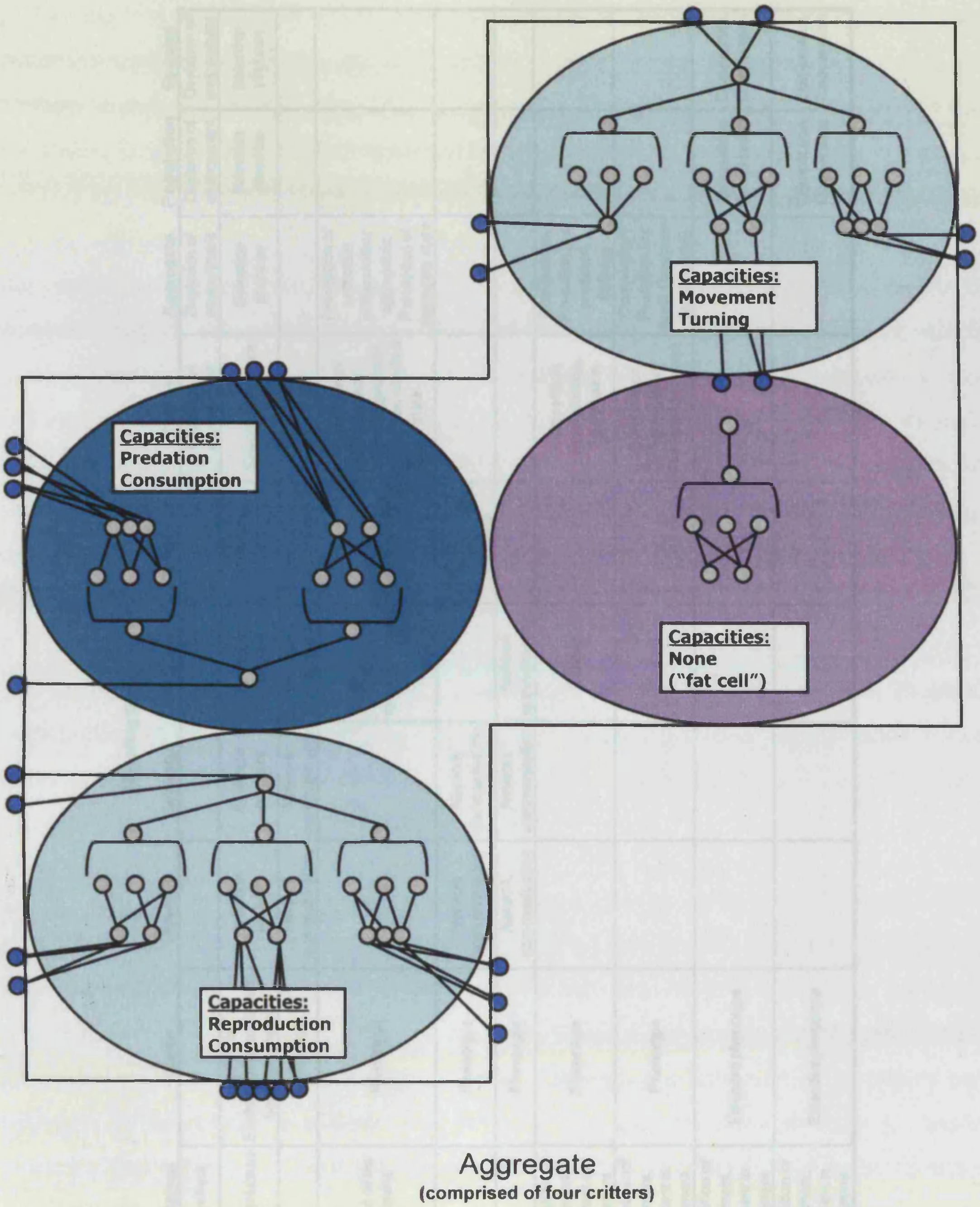


Fig. 8.1: The object model of the aggregate. The aggregate described here comprises 4 critters, each possessing its own structure and capacities (described later in the chapter).

	Affecting level									
Affected level	**Environment**	**Genes**	**Neuron**	**Receptor**	**Module**	**Control Network**	**Critter**	**Aggregate**	**Population**	**Species**
Environment	External effect						Depletion of environment	Depletion of environment	Depletion of environment	Depletion of environment
Genes	Selection pressure	Epistasis, Evolution/Reproduction, Selection pressure	Selection pressure	Selection pressure	Selection pressure	Selection pressure	Selection pressure	Selection pressure	Selection pressure	Selection pressure
Neuron		Phenotype	Network communication	Network communication	Network communication	Network communication				
Receptor	Perception of the environment	Phenotype			Network communication	Network communication	Perception of self/other critters/aggregates, Perception of critter state	Perception of self/other critters/other aggregates, Perception of aggregate state		
Module		Phenotype	Network communication	Network communication		Network communication, Activate				
Control Network		Phenotype	Network communication	Network communication	Network communication					
Critter	Consumption of environment, Movement in environment	Phenotype			Control		Competition, Reproduction, Aggregation	Competition, Predation (as predator), Splitting		
Aggregate	Consumption of environment, Movement in environment	Phenotype			Control		Competition, Aggregation, Predation (as prey)	Competition, Predation (as prey), Predation (as predator)		
Population	Consumption of environment, Movement in environment	Extended phenotype							Competition Cooperation	Competition, Cooperation
Species	Consumption of environment, Movement in environment	Extended phenotype							Competition, Cooperation	Competition, Cooperation

Fig. 8.2: Major interactions within the final version of Mosaic World

The metabolic rate is determined according to the actions the critter has the capacity of performing. Accordingly, a critter that can perform more actions will have a faster metabolism, and consequently, lose more energy every time step, whereas a critter that can perform no actions at all will lose a very low amount of energy every time step. Although the costs used do not capture the mechanisms of biology in detail, it can be argued that the model presents the critters with challenges similar to those faced by living organisms.

All critters are created with the capacity of performing all basic actions: the capacity to consume surfaces, the capacity to move/turn, and the capacity to reproduce (predation, which is a new feature that is shortly explained, is enabled by the capacity to prey and is not included in the critter's basic repertoire). By losing some of these capacities through evolution, the critters can decrease their metabolic rate. Critters that lose the capacity to perform a certain action cannot perform it; however, through evolution the critters' offspring can regain this capacity. Even a critter with no capacity to do any action still loses energy at a slow rate.

The basic metabolic rate for a critter is 10 units per time step, reproduction adds 30 units, consumption adds 30 units, moving/turning adds 30 units, and predation adds 30 units. E.g. a critter that can only reproduce and move, but not eat, loses 70 energy units per time step, which is 70% of the rate of a critter that can also eat.

8.2.2 Aggregates in Mosaic World

In order to investigate the transition to multicellularity, mechanisms for critter aggregation have been added (see fig. 8.3 for a screenshot of aggregates in Mosaic World). An aggregate can comprise up to 25 adjacent critters in any form within a 5x5 square, and is subject to all the costs and limitations that the critters sustain. Although the limitation of 25 critters per aggregate is biologically unrealistic, this design choice was necessary in order to enable running experiments in a realistic time frame; that said, this limitation did not appear to make any difference as aggregates rarely possess more than 10 members, and no aggregate was ever observed to possess 19 or more members.

The primary goal of adding this major feature was to discover the conditions that lead to aggregation rather than enforcing it: by making the aggregation methods optional, evolution is able to discover the utility (or not) of aggregation – there is no bias towards multicellularity or differentiation and no requirement for critters to aggregate.

Actions

Aggregates can use all abilities of their constituent members: if no members have the capacity to perform certain actions, the aggregate cannot perform them. Some actions can only done by the aggregate as a whole: reproduction, predation and splitting; therefore, as such actions involve all members, these decisions are determined 'democratically' – an aggregate performs these only if at least half its members wish to. Furthermore, because members that have lost the capacity to perform an action do not participate in the decision process, this may result in the effective specialisation of the aggregate's members. Thus, evolution can assign certain decisions to a single member by devolving the capacities to make these decisions for most members; this is Mosaic World's equivalent of a specialised organ.

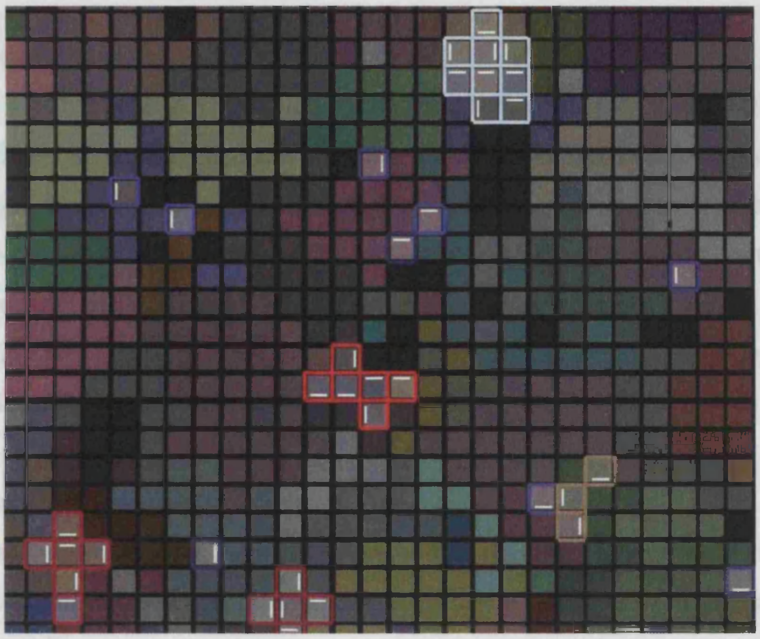


Fig. 8.3: A close-up of Mosaic World, demonstrating aggregates and critters living side by side.

Health and metabolism

Aggregates pool the energy of their constituent members; an aggregate's current and maximum health levels are the combined total of its members' current and maximum health levels. Similarly, an aggregate's metabolism is the combined metabolic rates of its members. These changes reflect the fact that an aggregate is literally the sum of its parts, which were previously individual critters (e.g. Dictyostelium – also known as slime mould – is an multicellular organism formed through the aggregation of individual cells [39, 138], thus, it can be stated that its 'health' is the overall 'health' of all its constituent cells).

Sensing and consumption

Aggregates enjoy the combined sensing capabilities of all their comprising members: every individual critter senses the environment and can affect the behaviour of the aggregate. This models the sensing capabilities of some aggregating organisms, for example, the Dictyostelium amoeba which has receptors for cyclic AMP that instruct it to move in a specific direction in order to aggregate [1].

In addition, every member that has the capacity to consume can still decide whether to consume a surface or not, although it is still subject to the same limitations faced by critters (i.e. it cannot consume while moving, and this depends on other members of the aggregate as well). This models the ability of evolution to determine the size and shape of the feeding organ of organisms. The energy gained (or lost) is added to the aggregate's energy pool.

Movement and turning

An aggregate's movement is determined by its members, and is effectively their combined movements. Since aggregate members can turn inside an aggregate, an aggregate's overall movement depends on its members' individual orientations. Consequently, the movement of an aggregate is difficult to coordinate. The movement and turning energy costs are identical to those of an ordinary critter – this models multicellular organisms using flagellates for swimming [32]. An aggregate does not fall from the world's edges as long as its central member is still on the surface matrix.

Reproduction

Aggregates can only reproduce asexually. To reproduce, an aggregate must not move for a given number of time steps and must also transfer a percentage (40%) of its maximum health to its offspring. All reproduction attempts incur an energy cost relative to the aggregate's size regardless of their success. When an aggregate reproduces, all its members are cloned and the outcome is mutated (i.e. every member undergoes the same mutations that a reproducing critter's offspring experiences). The members' spatial position is also copied, thus, the aggregate's shape is cloned as well. This type of reproduction is equivalent to budding, which is one of the forms of asexual reproduction seen in nature. In budding, a new individual grows as a bud out of the body of its parent, eventually detaching and becoming a full individual which is genetically identical to its parent [85]. Many animals reproduce through budding, for example: hydras and calcareous sponges.

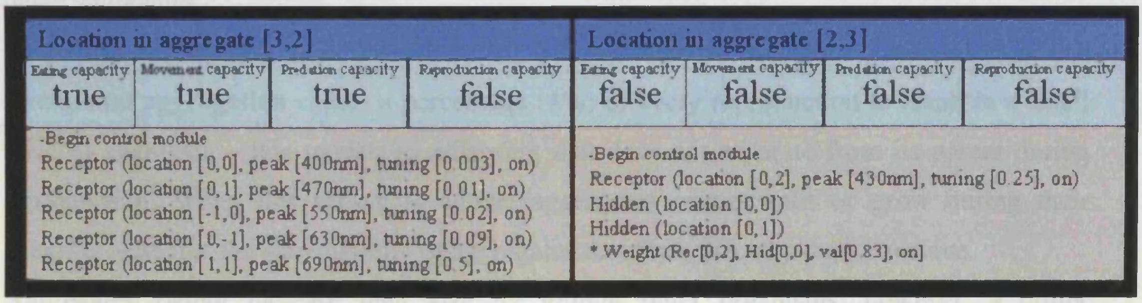
In addition to the 'standard' mutations, the offspring of an aggregate also undergoes the following three new types of mutations:

- *'Clone element':* this mutation causes one of the offspring's members (randomly picked) to be cloned twice at a given probability (4%). The new member is attached randomly to an existing member. This mutation also affects the aggregate's metabolic rate.

- *'Delete element'*: this mutation causes an offspring's member (randomly selected) not to be copied at a given probability (4%). The selected member must not be the only connection between two parts of the aggregate (i.e. it cannot split the aggregate in two). This mutation also affects the aggregate's metabolic rate.
- *'Shift element'*: this mutation causes an offspring's member (randomly picked) to change position (altering the aggregate's shape) at a given probability (4%).

Genome

When critters form an aggregate, their genomes combine and form the aggregate's genome (see fig. 8.4). The aggregate genome also contains additional genes that indicate every member's position and orientation in the aggregate. The genome defines all the traits of the aggregate, and by definition, of its comprising critters; thus, during reproduction this genome can be used to create the aggregate's offspring – and furthermore, if this aggregate splits, its members can be recreated as critters as well. Although in nature aggregating organisms do not combine their genomes, this mechanism was necessary in order to enable reproduction of aggregates; this has been the case because the mechanisms for true development are beyond the current capabilities of Mosaic World. Such mechanisms would enable a multicellular organism to grow from a single cell/critter that has a single genome; this cell/critter would divide multiple times with some of the offspring differentiating into different cell/critter types, and eventually form the multicellular organism.



Location in aggregate [3,2]				Location in aggregate [2,3]			
Eating capacity	Movement capacity	Predation capacity	Reproduction capacity	Eating capacity	Movement capacity	Predation capacity	Reproduction capacity
true	true	true	false	false	false	false	false
-Begin control module Receptor (location [0,0], peak [400nm], tuning [0.003], on) Receptor (location [0,1], peak [470nm], tuning [0.01], on) Receptor (location [-1,0], peak [550nm], tuning [0.02], on) Receptor (location [0,-1], peak [630nm], tuning [0.09], on) Receptor (location [1,1], peak [690nm], tuning [0.5], on)				-Begin control module Receptor (location [0,2], peak [430nm], tuning [0.25], on) Hidden (location [0,0]) Hidden (location [0,1]) * Weight (Rec[0,2], Hid[0,0], val[0.83], on]			

Fig. 8.4: Sample aggregate (size 2) genome; most genes for critters are not shown (see chapter 3)

8.2.3 Predation

The ability to prey on smaller aggregates and critters is added to this version of Mosaic World and requires evolving a capacity for predation. For this purpose, a new output unit is added to the critter's standard module; this unit must be activated in order to attempt predation. This feature was added because one of the investigated hypotheses in this chapter suggests that predation is one of the possible reasons multicellularity evolved [217].

In Mosaic World, an organism may prey on another organism if it is larger than its prey; this means that effectively only aggregates can prey on other aggregates and critters. Even though critters can evolve the capacity for predation, in practice this will only increase their metabolic rates without bestowing any additional abilities, except if the critter forms an aggregate or joins an existing one.

In order to prey on another organism, an aggregate must physically overlap at least 75% of its prey. Preying may not kill the target: only some of its energy is transferred to the aggregate (80% of the prey's maximum energy). Preying also incurs an energy cost that depends on an aggregate's size, regardless of whether it has actually successfully 'caught' a victim (i.e. the aggregate may attempt to prey on an aggregate that is larger than itself).

8.2.4 Aggregation

All critters have the ability to aggregate. For this purpose, a new output unit is added to the critter's standard module. There are two ways for critters to form an aggregate; each is used in different experiments.

Aggregation by choice enables critters to aggregate with other willing critters and aggregates that are in immediate contact with it. A critter may be in 'join' mode, where it adheres to any willing organism it is in contact with, 'neutral' mode where it does not initiate aggregation, but adheres to any other organism that attempts to adhere to it, and 'split' mode where it never aggregates.

Accidental aggregation causes a percentage (4%) of every reproduction to result in a small (size 2) aggregate – this models an offspring that does not separate from its parent during reproduction. When this setting is active, aggregates cannot split or grow during their lifetime. Note that the vast majority of aggregates that form this way do *not* survive.
Aggregates cannot increase their size by joining other organisms; however, a critter attempting to join an aggregate succeeds and adds its energy to the aggregate's (with a corresponding increase in its metabolic rate).

8.2.5 Splitting

An aggregate can decide to split; this causes the aggregate to split to its individual members. There is no way for a single member of an aggregate to leave it: the only way for a member to regain its individuality is if the entire aggregate disbands. When an aggregate splits, every critter receives the appropriate part of the full genome. Although all members of the aggregate have the ability to split, some may choose to forego participating in the splitting decision (which, as previously described, occurs 'democratically'). This feature parallels the ability of the fruiting body of aggregated organisms such as Myxobacteria and Dictyostelium to differentiate into spores that can be released to the world [1, 138]. It is important to emphasise that the vast majority of new aggregates split immediately after forming (and most of those that do not, die not long afterwards). As the results later in this chapter show, critters are *always* preferable to aggregates unless there is an advantage to being in the aggregate state which critters cannot duplicate.

Individual members were not allowed to leave an aggregate because this could have a very negative effect on the aggregate's ability to survive (which may depend on all its members), particularly when the aggregate is larger in size, where a single mutation may cause a member to leave. This is less of an issue in biological multicellular organisms which normally share the same genes and thus, members are less likely to behave in a way that does not contribute to the greater organism's benefit, however, for aggregates such as Dictyostelium there is a definite need to 'police' members that do not act in the aggregate's best interests. In fact, it is believed that the presence of such elements may be a serious problem for even simple forms of cooperation unless mechanisms for controlling it exist [226].

8.2.6 New mutation: mutate capacity

In addition to the new mutations that were described in the aggregate reproduction section, another mutation type has been added and affects both critters and aggregates during reproduction.

'Mutate Capacity': this mutation switches the action capacity of the critter or aggregate: 6% per action (i.e. if a critter does not have the capacity for an action, this mutation restores it – and vice versa). This mutation also affects the critter's or aggregate's metabolic rate.

8.2.7 Aggregate monitor unit

An additional sensor, the aggregate monitor unit, has been added to all critter modules (but not to the control network). This unit receives a signal if the critter is a part of an aggregate; the intensity of the signal is proportionate to the aggregate's size. Indeed, it is reasonable to assume that an individual cell must be able to tell whether it is within an aggregate and receive additional useful information for it to be able to function properly in this environment (for example, members of a Dictyostelium aggregate receive positional information in order to generate a prestalk-prespore pattern [112]).

8.2.8 The methodology behind these additions

In the course of the various investigations that were conducted using Mosaic World, it became obvious that Mosaic World's extensive model of evolutionary agents in a complex environment poses many challenges related to those faced by primitive unicellular organisms. Therefore, this version of the model aims to improve on the metaphor, and attempts to simulate the cellular environment: the critters represent unicellular organisms and the aggregates represent multicellular organisms. Accordingly, the controlling neural networks within each critter can be viewed more as abstractions of gene regulatory networks in a cell, and the receptors can be viewed as cells receptors (instead of biological cone photoreceptors in an eye). Indeed, as the rest of the chapter demonstrates, the behaviours that result from the interactions between critters, and the higher level they form, the aggregate, bears a strong similarity to behaviours seen in nature.

Certain environmental features (specifically, multiple illuminants) are unnecessary and are thus disregarded in this particular study. It is also important to separate the modelled phenomena from the algorithms used to model it; specifically, the controlling neural networks within each critter are used as a learning mechanism and are not intended to represent biology (as unicellular organisms do not contain neural networks).

Biological relevance: by emulating specific conditions theorised to have affected the emergence of multicellular life in nature, the expansion of the model enables to directly examine several biological theories. As the results section demonstrates, these additions to the model are clearly biologically relevant. In addition, by showing that simulated aggregates that are formed of several different critters, each specialised in certain functions, are a successful alternative to simulated critters, it can be argued that cooperative distributed specialised systems are a useful alternative to standard non-modular systems.

Level: the version of the model described in this chapter contains a new level and consists now of: genes (level 1), neurons and receptors (level 2), modules (level 3), control networks and critters (level 4), aggregates (level 5), population and species (level 6). The model presented in this chapter is the full version of Mosaic World, thus, it can be used to explore many different complex interactions. This type of model can be used to gain a better understanding of a modelled phenomenon. For example, in this chapter it will be shown how incorporating aggregation into the model affects all levels of the model, and more so, how these various effects provide insight into the nature of the modelled phenomena that normally may not be apparent.

Generality: although the changes to the model were incorporated in order to address specific questions about aggregations, multicellular organisms and differentiation, the model can still be considered to be a general model.

Abstraction: all changes in this chapter are related to the critter model and aim to emulate the biological features of aggregation and differentiation. These changes can be said to abstract the target phenomena to a large degree. Some assumptions have been made, for example, in assigning specific metabolic rates for action capacities; primarily because modelling this at greater detail (and more accurately) would be impossible, as the critter model is vastly simpler than its biological counterpart.

Accuracy: generally, the changes to the model are biologically accurate. However, as mentioned in the previous item, the changes to the critter model simplify reality to some extent, thus, are inaccurate to a degree. Specifically:

- The aggregation feature generally captures the biological phenomenon of aggregation; however, clearly its implementation is greatly simplified.
- The accidental aggregation feature aims to model multicellular life that occurred through cell division accompanied by adhesion (specifically, the biological mutation that prevented offspring cells from separating [33]). The general concept is accurately modelled; however, the probabilities used in this work are not based on biology.
- The aggregation by choice feature aims to model the concept of multicellular life through aggregation. This feature correctly captures the general idea of aggregation, but is otherwise not biologically accurate.
- The relative metabolic costs assigned for each cell type are not based on biological constants which would have been impossible to apply in a model so different from biology. However, the general concept is correctly modelled.

Match: as the result section shows, all three hypotheses that have been suggested to affect the emergence of multicellularity, and the behaviours and characteristics of evolved aggregates and ecologies, bear a striking similarity to the real world. Therefore, it can be said that the model behaves like the target phenomena

8.3 Experiments

In order to be able to investigate the interactions between aggregates and critters, and the interactions between critters within a formed aggregate, it became necessary to discover the conditions that lead to aggregate formation. Interestingly, as briefly mentioned before, this study mirrors the biological search for the origins of multicellularity. Consequently, five experiments were run with the aims of:

(i) Obtaining relevant data regarding the interaction between individual critters that leads to the formation of aggregates, as well as the effect predator aggregates have on this process (which is another type of interaction between critters and aggregates). This data will directly test existing theories for the emergence of multicellularity in nature.

(ii) Examining the interactions within evolved aggregates that make aggregation feasible – and determine whether the evolved aggregates share characteristics common to natural multicellular systems (i.e. differentiation).

(iii) Analysing the evolved ecosystems and discerning whether there is any consistent correspondence between the structure of the aggregate and its ecosystem.

In each experiment, the environmental conditions are set to emulate conditions suggested to have affected one of three different hypotheses regarding the emergence of multicellularity. The data collected measures the percentage of runs in which aggregation occurred. In addition, a representative aggregate is taken from all runs (where applicable) and its genome analysed; this data, together with the population statistics is used to characterise the type of ecosystem that was evolved. Behavioural analysis of aggregates is done by presenting the selected aggregates to 500 random surfaces at two levels of consumption ('full' and 'eaten') while recording their actions; this enables characterising the behaviour of members of the aggregate and understanding the task they perform.

All experiments require a random population of evolving individual critters to be placed in a test world, and end after 400,000 time steps. Once finished, the critter population is stored and analysed. Each experiment is repeated at least 10 times.

The examined hypotheses are:

- Hypothesis 1: predation is a sufficient condition to cause the emergence of multicellularity [217].
- Hypothesis 2: accidental aggregation, without any explicit immediate advantages, is a sufficient condition to cause the emergence of multicellularity [33].
- Hypothesis 3: member differentiation is important to multicellular organisms [173].

Experiments 1-3 examine hypothesis 1 by attempting to discern what aspect influences multicellularity: the ability to prey or the actual presence of predators. In all runs, the aggregation mode is 'aggregation by choice'. Experiment 4 examines hypothesis 2 by attempting to determine whether random occurrence of aggregation without any immediate advantages is enough to initiate multicellularity without any guiding selection pressure. Experiment 5 examines hypothesis 3 by attempting to discover how crucial the presence of differentiation is for multicellularity to occur.

Experiment 1: 'predation' is disabled – aggregates must be herbivores.

Experiment 2: 'predation' is disabled – aggregates must be herbivores, however, every 1000 time steps, 7 sterile predators are placed in the population. These predators cannot reproduce, split, or consume surfaces, and die unless they can catch prey. Furthermore, they are very small (size 2), and so can only eat critters but not other aggregates.

Experiment 3: 'predation' is enabled – evolved aggregates may prey on organisms.

Experiment 4: the aggregation mode is set to 'accidental aggregation'. 'Predation' is disabled so it would not affect aggregation.

Experiment 5: the ability of aggregates to evolve the capacities for different behaviours is turned off; in other words, the aggregates' differentiation is disabled – they are always capable of performing all actions. A secondary effect of this condition is that evolved aggregates have multiple redundancies of all behavioural capacities, consequently, a very high metabolic rate. The aggregation mode is set to 'aggregation by choice', and 'predation' is enabled (to encourage multicellularity).

8.4 Results

Table 8.1 shows the percentage of runs that evolved aggregates for every experiment. As the data shows, preventing evolution of predators when critters 'choose' to aggregate, results in no aggregates evolving (exp. 1). However, the presence of predators is enough to encourage some aggregate formation (exp. 2). When predators can be evolved, aggregates form very frequently (exp. 3). Furthermore, accidental aggregation is sufficient to cause aggregation quite frequently even when predators cannot evolve and there is no immediate advantage of aggregation. Finally, although differentiation is disabled, multicellularity still occurred according to exp. 5, albeit less frequently than when differentiation is enabled (exp. 3).

Table 8.1. Percentage of runs that evolved aggregates for every experiment

#	Experiment	% of Runs with Aggregates
1	Aggregation by choice, predation disabled	0.00%
2	Aggregation by choice, predation disabled, sterile predators present	30.00%
3	Aggregation by choice, predation enabled	76.92%
4	Accidental aggregation, predation disabled	60.00%
5	Aggregation by choice, predation enabled, differentiation disabled	60.00%

When the stored populations and representative aggregates are analysed, it becomes apparent that there are recurring patterns: Three types of aggregates and four types of ecosystems consistently appear. A description of these with details of a run that exemplified them is listed in fig. 8.5.

Types of aggregates:

- **Herbivore**: an aggregate that consumes surfaces and cannot prey.
- **Carnivore**: an aggregate that survives on prey (but may occasionally consume surfaces).
- **'Coral' Carnivore**: a carnivore that cannot move and only eats prey that moves into its area.

Types of ecosystems:

- **Herbivorous Aggregates:** this ecosystem is dominated by herbivorous aggregates – there are few or no unaggregated critters. E.g. exp. 3, run 5: total of 248 herbivorous aggregates, 16 critters.
- **Coexistence - Herbivorous Aggregates and Critters:** this ecosystem contains stable amounts of herbivorous aggregates and unaggregated critters. E.g. exp. 4, run 4: total of 20 herbivorous aggregates, 227 critters.
- **Predator/Prey:** this ecosystem contains stable amounts of carnivorous aggregates and unaggregated critters. E.g. exp 3, run 11: total of 45 carnivorous aggregates, 158 critters.
- **Predator ('Corals')/Prey:** this ecosystem contains stable amounts of 'coral' carnivorous aggregates and unaggregated critters. E.g. exp 3, run 2: 280 'coral' carnivorous aggregates, 149 critters.

Fig. 8.5: Types of aggregates and ecosystems that were repeatedly evolved during the experiments

Since the number of shapes and structures the aggregates evolved was large, 4 sample aggregates were picked for close analysis (fig. 8.6). Aggregates A,B,C were taken from exp. 2-4. Aggregate D was taken from exp. 5, and was picked in order to demonstrate the effects of limiting explicit differentiation.

Aggregate A: this aggregate was taken from a 'predator/prey' ecosystem. It consists of 6 members and possesses a metabolic rate of 270 units. Member 3 performs all actions: it is able to consume surfaces, move/turn, and participate in decisions for reproduction, predation, splitting. Member 5 is able to consume surfaces and participates in decisions for reproduction and predation. Members 2 and 4 do not perform any task, but participate in decisions for splitting. Members 1 and 6 do not perform any task, and thus, can be considered as 'fat cells'. Although this aggregate is also capable of consuming surfaces, based on its capability to act as a predator and its originating ecosystem, this aggregate can be defined as a carnivore with a relatively unoptimised division of tasks.

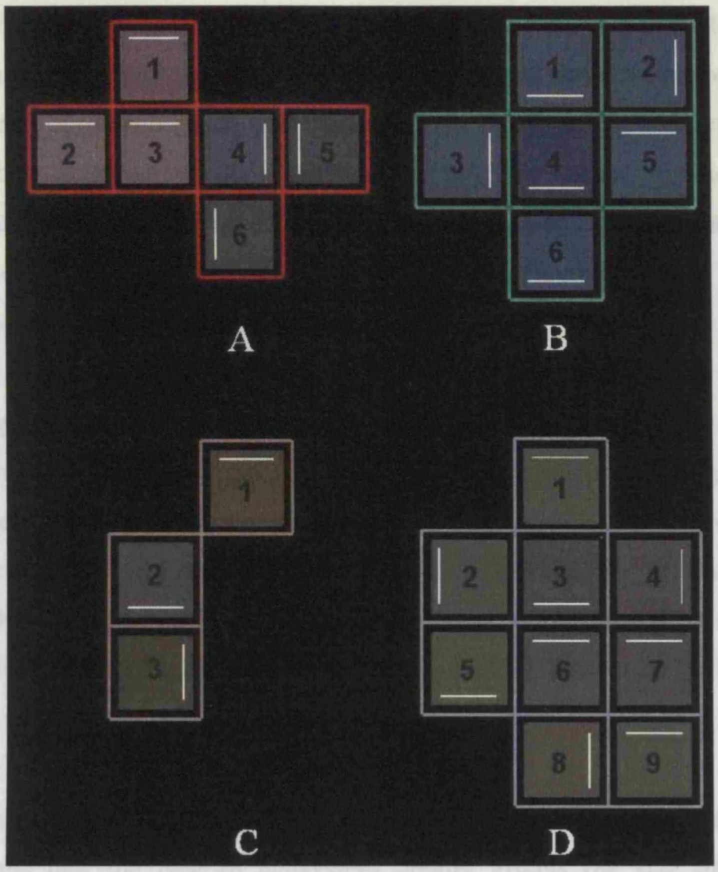


Fig. 8.6: Four representative aggregates. Note: every member has an orientation (the white line).

Aggregate B: this aggregate was taken from an 'herbivorous aggregates' ecosystem. It consists of 6 members and possesses a metabolic rate of 210 units. Member 3 is able to consume surfaces, and move/turn. Member 5 is able to consume surfaces and participates in decisions for splitting. Member 6 is able to consume surfaces, participates in decisions for splitting, and controls reproduction (is the only decision maker). Members 1, 2 and 4 do not perform any task ('fat cells'). Based on its behaviour and ecosystem, this aggregate can be defined as an herbivore with a relatively optimised division of tasks.

Aggregate C: this aggregate was taken from a 'coral predator/prey' ecosystem. It consists of 3 members and possesses a metabolic rate of 90 units. Member 1 controls reproduction. Member 3 determines when to prey (actively try to catch prey). Member 2 does not perform any task ('fat cell'). As this aggregate cannot move, has a perfect division of tasks, and a metabolic rate lower than an ordinary critter's, it can be said to be a coral predator – and one which is very well adapted to its environment (highly optimised).

Aggregate D: this aggregate evolved in an environment where explicit differentiation was disabled (exp. 5), and was taken from a 'predator/prey' ecosystem. It consists of 9 members and possesses a metabolic rate of 1170 units. Member 5 performs all actions: it is able to consume surfaces, move/turn, and participate in decisions for reproduction, predation, splitting. Member 1 is able to consume surfaces and turn (but not move), and participates in decisions for predation and reproduction. Members 2 and 6 can consume surfaces and participates in decisions for predation and reproduction. Members 3, 4, 7, 8 and 9 can consume surfaces and participate in decisions for predation.

Based on the aggregate's capabilities and ecosystem, it can be defined as a carnivore – and one which is, unsurprisingly, very inefficient in terms of metabolism; although some division of tasks has occurred, there is still a great deal of redundancy in the aggregate's member behaviours. Interestingly, one member affects movement and turning and another can only affect turning: this would normally never take place, as the same action capacity controls both – but apparently was able to evolve in this run because this division of labour occurred implicitly.

Table 8.2 shows the average size of aggregates per type of ecosystem using the definitions of fig. 8.5. It seems that the type of ecosystem greatly affects the size of the aggregate: carnivores are significantly larger than herbivores and 'coral' carnivores. In addition, herbivorous aggregates that coexist with critters are larger than herbivorous aggregates that reside in an ecosystem unpopulated with critters.

Table 8.2. Average size of aggregate per type of ecosystem (classified using fig. 8.5)

Type of Ecosystem	Ave. Size of Aggregate
Herbivorous Aggregates	2.22
Coexistence: Herbivorous Aggregates and Critters	3.04
Predator/Prey	5.64
Predator/Prey ('Corals')	2.06

8.5 Discussion

After analysing the results, it is possible to draw several conclusions with regards to the three hypotheses. First, regarding hypothesis 1, it is clear that when there is no threat of predators and the aggregation mode is 'aggregation by choice', there is not enough selection pressure for critters to interact and form aggregates – individual critters are more adequate as they need less energy and can more easily reproduce. However, the threat of predation is enough to cause critter aggregation, primarily in order to gain protection from predation, but possibly also to obtain a new energy source: prey.

With regards to hypothesis 2, it is clear that leaving aggregation to random chance by enabling 'accidental aggregation' is sufficient to induce multicellularity: although at first aggregates are inefficient in comparison to critters as there are no advantages to this state, and furthermore, considerable challenges of member coordination must be overcome, eventually evolution learns to exploit the benefits multicellularity offers and overcome the difficulties.

Finally, with regards to hypothesis 3, in runs where the aggregates could not differentiate, the percentage of multicellularity was somewhat lower, supporting the notion that differentiation is important. More so, of particular interest is the fact that evolution found a way to implicitly differentiate: although the aggregate‘s members had the capacity to perform all behaviours, *and the aggregate 'paid' the metabolic rate cost for these capabilities*, most members still chose not to perform certain tasks (e.g., members 3,4,7,8 and 9 in aggregate D in fig. 8.6 do not, rather than cannot, move, turn, and participate in decisions for reproduction and splitting). This result clearly supports the idea that differentiation is a major benefit for aggregation: both because a differentiated aggregate is more optimised, and also because it is much more difficult to coordinate members with multiple behaviours (e.g. movement, turning).

In addition, even from only viewing the 4 representative aggregates, it is possible to state that many shapes and specialisations were evolved, ranging from complete redundancy to a perfect division of labour. A common pattern was to evolve several 'eater' members (as each member eats independently), a single 'mover' member (to minimise coordination issues), and several prey/reproduce/split members (allows several critters to affect the overall behaviour of the aggregate - e.g. fig. 8.6, A, B). Also, members without any capabilities were often evolved and were apparently used as 'fat cells'; their only purpose was to grant the aggregate a larger maximum health capacity.

Of particular relevance is that there was a consistency in the various types of evolved ecosystems. Furthermore, different types of aggregates appear to require different structures (indicated by the consistency in average size). This is unsurprising: herbivores eat often while carnivores have to catch their prey so are not likely to eat as frequently, thus, require larger energy storage. Another explanation is the predation ability: larger predators can eat more types of organisms, and are harder to eat. Likewise, the emergence of 'coral' carnivores was intriguing: in these ecosystems, there were enough critters that 'corals' would rarely starve and had no need to move. As 'corals' reproduced in the vicinity of their parent, reef-like structures consistently emerged.

To conclude, the described results indicate that aggregation can occur from two different reasons: first, in order to avoid a potentially lethal interaction with a higher organism such as a hunting predator, critters will interact and form aggregates. Second, in order to benefit from a useful interaction between internal members, critters will interact and form a differentiated aggregate. Although not explicitly studied, the ability to benefit from a new food source, prey, may be another motivation for critters to interact and form aggregates.

The system described here has investigated perhaps the earliest, most primitive form of multicellularity using the notions of aggregation for growth and fission for reproduction. This can be seen as analogous to the hypothesised symbiosis that resulted in mitochondria becoming incorporated into modern cells [138]. Multicellular organisms comprising more complex cells are capable of developmental growth via mitosis and differentiation, and reproduction via a specialised gamete cell, resulting in all cells sharing identical genes and thus all genes benefiting from the collaboration. This work can be seen as the first evolutionary step towards this ultimate form of multicellularity.

8.6 Aggregation and the rest of the model

In this section it is demonstrated how the addition of aggregation affects all levels of the model, and how this effect provide insights into the modelled phenomenon and enables gaining a more complete understanding of it. For this purpose, a single aggregate has been picked and was analysed in brief from the perspective of every level. This aggregate was exposed to 500 different surfaces under several different conditions and its behaviour, specifically of its constituent members and their underlying control networks/activated modules, was noted down. The conditions were (i) full (uneaten) surfaces, randomly picked from the test world (ii) very positive surfaces, randomly picked from the available potent surfaces in the test world (resource value>30) (iii) very negative surfaces, randomly picked from the available lethal surfaces in the test world (resource value<-30) (iv) Only hole surfaces (v-xi) full surfaces, when health level is set to 0%, 10%, 30%, 50%, 70%, 90%, 100%. In addition, the individual members of its population were analysed.

Table 8.3. Analysis of the population the selected aggregate

Type	Number of individuals	Percentage of population
Critters	28	19.31%
Aggregates (size 2)	1	0.6%
Aggregates (size 3)	74	51.03%
Aggregates (size 4)	6	4.13%
Aggregates (size 5)	27	18.62%
Aggregates (size 6)	10	6.89%
Aggregates (size 7)	1	0.6%

Species (level 6):

Speciation is the process by which two new species are formed from a single species [23]. Two organisms are recognised as being of the same species if they could, at least in principle, breed together in nature and this would produce a fertile offspring. That said, this definition is not really used by biologists as a way of recognising a species because it requires too much time and resources which are not available – and it is also problematic when asexual reproduction is considered [23]. One of the ways in which species are classified is character based, that is, an organism is a member of a species if it possesses a specific observable characters or combination of characters regardless of the origin of these characters [18].
Using the above definition and picking 'size of aggregate' as a defining character, the population of the selected aggregate was analysed (table 8.3); the goal was to see whether speciation took place within this population as a result of the addition of aggregation.

This table does not state there are 7 different species within the population – obviously individual aggregates do not qualify as species, but rather intended to demonstrate the natural variation within this evolving population. That said, it is also possible that more species are present in the population based on other parameters (such as number of modules of members, specific shape of aggregate, or the presence of certain genes). Furthermore, other characters for species' classification that relate to aggregation are noticeable (e.g. ecological behaviour: carnivores and herbivores, ability to aggregate: aggregates and critters). Consequently, it is possible to argue that speciation took place within this population because of the incorporation of aggregation.

Aggregates (level 5)

After analysing the behaviours of each member under the conditions described in the analysis, it is possible to assign 'roles' for every member (see fig. 8.7). Member E is the brain of the aggregate and also is its reproductive unit: it controls reproduction, movement and turning, and controls behaviours for different health levels (see next item). Furthermore, by determining *when* to move, it effectively controls the decision of consumption for the entire aggregate (despite not eating anything itself). Member C is an eater/predator unit: it always attempts to consume surfaces and prey on critters. Member B is an eater unit as well. Members A, D and F are 'fat cells' – they only store energy and do not fulfil any other function.

Control network and modules (levels 4 and 3)

An analysis of functional modules of all members discovered that only members E and C utilise more than a single functional module. Naturally, these two members also exhibit the most sophisticated behaviours. Both control networks of members E and C break the stimuli according to whether an empty (eaten) or a full (uneaten) surface is viewed: in exactly the same manner as the evolved critters in chapter 7.

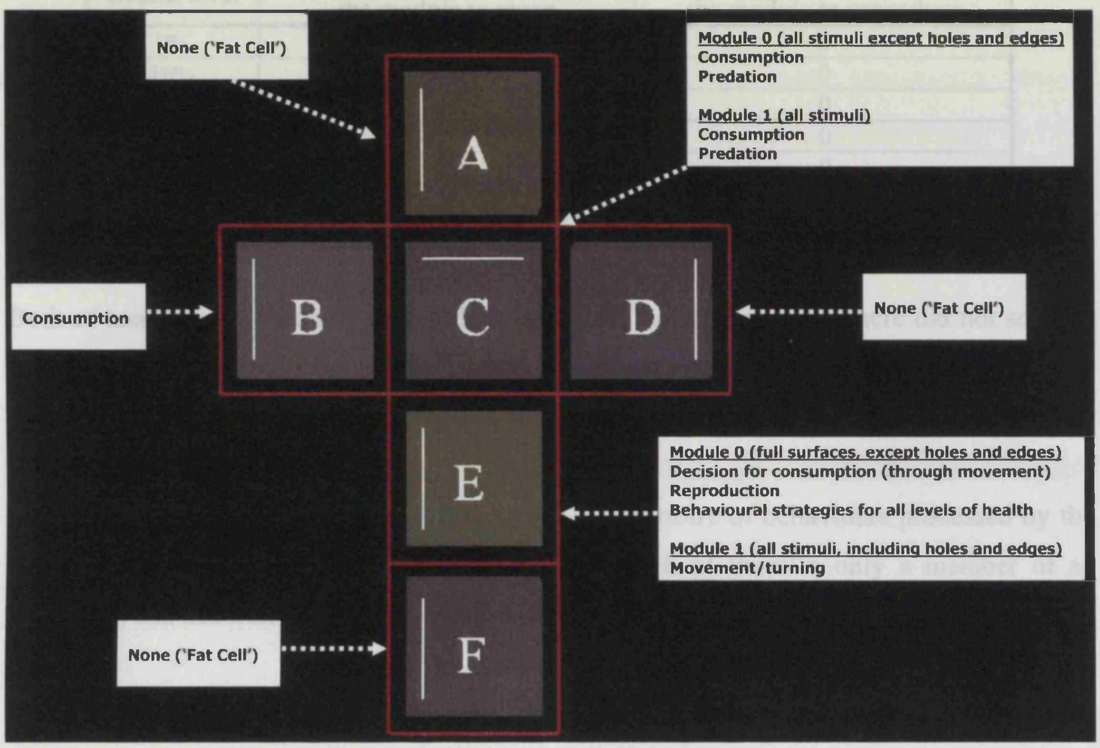


Fig. 8.7: An analysis of the roles of every member of the selected aggregate, its control network and subordinate modules

Table 8.4. The percentage of stimuli that causes member E's control network to activate module 0; broken down according to the stimuli type

Stimuli types	Percentage of stimuli that cause activation of module 0
Positive	56.20%
Random	69.00%
Negative	88.60%

When evaluating how member E's responsibilities are divided between its modules, it appears that member E's module 0 determines when to consume surfaces and how to behave in various levels of health, whereas module 1 controls all aspects of movement and turning (and how to avoid edges and holes). Furthermore, as table 8.4 demonstrates, it appears that the control network of member E is much more likely to assign negative surfaces than positive surfaces to module 0. Based on this behaviour, it seems that the aim is to minimise consumption of negative surfaces by assigning them to the 'specialist' of consumption, which is module 0 – thus, its activation is much higher when there are more negative surfaces than when there are positive or random surfaces.

Table 8.5. Member E unit 0's behaviour under various health levels, specifically, the number of times the reproduction and movement output units were activated in response to the test stimuli

Health level	Number of stimuli that caused the module to move	Number of stimuli that caused the module to reproduce
0%	363	0
10%	354	0
30%	292	0
50%	107	0
70%	9	0
90%	0	23
100%	0	89

Both of member C's modules appeared to display similar behaviours – there did not seem to be any particular situation where the control network showed a preference to one module or the other; thus, it is possible the process of specialisation is still incomplete in this case.

Interestingly, neither member C nor E has the full repertoire of behaviours possessed by the evolved critters in chapter 7, presumably because each of these is only a member of an aggregate, and accordingly possesses only a subset of its behaviours.

Another interesting observation is the fact that none of the modules appeared to be sensitive to the aggregate's health level except for member E's module 0. According to this analysis, it appears that the same behavioural strategy that is described in chapter 6 is also exhibited by the selected aggregate and is controlled by member E, module 0. As table 8.5 indicates, when the aggregate's health is low, the module never initiates reproduction, but many types of stimuli cause it to initiate movement. However, once the aggregate's health increases, fewer types of stimuli cause it to initiate movement, and at one point (when the health is 70%) it stops the movement and begins to initiate reproduction. As the health further increases, so do the occurrences of reproduction. Thus, this behavioural strategy appears to be advantageous for aggregates as well as critters.

Receptors (level 2)

Since member E is the sole member which makes behavioural decisions for the aggregate, only its visual system is analysed (fig. 8.8). The control network of member E has 2 receptors, both insensitive (wide) and peak at the long wavelengths. Module 0, which controls consumption decisions, has 5 very sensitive receptors (appropriate for surface classification), yet none of them peak in the long wavelengths (600nm+). However, this region of the spectrum appears to be well covered by the visual system of the control network. Thus, similarly to the analysed critters in section 7.7, the visual systems of the control network and module 0 appear to be working in sync; the control network evaluates the dangerous elements of the stimuli: if the surface is estimated to be dangerous (rich in very negative wavelengths), module 0 is activated – this is evident by the fact that the control network is more likely to transfer stimuli to module 0 that are negative (see table 8.4). Because module 0 specialises in short and medium wavelengths, it can apparently estimate whether the surface possesses enough positive wavelengths to warrant consumption, thus, it is able to provide a better estimate of whether the surface should be consumed or not. Note that the behaviour here is comparable, yet different, to the behaviour exhibited by the critters in section 7.7, where the control network activates the module in charge of consumption when the surfaces are estimated to be *positive* rather than *negative*.

In addition, the fact that all the receptors module 1 possesses are very insensitive suggests that it is indifferent to the colour of stimuli (similarly to the modules in section 7.7 that control movement); however, since 3 receptors are certainly sufficient for colour vision, this may not necessarily be the case.

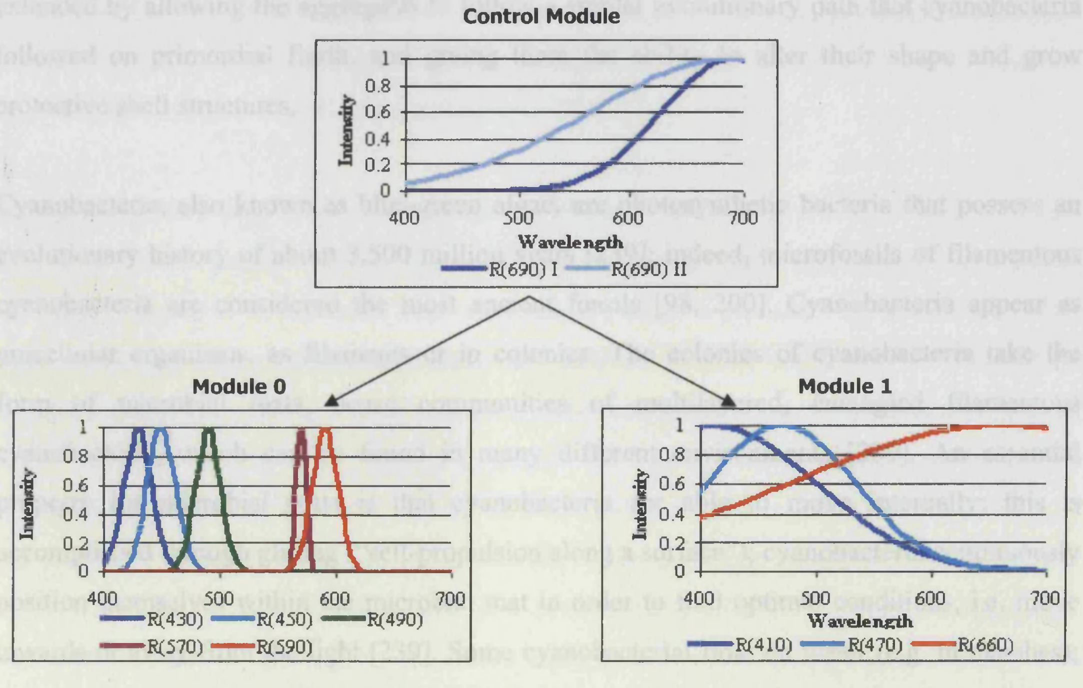


Fig. 8.8: The receptors of the control network and modules 0 and 1 of member E

Genes (level 1)

Unsurprisingly, enabling aggregation makes a large difference with regards to the genes. The average genome size of critters is 4,794 bytes in the analysed population, whereas the average genome size of aggregates in the analysed population is 17,944 bytes.

Although this specific example combines aspects of multiple domains (multicellularity with vision and behaviour), and is thus somewhat contrived, it serves to illustrate how both lower and higher levels of the model interact in a way that is useful towards gaining a comprehensive understanding of the studied phenomenon. In this specific example, the study of the visual layer (level 2) of all modules is necessary towards understanding the behaviour of the control network (level 4), and understanding its part in the critter and the overall aggregate. Additionally, this example further demonstrates the notion that differentiation/specialisation occurs across all levels. Therefore, to abstract away some of these details would be ill advised, as the complex interactions that occur in the target must be present in the model as well.

8.7 Part II: the evolution of form

The previous study investigated a primitive form of multicellularity that is formed through aggregation and reproduces through budding. It can be argued that Mosaic World's aggregates parallel many characteristics of both dictyostelium and cyanobacteria (which were mentioned in sections 8.1, 8.2.2, 8.2.5 and 8.2.7). In the following section, this work is extended by allowing the aggregates to follow a similar evolutionary path that cyanobacteria followed on primordial Earth, and giving them the ability to alter their shape and grow protective shell structures.

Cyanobacteria, also known as blue-green algae, are photosynthetic bacteria that possess an evolutionary history of about 3,500 million years [239]; indeed, microfossils of filamentous cyanobacteria are considered the most ancient fossils [98, 200]. Cyanobacteria appear as unicellular organisms, as filaments or in colonies. The colonies of cyanobacteria take the form of microbial mats, dense communities of multilayered, entangled filamentous cyanobacteria, which can be found in many different environments [239]. An essential property for microbial mats is that cyanobacteria are able to move internally: this is accomplished through gliding ("self-propulsion along a surface"); cyanobacteria continuously position themselves within the microbial mat in order to find optimal conditions, i.e. move towards or away from the light [239]. Some cyanobacterial float on water (e.g. in marshes); consequently, these mats are mobile [186].

In some conditions, microbial mats build rock-like structures. Stromatolites, which are widely researched, are formed through the accumulation of many layers, each created by the precipitation of minerals by the bacteria, primarily calcite, and/or through the trapping and binding of sediment grains [57, 239]. Additional structures are thrombolites which are created in a similar manner, however, unlike stromatolites, which have an internal laminated structure, thrombolites have an internal clotted structure and are primarily formed through calcification [102] and oncolites, which are like small mobile stromatolites: they grow around a part of a detached microbial mat and are moved by tidal action [52, 179].

Many stromatolites are formed through calcification [239], but stromatolites can also be formed through silica precipitation [174], silica and iron precipitation [175], dolomite or celestite minerals [195]. The process of lithification (turning into rock) is extremely rare and is not well understood [115, 239]; however, it is known to be mostly under biological control by the cyanobacteria [239]. The bacteria may enhance, inhibit or passively witness the lithification process [57]. The lithification process and the growth of stromatolites are dependent on certain environmental parameters [10]. For example, in order for the mats to precipitate iron, there need to be sufficient amounts of it in the environment [175]. Furthermore, the growth, shape and size of stromatolites depend on the interactions between the microbial mat and the environment [57, 115]. Environmental aspects that affect morphology are salinity, supply of nutrients, the turbulence of the environment, sediment grain size, and saturation of calcium carbonate [57]. Although it is argued by some that the environment is the only parameter that affects the crystal shape [62], others believe that certain types of cyanobacteria grow specific morphologies (e.g. cup shaped forms) and that these shapes are under direct biological control [57, 62].

Stromatolites have been mainly formed during Precambrian times; indeed, stromatolites that date 3,500 million years have been found [239]. Although very rare, there are also few places on modern Earth where stromatolites continue growing; some are very similar to fossil stromatolites [239]. It is believed that the lack of grazing organisms is the reason stromatolites were primarily formed in ancient times and not today, as the presence of grazing organisms (e.g. nematodes, crabs and fish) can affect the diversity of the microbial mats [115]. This is supported by the fact there was a sharp drop in their number in the beginning of the Cambrian believed to be linked to the rise of the metazoan (a group of multicellular organisms) which appeared at the same time [115], and also by the fact that contemporary stromatolites normally grow in environments which grazers cannot or rarely reach [239]. It is also believed that the greater alkalinity of the ancient marine environments is another reason for their greater numbers at the time, as cyanobacterial mats are very often found in hot springs or other areas with alkaline conditions [239].

The morphology of stromatolites may be potentially explained by several elements. It was suggested that the morphology of the microbial mat (and thus, of the formed stromatolites) is an attempt to optimise access to solar energy [57]. An additional explanation may be gaining protection from an environmental hazard: because in primordial times the ozone layer has not been formed yet, the environment was exposed to high intensity UV radiation [175]. This is very dangerous to bacteria in shallow water environments (such as cyanobacteria) as they are particularly vulnerable to the harmful UV radiation (which does not reach deep water) [174]. Interestingly, it was demonstrated that cyanobacteria that reside in contemporary stromatolites that were encrusted with silica are protected to a considerable degree from UV radiation [174]. Furthermore, it was shown that cyanobacteria that mineralise iron and silica have a high resistance to UV light in comparison to non-mineralised cyanobacteria; thus, by precipitating iron and silica, ancient bacteria gained an effective UV shield [175]. Finally, some cyanobacteria microbial mats that grow stromatolites are able to colonise areas which are normally inhospitable (such as gypsum crystals). Such mats precipitate dolomite or celestite minerals as a by product of the adaptation that enables them to survive in such environments [195].

Thrombolites appeared much later in time than stromatolites, in the early Cambrian period. It has been suggested that the appearance of heavily calcified cyanobacteria and thrombolites is an evolutionary adaptation meant to protect cyanobacteria against grazing and burrowing organisms which appeared at the same time [102].

This section describes the second study in this chapter, which was conducted in order to examine the effect of environmental change on aggregates capable of altering their shape and growing protective structures around themselves. By adding a new type of environment, one which offers new benefits but also creates new dangers, the aggregates gain an incentive to evolve adaptations that enable them to utilise the new environment while overcoming the dangers. It is believed that enabling aggregates to control their shape will allow them to evolve shapes advantageous for life in Mosaic World: this work will examine the nature of these adaptations. In addition, this work continues the previous investigation into the beginning of development: if the aggregates are able to evolve specific shapes and/or build protective structures of specific shapes for a specific purpose (in this case, gain protection from an environmental hazard while gaining benefits of this new environment), it can be said that this work achieves a third primary process of development: morphogenesis, the process which enables development to accurately control the form of an organism using cell movement for a specific purpose, in addition to two primary processes which were evolved in the previous work: differentiation and growth [117]. Finally, this work continues the investigation of complex interactions of the first part, by examining the effect of environmental change on the evolved shapes and strategies of shell growth of the aggregates. For these purposes, several new features have been added to Mosaic World.

8.8 Additions to the model

The following changes introduce a new type of environment to Mosaic World, one that provides new benefits but also new dangers. In addition, new abilities are given to the aggregates; these mirror the ability of colonies of cyanobacteria to grow protective structures and determine their shape.

Two new interactions are added to the table in figure 8.2:

- critter→aggregate: a member with the evolved capacity now has the ability to move within an aggregate. The result is that the aggregate's shape is altered.
- critter→aggregate: a member with the evolved capacity now has the ability to grow protective shells. The result is that the aggregate possesses new benefits but also new costs.

8.8.1 New environment

Until now, no assumptions were made regarding the nature of the surface matrix, other than the fact it is modelled after a natural visual environment. Therefore, there is no reason not to be able to expand the metaphor, and assume the critters and aggregates have always inhabited a type of aquatic environment: deep water. In this section, a new environment type is added: shallow water. Critters and aggregates may move between deep and shallow water as they please, however, unless they have some form of protection from UV radiation, they are very likely to perish quickly (this is analogous to the scenario described in [174]). Nonetheless, the risk is accompanied with advantages: as a new and unutilised environment, shallow water offers more potent nourishment than deep water. Consequently:

- In shallow water, positive surfaces provide 20% more energy than they would in deep water.
- In shallow water, the metabolic costs paid every time step by critters and aggregates are 400% of the standard costs to reflect the damaging effect of UV, the new environmental hazard, on metabolism.

From a visual perspective, both deep and shallow water are identical – this was done on purpose in order to prevent a case where one environment is preferred based on the ability to visually recognise resources within them; however, in order to tell apart between deep and shallow water, a new type of receptor was added (shortly explained).

8.8.2 Shells: protective structures

The capacity to grow shells which serve as protective structures has been added; critters may evolve this capacity, which increases the metabolic cost (by a rate identical to the other metabolic costs) to a critter/aggregate that evolves it. However, because of the shell weight, only aggregates may grow shells.

In adding this feature, several goals were aimed for:

- Shells may be used as a way of protection from predators, i.e. in a fashion similar to the way molluscs protect their soft bodies with protective shells [85]. In addition, as stated, it has been suggested that thrombolites were grown to act as a protective measure against grazing organisms for colonies of bacteria [102].
- Shells may be used as a way of protecting an organism from UV radiation, the new environmental hazard. As stated, cyanobacteria that precipitate iron or silica and use these to grow stromatolites gain considerable protection from UV radiation [174, 175]. Of course, aggregates may choose to remain in deep water, which are safe from UV radiation (and this is true in nature as well, as meters of water block UV light).
- The disadvantages of shells in Mosaic World mirror, to some extent, those in nature. For example, a marine mollusc that grows shells sustains an energy cost [168].
- Because certain floating microbial mats are mobile [186] and oncolites are mobile [52, 179], aggregates who build shells are capable of moving in Mosaic World. Although in nature oncolites do not control their movement, enabling aggregates who build shells to move is a necessary compromise: preventing some aggregates from controlling their movement would be too destabilising to the Mosaic World ecology as it may prevent predators from evolving and may thus result in aggregates rarely evolving as well.

For the purpose of shell growth, two output units were added. The first unit determines whether a critter wants to grow a shell, and the second determines the grown shell's width (measured in shell segments, 1 to 3 surfaces across). Note that 'shell segment' refers to a shell element in a specific location, and 'shell' refers to the entire structure the aggregate has grown.

- A member may grow up to 3 shell segments simultaneously: the first shell segment occupies the space directly in front of it, the second occupies the space diagonally to its left, and the third occupies the space diagonally to its right. A member may grow a shell segment in a space only if another member of the aggregate does not occupy it. Obviously, if a member turns, it can grow more shell segments in the next time step if the space is open.
- The aggregate pays an immediate energy cost for every shell segment it grows.
- The shell of the aggregate increases its weight, thus, potentially decrease its speed. Every member of the aggregate may carry up to 4 shell segments (not necessarily grown by it)

without any effect on the aggregate. However, every additional shell segment decreases the speed of the aggregate; the aggregate may continue moving at its previous speed but must pay an energy cost proportional to its extra weight.

- Shells enable aggregates to resist being preyed on by larger aggregates: the grown shell segments count towards the aggregate size when gauging whether a predator is larger than it is and the 75% required overlap. Similarly, the shell segments count towards the predator's size when attempting to prey on other aggregates.
- Shells offer aggregates protection from UV radiation in shallow water. In Mosaic World, these dangers result in an increase of the metabolic costs paid by the aggregate. Adequate protection decreases the metabolic costs to levels lower than in deep water. An unprotected aggregate suffers the standard 400% metabolic costs, whereas a fully protected aggregate pays only 30% of the standard metabolic costs. Intermediate degrees of protection offer a proportionate decrease or increase in the metabolic costs (e.g., 50% protection would result in 215% metabolic costs).
- The offspring of an aggregate does not inherit the shell of its parent. However, it can grow a similar shell structure.
- A critter may not join an aggregate if a shell segment has been grown in that location.

8.8.3 New receptor types, and the shell indicator unit

Several types of receptors have been added:

- Environment detection receptor: this receptor receives a positive signal if it detects stimulus from a deep water surface, and no signal if it is a shallow water surface. This signal represents the different pressures encountered by critters and aggregates in the different environments (as the pressure of water is greater in deep water).
- Organism viewer receptor: this receptor does not receive signals from the surfaces, but instead views the transmittance of a critter if one is present in its receptive field. In addition, this receptor receives a signal if another aggregate's shell is in its receptive field, and a different signal if its own shell is in its receptive field. This offers aggregates a simplified way of detecting the presence of other aggregates and shells, and was deemed necessary because the ability to extract the visual element of critters/aggregates and shells from the stimuli has proven to be too difficult to evolve in this context.

Additionally, there is a shell indicator unit for every critter and aggregate member that receives a signal proportionate to the number of shells the member has grown.

8.8.4 Member migration

All members of an aggregate may migrate within it: this enables an aggregate to change its morphology. A member may move up, down, left or right as long as: (a) the space is unoccupied (b) it is still connected to the aggregate in its new location and (c) this move does not split the aggregate to two separate parts. This feature parallels the required ability of cyanobacteria to move within a microbial mat [239].

Member migration may cause shells to be left unattached: when a shell is attached to another shell, it stays with the aggregate – otherwise, it is removed.

8.8.5 The methodology behind these additions

Biological relevance: the additions to the model described in this section grant aggregates the ability to alter their shape in real time and grow protective shells. As the results show, these additions are clearly biologically relevant as they enable investigating both the effect of environmental change on the evolved shape and function, and also an important developmental principle: morphogenesis, by examining what shapes the aggregates evolve and how these shapes are controlled.

Level: the additions to the model described in this section do not affect this parameter.

Generality: the additions to the model do change the fact the model is general.

Abstraction: the added changes can be said to be abstract in nature.

- New environment/dangers: the addition of shallow water and UV radiation can definitely be said to be abstract and not specific as no specific biological aspects are modelled, except for the fact that advantages are bestowed (more potent nourishment in shallow water) and costs are incurred (increased metabolic costs that reflect UV radiation).
- Shell growth: this addition enables aggregates to grow protective shells that are abstract and do not specifically model any particular biological system. As such, they can be said to emulates the ability of multicellular colonies (such as cyanobacterial mats) to grow stromatolites as well as the ability of higher organisms to grow protective shells.
- Shape alteration: these changes enable the aggregate's members to move to new locations, thus, enabling the aggregate to alter its shape. These changes are more specific than those described in the previous two items as they specifically grant every member the ability to decide whether to move for its 'own' purposes, which is similar in concept to cyanobacteria moving within a microbial mat (the bacteria move to find optimal conditions [239]).

Accuracy: generally, the changes to the model that emulate specific biological elements can be said to be biologically accurate. However, the fact that most additions are abstract makes this item less relevant. For example, the precise advantages and disadvantages associated with shallow water are reminiscent of some environments in nature but since no particular environment has been modelled, these changes are neither biologically correct nor incorrect.

- Shell alteration: these changes aim to model certain biological elements and can be said to be accurate to a degree.

Match: as the result section shows, the evolved behaviours certainly resemble those exhibited by microbial mats in nature in terms of shape alteration and shell growth. Furthermore, it can be argued that the growth of stromatolites by colonies of cyanobacteria is among the first examples of morphogenesis in nature; therefore, the behaviour of Mosaic World's aggregates is particularly reminiscent of its natural equivalent.

8.9 Experiments

The hypothesis which was investigated in the course of the experiments is:

- Significant environmental variation can affect the evolution of morphogenesis.

Three sets of experiments were run with the aim of:

(i) Examining the form of aggregates that are capable of altering their shapes: do any specific forms affect aggregates positively?

(ii) Examining the protective structures that aggregates grow: in what manner are these shells used? How are these shells grown?

(iii) Examining the evolved ecosystems: are there new recurring types of behaviours and organisms?

All experiments require a random population of evolving individual critters to be placed in the test environment and end after 250,000 time steps. In each experiment, certain conditions are different (see table 8.6); these conditions examine the effect of enabling aggregates to change their shapes with and without the ability to grow shells. Once finished, the population is stored and analysed. Each experiment is repeated until at least 9 successful runs are collected.

Table 8.6. The three types of experiments

Experiment	Aggregates can change their shape?	Aggregate can grow protective shells?
1	Yes	Yes
2	No	Yes
3	Yes	No

8.10 Results

In all three experiments aggregates and critters were evolved. In these runs, the evolved aggregates often grew shells, and occasionally changed their shape in real time; however, most often a static shape was used. A study of several sample aggregates from every run was conducted, and the evolved shapes and grown shells were analysed.

It is important to stress that this study was exceptionally difficult to accomplish because three stages in evolution were required: first, critters must successfully establish a thriving population; second, a stable species of aggregates must emerge afterwards; and third, these aggregates must utilise these new mechanisms (in order for them to be studied).

Morphologies

Although the ability of aggregates to change their morphologies in real time was not often seen by observers, clearly it has been used through the course of evolution by aggregates as is evident by the fact that aggregates with this ability tended to have long and diagonal shapes whereas previously this was not a common trait; therefore, it appears that this ability was used in order to increase the aggregate's chances of survival. These recurring shapes appear to be a useful morphology, as an aggregate can minimise its size (thus, the need for food) while still covering as large an area as possible, both in terms of ability to consume surfaces and the ability to catch prey. This is also an advantage for an aggregate that wishes to move in different directions, as an aggregate cannot change its orientation (only individual members can). Interestingly, there were no observed differences between aggregates that primarily evolved to live in deep water and aggregates that exploited both deep and shallow water. However, since the evolved shapes appeared to be sufficient for survival, it can only be concluded that specific shapes (regardless of the grown shells) were not necessary for survival in Mosaic World's implementation of shallow water.

Figures 8.9 and 8.10 provide examples of aggregates which can alter their shape and aggregates that cannot. Each of these aggregates was picked from a different run where a majority of aggregates evolved the same or similar forms.

An analysis of the manner in which evolved shells were used by aggregates that evolved this capability was performed together with a real time analysis of the aggregate's behaviour within its ecosystem, revealed that there appear to be two reasons for shells to be grown by aggregates:

I) **Surviving in shallow water:** aggregates grow shells in order to be able to avoid UV radiation and exploit the new niche, shallow water. This is indicated by the fact that in the vast majority of runs aggregates grow shells and successfully manage to populate both deep and shallow water.

II) **Predation:** in many runs the aggregates evolved both the capacity to prey on other organisms and the capacity to grow shells, although no critters are present in the run. It is clear that the aggregates prey on each other, and clearly the shells are a mechanism for avoiding predators as well as a mechanism for overcoming this defence.

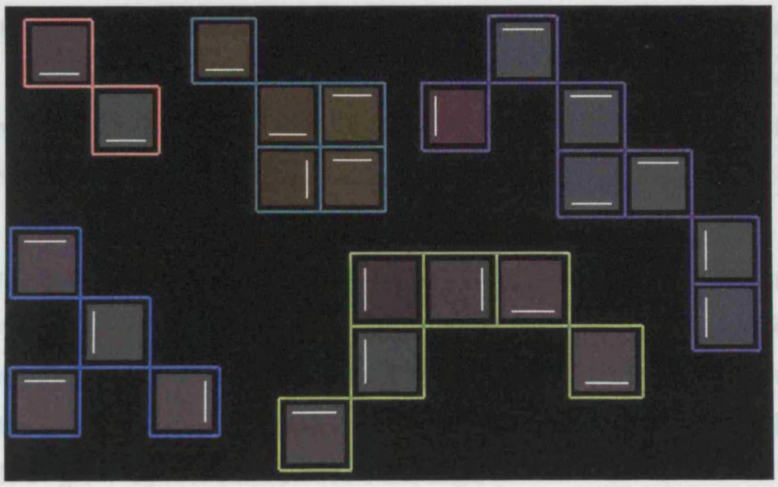


Fig. 8.9: Five examples of aggregates that could alter their morphology in real time.

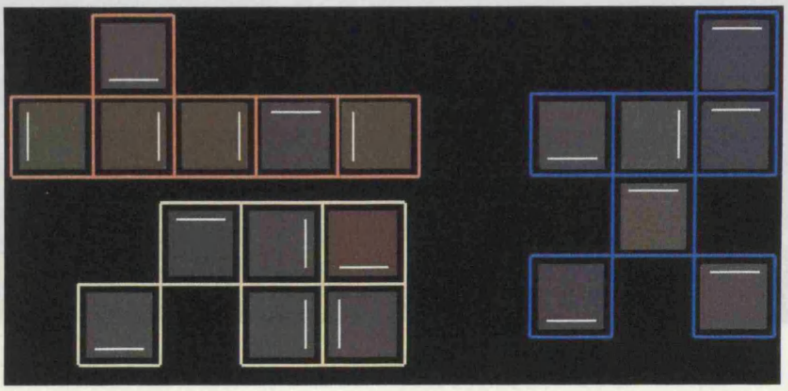


Fig. 8.10: Three examples of aggregates that cannot alter their morphology in real time.

Shell growth

Shells are grown in three different ways.

- **Static growth:** This method of growing shells occurs when one or more members evolve the capacity to grow shells and grows them around their immediate area. This was the most frequently used mechanism.

- **Dynamic growth:** this method of growing shells occurs when one or more members evolves the capacity to grow shells and the capacity to turn; this enables the members to turn and coat a large part of the aggregate with shells. This mechanism was occasionally used by one or more members.
- **Dynamic growth with cell migration:** this method of growing shells occurs when one or more members evolves the ability to migrate within the aggregate (change its shape) in addition to the capacity to grow shells and the capacity to turn: by combining movement with turning and growing shells, this type of mechanism enables growing relatively sophisticated shells. This mechanism was rarely used, probably because of the coordination issues involved in using three different abilities for a single purpose, and because these mechanisms may increase the difficulty of evolving the aggregate, for example, if one member controls movement/turning and another member creates shells in this manner, the second member can affect the aggregate's movement by default, and will have to evolve additional strategies to avoid this situation.

Fig. 8.11 demonstrates some of these mechanisms using two evolved aggregates. Within aggregate 1, member A is able to both turn and grow shells and is thus responsible for a large portion of the aggregate shell while members B, C and D grow shells in their immediate area. Similarly, within aggregate 2, member G is able to grow shells while turning, while member I is only capable of growing shells in its immediate area.

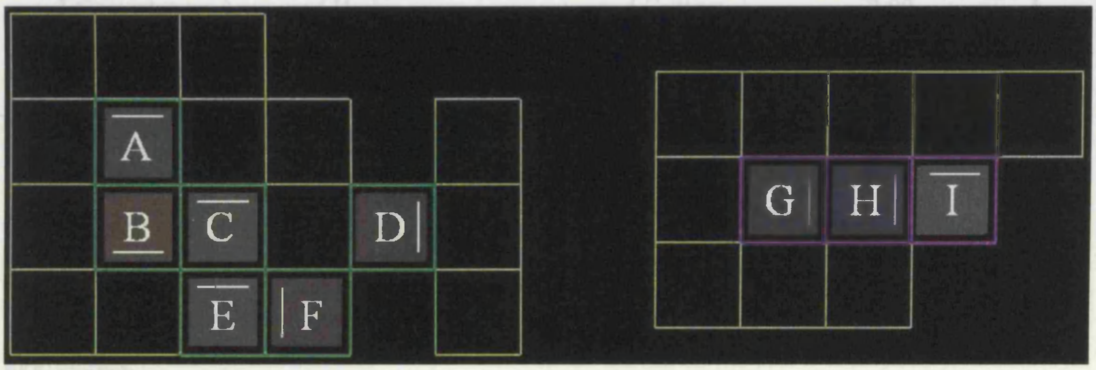


Fig. 8.11: A close-up of two sample aggregates with grown shells. Aggregate 1 consists of members that are denoted by the letters A,B,C,D,E,F, and marked in bright green. Aggregate 2 consists of members that are denoted by the letters G,H,I and are marked in purple. The thin yellow squares around both aggregates are grown shells.

Ecosystems

The addition of the ability to grow shells (experiments 1 & 2) appears to have influenced the types of ecosystems that can be evolved (table 8.7). These ecosystems are mostly variations of the ecosystems which appear in fig. 8.5, however, new types of ecosystems were evolved as well, including:

- **Aggregate carnivores (unarmoured):** aggregates that can both consume surfaces and prey on other aggregates; these aggregates evolved in runs where no critters were evolved.
- **Armoured aggregate carnivores:** an armoured version of the previous aggregates.
- **Armoured herbivores:** an armoured version of herbivorous aggregates ecosystem.
- **Armoured predators/prey:** an armoured version of the predator/prey ecosystem.
- **Armoured corals: predator/prey:** an armoured version of the coral predator/prey ecosystem.

In addition, in some of the runs the aggregates do not appear to grow shells. Interestingly, occasionally armoured aggregates showed a preference for deep or shallow water: but mostly they were capable in surviving in both types of environments. Finally, it appears that aggregates are generally larger than in the previous set of experiments (but not always). This can be explained by the greater need for size in order to be able to carry the weight of the shells.

Table 8.7. Average size of aggregate per type of ecosystem

Type of Ecosystem	Ave. Size of Aggregate
Armoured Herbivorous Aggregates	4.38
Coexistence: Armoured Herbivorous Aggregates and Critters	2.00
Armoured Aggregate Carnivores	5.32
Armoured Predator/Prey	5.86
Armoured Corals: Predator/Prey	2.43
Aggregate Carnivores (Unarmoured)	4.75

8.11 Discussion

It is interesting to note the similarities and differences between the construction of protective structures by cyanobacteria and the growth of protective shells by Mosaic World's aggregates.

First, it appears that when a new environmental niche is created, one which provides new rewards, an attempt to exploit it is made despite the fact that additional difficulties are involved in this process, specifically, the need to obtain protection from an environmental hazard (UV radiation). This is true for organisms that evolve both in Mosaic World and for cyanobacteria in nature. Second, this attempt requires aggregates to control their shapes and the shape of the grown shells – this resembles the behaviour which the model aimed to capture. Third, although Mosaic World's environment is very simple when compared to the natural environment, evolution discovered a way of utilising the ability to change an aggregate's shape to better exploit this environment; that being said, there were no differences observed between the shapes of aggregates that were evolved primarily for deep water and the shape of aggregates that were evolved for deep and shallow water. Fourth, although aggregates frequently grew shells, more often they grew partial shells rather than complete shells – this may be explained by the need to balance the trade-off between management of shell construction and the rewards the shallow water environment provides. Finally, even though only occasionally aggregates changed shapes in real time, and no elaborate movements were evolved (mostly a single member moved member back and forth in a way that was used to consume additional surfaces), this clearly mirrors the behaviour of moving cyanobacteria in microbial mats: to optimise access to resources (light).

To conclude: in this study, it was shown how the environment's interaction with the aggregate affects both its shape and the shape of its grown shell. Clearly, the selection pressures involved with the addition of a new type of resource are significant enough that they provided an evolutionary incentive for aggregates to evolve the mechanisms required to benefit from these. Even more interesting is the fact that the aggregates were able to evolve mechanisms for precise control of their shape and the shape of their shell structure in order to benefit from shallow water; for that reason, it can be said that the aggregates were able to exhibit another primary process of development: morphogenesis, in addition to growth and differentiation. Thus, the examined hypothesis can be said to be true: significant environmental variation can indeed affect the evolution of morphogenesis.

8.12 Complex interactions analysis

The work described in the first part of this chapter primarily deals with the interactions that take place between aggregates and critters and the interaction between critters within an aggregate. In order to examine these interactions, five experiments that exposed a critter population to several types of evolutionary and environmental conditions were conducted.

The results of these experiments showed that the potential interaction between predator aggregates and critters is sufficient to cause critters to interact and form aggregates in order to avoid the threat of predation. Additionally, the interactions between critters within a formed aggregate, which occurs through differentiation, appears to be crucial towards the aggregate becoming an attractive alternative to critters: this is the true because differentiation makes the aggregate more efficient and also because reducing capabilities makes coordination of several behaviours an easier task. Therefore, both these types of interactions, critter→critter and critter→aggregate, are crucial towards accomplishing the challenge set in the beginning of this chapter. These interactions take place between two different levels of the model, however, their effects reach all other levels as well.

The interaction(s) that takes place are in parenthesis at the end of each sentence.

1) Every critter attempts to survive – this requires several different behaviours:
    (a) **Perception:** the environment is perceived by the critter's control network's receptors (environment→receptor). It is important that the receptors relay relevant information to the control network so it could activate the appropriate module.
    (b) **Communication:** the receptors relay this information to the control network through neurons (receptor→neuron, neuron→control network).
    (c) **Activation:** the control network determines using the received stimuli which module to activate (control network→module).
    (d) **Perception:** the environment is perceived by the activated module's receptors (environment→receptor). It is essential that these receptors relay information that is relevant towards the task the module is in charge of. In the context of the chapter's experiments, it is crucial that the receptors relay information regarding the presence of predators in order for the critters to be able to avoid them (run away). In addition, the receptors should inform whenever other critters that can aggregate are nearby.
    (e) **Control:** the activated module controls the critter's behaviour (module→critter).
    (f) **Consumption:** the critter may consume surfaces (critter→environment); in this case, energy is transferred from the environment to the critter (environment→critter).
    (g) **Movement:** the critter may choose to move (environment→critter).
    (h) **Reproduction:** the critter may choose to reproduce (critter→critter). Under the 'accidental aggregation' scenario, this action may result in the formation of a size 2 aggregate. The vast majority of these aggregates do *not* survive, as no coordinated behaviour of both critters has been evolved yet (frequently such aggregates fall from the edges or into a hole).
    (i) **Aggregation:** under the 'aggregation by choice' scenario, a critter may choose to aggregate with another critter or aggregate. Although this may occasionally happen, the choice to aggregate by no means guarantees the survival of the new (or extended) aggregate (critter→critter, critter→aggregate).
2) **Selection (to better break down the task):** many critters die during stages 1-f to 1-i, either by consuming negative surfaces, or by falling from the edges/into a hole, or by running out of energy, or by reproducing when not possessing enough energy. Critters whose control networks have learned to break the task ideally are far more likely to survive than critters whose control networks break the task incorrectly or do not break

the task at all. Thus, the advantages such control networks grant directly affect the selection of the genes that define them (control network→genes)

3) **Selection (to evolve appropriate behaviours and structures):** the critters that survive are likely to have appropriate structures for their modules and also exhibit appropriate behaviours in various situations; thus, the advantages gained as a result cause the selection of the genes that define these modules (module→genes).
4) **Selection (to better compete):** the critters that survive compete on resources; critters that are fitter are more likely to out-compete others, thus, all features which increase fitness affect the selection of the genes that define them (critter→genes).
5) **Selection (to aggregate):** as was shown, even when predators are only occasionally present, there is a strong selection pressure on critters to aggregate as a way of overcoming the threat of predation (aggregate→critter, critter→genes). Once aggregated, the fact that these newly formed aggregates are difficult to prey on, can now obtain a new energy source (prey), and can differentiate (and optimise their metabolic rates) causes the selection of genes that prevent the aggregates from splitting (aggregate→genes).
6) **Reproduction:** continuing (1-i), the critters that survive past steps (2)-(5) and are now able to reproduce are fitter than those that died (genes→genes). Their offspring's phenotype is likely to be fit as well, as affected by the selection pressure in (2)-(4).
7) In the course of evolution a stable population of critter often emerges. It is very important to emphasise that it is *only* at this moment in time that stable species of aggregates can emerge. Although occasionally aggregates are formed before this moment, they never manage to survive and continuously reproduce; to achieve this goal, a stable base of fit critters *must* be present. However, if enough selection pressure is present (as indicated in (5)) or if 'accidental aggregation' is enabled, eventually a stable species of aggregates emerges.
8) **Aggregate behaviour:** the average aggregate attempts to survive and exhibits the following behaviours through its members. During every time step, all members of the aggregate generate behaviours depending on their capacities:
   (a) **Standard behaviours:** Like an ordinary critter, the member's control network perceives the environment (environment→receptor) and relays this information to the control network (receptor→neuron, neuron→control network). The control network determines which module to activate (control network→module). The activated module perceives the environment (environment→receptor), and controls the member's behaviour (module→critter).
   (b) **Consumption:** a member who has the capacity to consume surfaces can attempt to do so; if the aggregate does not move at the moment, it succeeds

(aggregate→environment). In this case, positive or negative energy is transferred to the aggregate's energy pool (environment→aggregate).

(c) **Movement:** a member who has the capacity to move or turn can do so (environment→aggregate); since this behaviour affects the rest of the aggregate, coordination of behaviours must evolve. Otherwise, for example, two members may push in different directions and the aggregate will not move – certainly the aggregate is unlikely to survive.

(d) **Reproduction:** a member who has the capacity to reproduce may attempt to do so. Since this ability is 'democratic', the aggregate only reproduces if the majority of members with this capacity wish to do so simultaneously (aggregate→aggregate).

(e) **Predation:** a member who has the capacity to prey may instruct the aggregate to attempt catching prey which could be critters and other aggregates. Since this ability is 'democratic', the aggregate only performs this action only if the majority of members with this capacity activate it (aggregate→aggregate, aggregate→critter).

(f) **Splitting**: a member may attempt to initiate splitting. Although this ability is 'democratic', only members who evolve the ability to participate in this decision affect the outcome. If the majority of members wish to split, the aggregate dissolves and every member becomes a standard critter (aggregate→critter). Note that most of these critters will not survive if the aggregate is differentiated.

9) **Selection ('standard' pressures):** many aggregates die during stages 8-b to 8-e. Those that survive face the same selection pressures critters face in steps (2) to (5): selection for every member's control network to better break down the task, selection for every member to evolve appropriate structures and behaviours, selection to better compete – both with critters (aggregate→critter) and with other aggregates (aggregate→aggregate) – (module→genes, control network→genes, critter→genes). In addition, aggregates face several additional selection pressures.

10) **Selection (to grow):** because aggregates are also susceptible to predation, there is a constant pressure on them to become larger in order to escape the threat of larger predators. In addition, there is pressure on predator aggregates to become larger in order to become more effective predators (aggregate→genes). This is evident in results of the experiments: aggregates that are predators are larger than aggregates that are herbivores.

11) **Selection (to split or shrink):** since it is much easier to find enough resources to survive as a critter or a smaller aggregate, there is constant selection pressure on aggregates to split or become smaller. This is evident in those runs that had 'aggregation by choice' enabled and no predators: in these runs, no aggregates were evolved at all (critter→genes, aggregate→genes).

12) **Selection (to differentiate):** an aggregate that is differentiated is more likely to survive,

both because it is more efficient, and also because it is far more likely to be able to coordinate the various actions of its constituent members (aggregate→aggregate). This is evident in all runs, but in particular in those runs where explicit differentiation was disabled; in this case, aggregates implicitly differentiated, by only utilised some of their abilities despite enormous metabolic costs. Thus, because differentiation increases an aggregate's likelihood of survival, the advantages it confers directly affect the selection of genes that encode this trait (aggregate→genes).

13) Steps (1)-(12) are repeated until the run ends. Depending on the evolutionary conditions, some runs only result in species of critters, other result in both critters and aggregates (predator/prey, coexistence), and yet others result in the extinction of critters and only aggregates remaining. The critters and aggregates that survive tend to be very fit, in terms of structure and behaviours, as well as in terms of internal differentiation.

8.12.1 Complex interactions analysis: part 2

The second part of the chapter continues investigating the challenge set for this chapter by adding a new type of environment to Mosaic World, shallow water, and by enabling the aggregates to alter their shapes and grow shells. These additions affect the interactions that take place in Mosaic World within aggregates and between critters and aggregates. Although these effects are (mostly) beneficial for aggregates, they are not crucial towards exploring the challenge; however, they do provide an opportunity to examine very interesting effects on the interactions in the system.

As the results show, aggregates increase their adaptation to the environment by evolving shapes that grant advantages, both in order to better utilise deep water and also to exploit the new environment, shallow water; by doing so, the aggregates exhibit morphogenesis. This is evident in the long and diagonal shapes that were frequently evolved by aggregates, and also in the shells that were grown to protect the aggregates from the environmental hazards (UV radiation) that are present in shallow water.

Because the work in part 2 extends the work in part 1, the vast majority of complex interactions are identical. Therefore, only the new interactions that take place within Mosaic World are described in this section.

1) **Expanded aggregate behaviour:** aggregates that can alter their shape and grow shells have all the behaviours described in (8) and are also subject to the same selection pressures described in (9) to (12); they do have additional behaviours and selection pressures:
    (a) **Member migration:** a member who has the capacity to migrate within the aggregate

can attempt to do so. This works as long as the movement does not split the aggregate in two or causes a member to migrate to a location where a shell is present (critter→aggregate). This ability enables the aggregate to change its overall shape through its members, and has the potential of increasing the aggregate's ability to survive.

(b) **Shell growth:** a member who has the capacity to grow shells may do so (critter→aggregate). These shells provide benefits (protection from UV radiation) but also costs (additional weight, cost of growth) to the aggregate. As the results indicate, gaining protection from UV through shell growth is necessary in order to safely utilise shallow water. In addition, shells make aggregates better predators but also more efficient at avoiding predators as the shell count towards the aggregate's size for predation purposes. However, an aggregate that carries too many shells may face additional – at times significant – energetic costs for movement.

2) **Selection (to grow shells or not):** aggregates face additional pressures in addition to the selection pressures described in the previous section. On one hand, growing shells certainly provides advantages as it enables the aggregate to safely exploit the new environment and also become a better predator and less of a prey; these issues certainly affect the aggregate, selecting traits that cause it to grow more shells. However, shells are *not* crucial: as many runs have shown, aggregates can certainly survive without the extra costs and weight of shells, and in fact, can also utilise shallow water, albeit, only to a limited degree. Thus, there is also pressure on aggregates for selecting traits that cause aggregates not to grow shells. Consequently, whether the aggregates grow shells, and how many, depends on the balance between the advantages and disadvantages of the shells in comparison to the benefits of shallow water (aggregate→genes). Moreover, the fact that aggregates compete against other aggregates (through predation and competition on resources), affects selection of genes that cause growth of shells as well (aggregate→genes). This is also affected by other parameters, e.g. if many aggregates choose to exploit shallow water then there would be pressure towards not growing shells and staying in the (now relatively empty) deep water, and vice versa.

3) **Selection (to evolve an appropriate shape):** since now aggregates are much more capable of finding an advantageous shape at a very low cost (only the cost of the immediate move), there are considerable pressures towards the selection of genes that encode shapes that are useful in Mosaic World (aggregate→genes).

4) **Selection (to differentiate):** in addition to item (12) in the previous section, as there are more capabilities for the aggregates to 'divide' between members, the benefits of differentiation become greater, thus, the pressure towards genes that encode differentiation is greater than before as a result of competition (aggregate→genes).

5) **Selection (to grow, to split or shrink):** in addition to items (10) and (11) in the previous section. The fact that aggregates are in a sense 'better' than before, since only aggregates can grow shells and safely exploit shallow water, affects the selection of genes that cause critters to aggregate, grow, split or shrink. In addition, the fact that aggregates can now 'optimise' their shapes confers additional advantages to aggregates in comparison to critters. Also, as shells affect both predators and prey, this affects the selection pressure leading for aggregation as well – although it is difficult to estimate in what direction. Finally, as the previous item described, differentiation is now more advantageous; this is another benefit only aggregates can utilise. It is difficult to estimate the precise effect of these changes on selection pressures (as they were not explicitly measured), however, it is logical to assume that these additions increase the likelihood of aggregation, simply because aggregates gain more benefits than critters as a result (aggregate→genes).
6) Steps (1)-(12) from the previous section and (1)-(4) in this section are repeated until the run ends. As the results section described, the evolved ecologies are more varied, showing multiple types of behaviours and ecologies. In addition, the aggregates have evolved appropriate morphologies and utilise the ability to grow shells to their advantage when exploiting the new environment, shallow water.

8.13 Conclusions

The goal of the work described in this chapter was to investigate several interesting interactions that take place between critters and aggregates and between members of an aggregate. This investigation also provided evidence that supports several biological theories regarding the emergence of multicellularity, namely that both the presence of predation and accidental aggregation are sufficient to initiate the transition to multicellularity, and also that differentiation is indeed a major benefit for aggregates and will occur even if an aggregate pays a large metabolic cost for it. In addition, the evolved results shared many parallels with natural systems, from the emergence of a division of labour within an aggregate, to the life-like dynamics of the evolved ecosystems.

The second part of the chapter continued investigating these interactions, by examining the effect of environmental change on the behaviour of aggregates that are capable of altering their shape and growing protective structures around themselves. The results showed that despite the additional costs associated with the required changes, evolution utilises these new additions in order to exploit the new environment, by evolving mechanisms that enable aggregates to precisely control their shape and the shape of their grown shells; it is interesting to note that by doing so, the aggregates exhibited an additional primary process of development: morphogenesis.

Chapter 9

Conclusions

9.1 Investigating complex interactions: an overview

As all model builders know, it is impossible to simulate every aspect of complicated real world phenomena. This is normally not an insurmountable challenge when simulating simple systems (non-complex systems) as it is generally possible to identify the important components in the target and only incorporate these into the model. However, because a complex system's behaviour is generated by highly nonlinear interactions between many different components, building a model that successfully captures the emergent behaviours of the target phenomena can be challenging.

Consequently, there is a recurring flaw in most models of complex systems. Whereas natural complex systems are frequently hierarchical – they are composed of hierarchies of nested complex systems – in most models only a limited range of levels of the phenomena, mostly one, is incorporated into the model. This means that an aspect of the model that is modelled as a simple component is often in reality a complex system in its own right, capable of expressing emergent and unpredictable behaviours. This oversimplification introduces an element of inaccuracy into the model because the emergent behaviour of an elementary component is modelled too simply. In addition, this prevents the examination of the relationship between components that are placed in different levels of the modelled phenomena, since these levels do not exist in the model. Most importantly, this prevents the systematic exploration of multilevel interactions in a hierarchical complex system model.

The aim of this thesis was to create a hierarchical complex system model in order to systematically investigate complex interactions. The concept of complex interactions includes both multileveled interactions and interactions that take place between components of the same level. The construction of such an analysis was intended to provide new insights into complex systems in general. At the same time, this thesis aimed to demonstrate the importance of incorporating hierarchical complexity into model design, by demonstrating that a more comprehensive understanding of the target phenomena can be gained as a result. For this purpose, the Mosaic World model was created and systematically investigated in the course of the thesis.

9.2 Summary of work

Chapter 1 provided an introduction to the problem that is addressed in this thesis, the fact that most models disregard the hierarchical nature of complex systems. Additionally, it described the underlying hypothesis behind this work, that creating a model that focuses on interactions, specifically complex interactions, may provide novel insights, and stated the aims and objectives of this thesis and the contributions that are expected to be created in solving this problem.

Chapter 2 provided the full background necessary to understand the context of the work this thesis addressed. This required providing a detailed description of complex systems with a focus on systems that exhibit hierarchical complexity. In addition, the concept of emergence, which is integral to many aspects of the thesis, was explained, and a definition of complex interactions was created and provided together with a critical review of related research that explores complex interactions. Because the work described in this thesis belongs to the artificial life field as well, a relevant review of this field was given.

The second part of the chapter supplied the essential background in order to create a model of a hierarchical complex system. For this purpose, two types of models were described, and a useful methodology [233] for the creation of models of biological phenomena was given. The creation of Mosaic World required creating a framework of evolving agents: hence, the field of evolutionary computation was introduced, and the usage of genetic algorithms was thoroughly explained. Because every agent is controlled by one or more neural networks, their operation was also described. Finally, some methods and considerations regarding the usage of genetic algorithms to evolve neural networks were provided.

Chapter 3 presented a detailed technical description of the initial version of Mosaic World which was used for this work (and was continuously expanded in the course of this thesis). This required elaborating on the concept and goals underlying the model, describing several basic terms which were frequently used, and providing a thorough overview of the model in terms of the complex interactions that take place within. In addition, the environment: the surface matrix and the illumination matrix were outlined, and a full description of the algorithm used to create each was provided. A complete description of the inhabitants of Mosaic World, the critters, was also given, including their behaviour (reproduction, movement, sensing), their genomes, their brains and the evolutionary process they undergo.

Chapter 4 described the first challenge presented to Mosaic World: *evolvability*. This challenge began the complex interactions investigation at the lowest level of the model, and so, focused on genes→genes interactions. The goal was to discover the nature of genes→genes interactions that improve the effective evolution of critters that adapt to an environment which becomes increasingly more difficult through time. This was accomplished through experiments that investigated the effect on evolvability as a consequence of the process used to evolve the neural networks used for critter control. It was discovered that when the process of evolution, as expressed in five different types of structural mutations, produces gradual changes to the neural networks and enables evolution to adapt elements of itself, the evolvability of the critters was promoted. Conversely, when the process enables duplication of existing network structures, the evolvability of the critters was inhibited.

Chapter 5 continued the complex interactions investigation at the next level of the model, thus, the focus was on receptor→environment interactions and the challenge was *colour vision*. The goal of the chapter was to discover the effect of environments of various visual characteristics on the visual system of critters that evolved in them. It was discovered that the necessity of adapting to the environment exerts pressure on the visual systems of the critter to provide the relevant information to the network; when it is useful to filter information and only use a part of the available stimuli, the visual system adopts this strategy, however, the visual system adopts a different strategy when survival requires extracting a greater amount of information.

Chapter 6 explored the next level of the model by focusing on network→environment interactions; therefore, the investigated challenge was *behaviour*. The aim in this chapter was to discover the effect of environments of various levels of difficulty on the behaviour of critters that evolved in these environments. Whereas the previous chapter demonstrated that by evolving specific structures (specifically, the structures of visual systems) the critter is able to adapt to its environment, this chapter continued this investigation by demonstrating another mechanism of adapting to the environment: behavioural changes. Thus, it was demonstrated that when the environment varies, the appropriate behaviour frequently changes as well, and so, a critter that wishes to survive must adapt its behaviour accordingly. This adaptation occurs through the interaction of the environment and the critter: the environment acts as a selective force that determines the behaviour an adapting critter will exhibit.

More importantly, by demonstrating that the evolved behavioural strategies strongly resemble those exhibited by natural organisms under equivalent conditions, this chapter has shown that there are universal behaviours that are appropriate for certain kinds of environments regardless of whether they are virtual or physical; these behaviours are used by the inhabiting organisms, which can be animals, insects or critters.

In chapter 7, the model's hierarchical nature was augmented by replacing the standard network used to control the critter's behaviour with a new control mechanism: the modular neural network. The interactions that occur within this new level, specifically, the control network→module interactions, were the focus of this level's investigation and the challenge was *modular specialisation*. The experiments that were set in the chapter examined the nature of the control network→module interactions that occur in order to improve the fitness of critters that adapt to an environment which changes in time. It was demonstrated that this improvement occurs through modular specialisation: the control network learned to break the task it faced in a meaningful way and assign each of these subtasks to its subordinate modules, and each of the subordinate modules specialised in its assigned task. This modular specialisation is what enabled the modular networks to increase the fitness of the critters.

In chapter 8, the model's hierarchical nature was expanded again, by enabling individual critters to aggregate and become multicellular organisms. The interactions that are associated with the new level, specifically, the interactions that occur between critters and aggregates, critter→aggregate, and the interactions that occur within aggregates, critter→critter, were the focus of this chapter's investigation. Consequently, the challenge in this chapter is *aggregation*. Experiments were carried out in order to examine the conditions that lead to aggregation, and the results showed that aggregation occurs when the environment provides an advantage for being big (as in the case of predators) or when aggregation enables greater efficiency (which is caused by internal differentiation). This demonstrated again two principles that appeared in the previous chapters: that the selection pressures exerted by the environment determine the nature of the adaptation that is required, and that this adaptation (improvement in fitness) is enabled by internal interactions, in this case, differentiation.

The second part of the chapter reinforced these conclusions by showing that when a new type of environment is introduced which provides new rewards but incurs new costs, aggregates demonstrate precise control of their morphology, by evolving specific shapes and by growing specific forms of protective shells in order to benefit from this environment in relative safety; it is important to stress that by doing so, the aggregates exhibited morphogenesis. Thus, the differentiation process is further extended by enabling each member to carry a greater number of possible tasks.

9.3 Evaluation and criticism of the model

To ensure that the design decisions of all aspects of Mosaic World are justified, Webb's comprehensive framework [233] for the design of models of biological phenomena was used throughout this thesis. This framework used 6 different dimensions to examine the model and its extensions: biological relevance, level, generality, abstraction, accuracy and match.

The modelled biological systems

In section 3.2 it was discussed why several different biological systems were chosen to be modelled in various degrees of accuracy instead of a single large biological system which could have been modelled very accurately. The reason given was that to model precisely a single biological system would be too limiting in terms of the range of interactions and hypotheses that could be explored. In this section it is argued that this appears to have been a correct design decision.

On one hand, there was a loss of accuracy in the model which prevented very detailed biological hypotheses from being explored. However, many more biological hypotheses which did not require extremely precise models were investigated, and overall, this enabled investigating a far greater range of hypotheses which were *still* biologically relevant and useful: this was demonstrated to be the case in chapters 4 to 8 in the respective methodology sections. More importantly, exploring few very detailed biological hypotheses *was not* the goal of this work; the goal was the detailed analysis of interactions in a hierarchical complex system, in addition to a demonstration that implementation of hierarchical complexity is necessary: as section 9.4 shortly demonstrates, these objectives were satisfied.

Number of levels of the model

One criticism of this work could be that a smaller number of levels in the model would have been sufficient to obtain the insights that were obtained. However, this is untrue; the number of levels in the final version of the model (6) is the minimum number required to discover *all* four observations that are reported (see next section). A choice of 4 levels (equivalent to a 'standard' model) could have discovered the first three observations (first: adaptation takes place, second: 'rate' of adaptation is determined by evolvability, third: adaptation occurs through differentiation/specialisation). A choice of 5 levels would have raised the possibility of the fourth observation (differentiation occurs across all levels), but examination of two levels (e.g. control network and modules) would not have been sufficient to prove that this occurs across all levels. However, a choice of 6 levels demonstrates that this consistently occurs across multiple levels. Even though it is possible to play devil's advocate and say that a choice of 7 levels would demonstrate that only 6 levels are affected by this principle, this is unlikely to be the case.

In addition, it is possible that further insights would have been found if more levels were incorporated to the model. Although this may very well be true, for practical reasons related to the length of a PhD, this number of levels in the model was used.

Underlying context of the model: the visual environment

It is possible to argue that the choice of the underlying context for the model, a visual environment, was perhaps not the ideal choice. Although it is impossible to state with confidence that no other choice of environment would have been better, this choice of environment can be justified in three ways. First, using this environment enabled creating conceptually simple environments that are very challenging. Furthermore, by altering few parameters of the environment, it was possible to create many types of environments of various levels of difficulty. This capability was extremely useful. Second, this type of environment also enabled performing experiments with environments that are inherently different from each other: for example, the highly complex ambiguous environments and the simple environments that are used in chapter 5. Finally, the usage of this environment enabled examining interesting biological hypotheses that relate to the evolution of visual systems, which is a worthy goal in its own right.

In hindsight, the main disadvantage of this environment was the fact that it is computationally demanding. Simulating thousands of detailed reflectance functions for both the surface and the illumination matrices sources took its toll on the system, and certainly reduced the scope of possible experiments that could have realistically been conducted.

Usage of an artificial life model

A common criticism of artificial life is that the construction of models can occasionally force the desired result, even if unintentionally. Thus, the results of all artificial life models have to be taken with scepticism.

Although this is a valid concern, and as every model designer knows, the choice of parameters and design certainly affects the model's behaviour, this is also the strength of the approach. When designing a model, while it is possible to enforce high-level behaviours on low level components, doing so would cause all conclusions that can be drawn from the model to become meaningless because the high level behaviours could not be explained by the behaviour of the components of the model. Conversely, because many artificial life models, Mosaic World included, examine the conditions that cause low level components to exhibit high level behaviours, when the hypothesised conditions cause these low level components to express the hypothesised high level behaviours, it is reasonable to assume that the model and its underlying assumptions are true. This is discussed at greater length in section 2.3.2.

It is important to state that this also makes certain artificial life models difficult to use. For example, it has proven to be remarkably difficult to find the conditions that cause aggregates to grow shells, since these also affect the conditions that cause critters to aggregate: altering some conditions often caused critters to never aggregate, thus, examining their shell growth was not possible. It is the view in this thesis that this difficulty demonstrates that once these conditions are found, they are meaningful.

Analysis of complex interactions

An additional criticism of this work could be that a mathematical analysis of complex interactions (e.g. measuring the precise flow of information between components of the model) might provide similar, yet more accurate, insights to those found by the process-level analysis used in this thesis. In response, it is argued that while this criticism is valid, and this type of analysis would in principle offer a more precise way of understanding the interaction dynamics within the system, in practice the challenges in performing such an analysis cause it to be beyond the scope of this thesis for several reasons.

First, even though the measurement of the precise flow of information in a system is possible, and this could potentially be used in order to achieve a more accurate quantification of the system's internal dynamics, in practice this may simply be too complicated to perform for an continuously evolving population of hierarchical agents within a complex system (such as Mosaic World).

Second, even though tracking the flow of information of some interactions in the system is likely to be feasible using this type of technique (e.g. measuring the flow of information from the environment to a receptor), tracking many other types of interactions is not a straightforward task at all; for example, how does one measure the selection pressure an environment exerts on a critter? or the selection pressures within a competing population that is exerted on its members? Furthermore, the fact that these interactions and many others are supposed to be tracked simultaneously lends an additional complication which must be overcome.

Finally, while it is conceivable that some of these challenges may be overcome, doing so would be too time consuming and prevent performing the investigations that are the primary focus of this thesis, which are establishing the interactions that exist in the model and their system-wide effects rather than the precise quantification of these interactions. That being said, this type of investigation is inarguably promising and so, could be performed as future work.

Choice of challenges

In this thesis, 5 different challenges were presented to Mosaic World: evolvability, colour vision, behaviour, modular specialisation and aggregation. It can be argued that this choice of challenges is rather arbitrary. In response it can be said that these specific challenges were selected for two reasons: primarily because they enable examining *every* level of the model, and also because they present interesting challenges that parallel those encountered by real world organisms, e.g. real organisms must be evolvable, perceive their environment, find appropriate behaviours for survival. It is important to state that coming up with other challenges is probably possible, but their choice is not likely to be better justified than those that were used in this thesis.

9.4 Objectives revisited

The aim of this work was to demonstrate that evolving a population of hierarchical visually guided neural network agents for the purpose of investigating complex interactions is useful, in the sense that it enables the demonstration and investigation of behaviours that normally do not appear in simpler, non hierarchical or less hierarchical, models, and thus enable finding new insights into complex systems in general. This section reviews the objectives described in chapter 1 deemed necessary to test this hypothesis:

1. **Explore biological systems and universal principles in nature that are suitable for investigation using a hierarchical complex system model.**

In the course of this thesis, several biological systems and universal principles were investigated using Mosaic World:

- In chapter 3, a generic simple ecosystem was picked as the primary model of Mosaic World, and an abstract visual environment was chosen to be the underlying context. In addition, the biological cone photoreceptor was selected as inspiration for the critter visual system.
- In chapter 4, the concept of evolvability was investigated using different types of structural mutations.
- In chapter 5, the concept of ambiguity was incorporated into the visual model. In

addition, the effect of various environments on visual evolution was investigated.

- In chapter 6, the behaviour of the Mosaic World ecosystem was likened to biological ecosystems, thus, the behaviour of the critters was compared to the behaviour of certain animals (e.g. Chacma baboons, Rana catesbeiana tadpoles) and insects (e.g. wolf spiders and drosophila flies).
- In chapter 7, the concept of modularity was incorporated to the brain model and enabled investigating the effect of modular brains and their operation. In addition, the effect of gene duplication, as expressed through the 'duplicate module' mutation was investigated.
- In chapter 8, the behaviour of the Mosaic World ecosystem was compared to the cellular environment; by enabling the ability of critters to aggregate, and as enabling the evolution action capacities, it was possible to investigate several hypotheses regarding the evolution of multicellularity. In this study, the behaviour of aggregates was compared to the behaviour of primitive multicellular organisms that are formed through the aggregation of individual cells, such as dictyostelium and cyanobacteria. In the second part of the chapter, a feature enabling aggregates to grow shells and alter their shape was added, and so it was possible to examine the effect of environmental variation on the evolution of morphogenesis. By adding these features, the similarity of aggregates to cyanobacteria was further extended since colonies of cyanobacteria in microbial mats are able to build rock-like structures such as stromatolites.

2. **Develop a computational multi-agent, hierarchical complex system model, Mosaic World.**

The initial version of the Mosaic World model was described in chapter 3. In chapters 4, 5, 7 and 8 additional features were incorporated into the model.

The initial version of Mosaic World that was described in chapter 3 comprises four distinct levels: 'genes' (level 1), 'neurons' and 'receptors' (level 2), 'networks' and 'critters' (level 3), 'population' and 'species' (level 4). In chapter 7 an additional level was added by replacing 'networks' with 'control networks' and adding 'modules'. In chapter 8 an addition level was added by inserting 'aggregates' between 'critters' and 'population'. These additions were necessary in order to explore increasingly hierarchical systems and a greater range of complex interactions.

3. **Identify key interactions in the model, and create accordingly a set of challenges that will focus on each one. Each challenge will consist of a small perturbation to the system or its context; the resulting effect on the interactions will be systematically investigated.**

A thorough analysis of the Mosaic World model and its behaviour showed that the following interactions are integral to many emergent behaviours exhibited by the model:

- Genes→genes (investigated in chapter 4: the evolvability challenge:), receptor→environment (investigated in chapter 5: the colour vision challenge), critter→environment (investigated in chapter 6: the behaviour challenge), control network→module (investigated in chapter 7: the modular specialisation challenge), critter→aggregate (investigated in chapter 8: the aggregation challenge), and critter→critter (investigated in chapter 8: the aggregation challenge).
- Since all changes are driven by selection pressure, the relevant interactions are integral. This thesis explored: genes→genes, receptor→genes, network→genes, module→genes, control network→genes, critter→genes, and aggregate→genes.

4. **Correlate and understand the behaviour of the perturbed aspects of the system (its elements or context) with the results of those interactions in the system as a whole.**

In every chapter, an aspect of the system (its elements or context) was perturbed, resulting in an overall effect on the system; this effect was thoroughly analysed in every chapter in the complex interactions analysis section.

The following describes the perturbation done to the system, and the overall effect of this perturbation. In chapter 4, different types of structural mutations led to different evolvability of the critters. In chapter 5, different types of environments resulted in different types of visual systems. In chapter 6, different types of environments resulted in different behaviours. In chapter 7, different types of brains resulted in modular specialisation and increased fitness. In chapter 8, different environmental conditions and incorporation of the ability to aggregate affected whether aggregates would evolve or not, and a new type of environment and the ability to change shape and grow shells affected the aggregates' morphology and their choice of habitat (deep water, shallow water, or both).

In devising the complex interactions analysis, the aim was that interesting properties of the system, which may not normally be easily detected in the data would become more apparent, and by becoming so, some general knowledge about complex systems (specifically, biological complex systems) would be obtained. This was found to be the case.

While performing the complex interactions analysis for the diverse challenges that were presented to Mosaic World, four major patterns were observed. These observations apply not only to Mosaic World, but also to real world biological systems. Note that the analysis of interactions, performed in a coherent and structured manner enabled the development of these insights.

First observation: adaptation takes place

The first observation is that an evolving virtual organism, just like its natural counterpart, has three ways of adapting to a difficulty that it faces. It may adapt its structure to better deal with the difficulty, as demonstrated by the visual adaptations in chapter 5. Alternatively, it may adapt its genetically encoded behaviour to better deal with the challenge, as demonstrated by the behavioural strategies in chapter 6. Or it may adapt both its structure and its genetically encoded behaviour to better deal with the challenge, as demonstrated by the aggregating critters in chapter 8: not only did the critters aggregate to avoid the threat of predation, but at times they also evolved different behaviours and began preying on other organisms. Note that in all cases, these adaptations were a result of the interactions between the environment and the organism which lead to a selection pressure that is exerted on the organism.

Although it can be argued that the reported behavioural changes are also a form of structural adaptation as these behaviours are genetically encoded, and this claim is certainly true, it is possible to view genetically encoded behaviour as a distinct subset of structure, thus, worthy of classification in its own right.

Second observation: the 'rate' of the adaptation is determined by evolvability

The second observation is that the 'rate' of the adaptations that take place in the course of evolution is determined by the organism's evolvability. As was seen in chapter 4, the way the genes interact, as indicated by different types of structural mutations, determines the population's ability to adapt to a changing environment, and that more evolvable populations are faster in their rate of adaptation (as those that were not fast enough perished because the changing environment became too challenging).

Third observation: adaptation occurs through differentiation

The third observation is that one significant and regularly exploited way for these structural and behavioural adaptations to occur is through internal specialisation (through interaction of internal components). In chapter 5, different environments caused critters to evolve specialised visual systems appropriate for these environments, thus enabling them to survive. In chapter 7, critters with modular brains increased their fitness through modular specialisation. This was achieved by breaking the survival task to subtasks, both behaviourally (different modules were activated in different types and performed different tasks) and structurally (different modules possessed different types of visual systems, appropriate for their tasks). In chapter 8, although new aggregates at first had no advantage, by differentiating the aggregate's members, they were able to gain an advantage: for example, they could obtain a metabolic rate lower than a standard critter's and still possess more capabilities. In the same chapter, section 8.6, it was also shown that the population speciated: multiple species were evolved to explore different niches; this is essentially the same principle, but on the scale of the ecosystem.

Fourth observation: the process of differentiation occurs across all levels of the hierarchy: each one specialises in its function.

The fourth observation is that the process of differentiation occurs across all levels of the hierarchy: in every level, the component specialises/differentiates in order to fulfil its task in an efficient (but not necessarily optimal) manner, and the nature of this differentiation is dependent on the differentiation that takes place at other levels. Since this finding is novel, this observation probably best demonstrates the validity of the hierarchical model.

In chapter 5 which deals with the initial version of Mosaic World, it is repeatedly shown that the visual system of evolving critters adapts to the environment by specialising.

In chapter 7, it is shown that the control network and its subordinate modules adapt to the environment by specialising: the control network specialises in breaking the survival task into meaningful subtasks and the subordinate modules specialise in their allocated subtasks. Furthermore, in section 7.7, the visual systems of the control network and subordinate modules are analysed, and it is demonstrated that both the visual systems of the control network and the visual systems of the subordinate modules become specialised as well; these *adapt to the specific subtasks* of the control network/module. For example, a module responsible for controlling movement contains a visual system that is colour-blind whereas a module responsible for consumption contains a sophisticated visual system. This interaction of the control network and the subordinate modules is what enables the improvement in fitness (e.g. as demonstrated by the visual systems of the control network and subordinate modules working together). It is important to emphasise that unless the model had these levels, these details would have been lost (the standard non-modular network would have a relatively generic visual system with some, but not all, of the capacities of the modular network).

In chapter 8, it is shown that members of an aggregate differentiate in order to increase the aggregate's fitness (as indicated by a lower metabolic rate), that is, the aggregate divides certain of its capabilities between its members: each is controlled only a subset of the aggregate's actions. Furthermore, in section 8.6, a thorough analysis of a representative aggregate demonstrated that this differentiation/specialisation takes places across all levels. Consequently, some of the aggregate's differentiated members had specialised modules, and these specialised modules had specialised visual system, appropriate for performance of a specific subset of the module's behaviours.

When one examines the speciation analysis (also in section 8.6), which demonstrates that multiple species of various sizes and behaviours (predators and non-predators) evolved in the ecosystem, it becomes apparent that differentiation truly occurs across all functional levels of the model: receptor (level 2), modules (level 3), control networks (level 4), aggregates (level 5) and species (level 6), and that the specialisation of lower levels clearly depends on the specialisation of higher levels.

In conclusion of this objective, even though this thesis provided an interesting opportunity to witness these four patterns in process in several different variations, it cannot be said that all of them are surprising (or novel). Clearly, evolving organisms adapt to a changing environment, and this adaptation can take the form of a structural and/or a genetically encoded behavioural adaptation. That said, witnessing some of these observations in natural organisms in real time would be impossible, and so, the fact that Mosaic World enables exploring such hypotheses and witnessing their results in real time is noteworthy and interesting (for example, examining whether different 'rates' of adaptation to environmental change of natural organisms can be achieved using different evolutionary mechanisms is currently impossible as present-day science does not have the ability of changing such fundamental aspects of evolution).

Furthermore, the fact that differentiation occurs across all levels of a hierarchical complex system is a novel observation which was not expected. This particular insight is a finding shown in detail for the first time in this work and was enabled by implementing hierarchical complexity and discovered through the investigation of complex interactions. It is believed that by continuously using this type of analysis, additional insights can be gained of real world biological and non-biological complex systems; these insights may be used to better predict and affect such systems.

5. **Demonstrate that incorporating hierarchical complexity into the model can provide an improvement in the understanding of the modelled phenomena, by finding novel observations that could not be made in a non hierarchical or less hierarchical model.**

As was demonstrated in the previous objective, had the model not incorporated hierarchical complexity, some interesting and novel observations would not have been apparent. A good example of such an observation is the fact that the process of differentiation/specialisation occurs across all levels of the hierarchical model; as was shown, in order to witness such a phenomenon, the model must possess at least six functional levels (this was discussed in section 9.3, 'number of levels of the model').

An interesting additional observation is the fact that some of the modules analysed in section 7.7 take the same strategy demonstrated in chapter 5 and filter information that is irrelevant: e.g. a module which controls movement is colour blind – it does not receive information about colour which is unnecessary. This demonstrates that evolved visual strategies for subtasks are consistent with known visual principles.

Clearly, for many types of studies, obtaining such observations can be very useful towards gaining a broader understanding of the modelled phenomena. It is also conceivable that at times such observations may be even necessary towards understanding the modelled phenomena. In addition, it is easy to imagine situations where disregarding hierarchical complexity has the potential of affecting the model's overall behaviour, thus, this may affect its validity (e.g. when emergent behaviours that appear at lower levels of the model are modelled too simply). Consequently, it can be said that incorporating hierarchical complexity into a model is useful, and in some situations, crucial, towards understanding the modelled phenomena.

6. **Demonstrate that the model can be used to support or refute existing and novel computational and biological hypotheses that cover some or all levels of the system including:**
    - **The usage of different types of structural mutations will affect the evolvability of neural network agents.**

This hypothesis was explored in chapter 4. It was discovered that adaptive evolution and gradual changes promote evolvability, while structural duplication inhibited it in Mosaic World.

- **Like biological visual systems, physical similarity or behavioural similarity of resources will affect the visual system of evolving virtual agents.**

This hypothesis was explored in chapter 5. It was shown that evolution does not 'care' about physical similarity; the only thing that matters is behavioural similarity. In Mosaic World, when resources are physically different but behaviourally similar, similar visual strategies are evolved. However, when resources are physically identical but behaviourally different, different visual strategies are evolved.

- **Like biological visual systems, increased physical similarity of resources will affect the visual system of evolving virtual agents.**

This hypothesis was explored in chapter 5. It was shown that increased similarity requires greater specialisation of the visual system in order to correctly recognise the various types of resources; in other words, suitable adaptations are evolved so that the visual system can fulfil its role. This resembles visual adaptations evolved by organisms that live in visually challenging conditions.

- **The need to deal with ambiguous environments is a possible reason for the evolution of colour vision in nature** [137].

This hypothesis was explored in chapter 5. It was shown that ambiguous environments result in critters that evolve visual systems that can be referred to as colour vision. Critters evolve this in order to gain a more reliable way of discerning the value of a resource, which becomes particularly useful in ambiguous environments.

- **Evolving virtual agents in environments of various levels of difficulty will result in behaviours that are similar to those encountered in nature under equivalent conditions.**

This hypothesis was explored in chapter 6. It was shown that the type of environment (in terms of difficulty) has a large effect on the behaviour of the critters. Additionally, critters exhibit different behaviours when they have different levels of health. Interestingly, both these types of behaviours mirrored many real world behaviours exhibited by animals and insects.

- **Virtual agents that are controlled by modular neural networks (specifically, a mixture-of-experts architecture) will be fitter than critters that use non-modular neural networks** [95, 96].

This hypothesis was explored in chapter 7. It was shown that utilising this type of architecture for critter control improved their fitness. This improvement resulted from modular specialisation: the control network found a useful strategy of breaking the overall task into smaller subtasks, and each one of the modules specialised in its assigned task.

- **Predation is sufficient to cause the emergence of multicellularity** [217].

This hypothesis was explored in chapter 8, and was shown to be true for aggregating critters that evolve in Mosaic World in the presence of predators (and is true even when the aggregates themselves cannot become predators).

- **Accidental aggregation, without any explicit immediate advantages, is sufficient to cause the emergence of multicellularity** [33].

This hypothesis was explored in chapter 8, and was shown to be true. When aggregation is involuntary, even though most new aggregates die, eventually enough survive and manage to obtain the advantages of multicellularity; this occurs despite the fact that aggregation does not provide any advantages at first.

- **Significant environmental variation can affect the evolution of morphogenesis.**

This hypothesis was explored in chapter 8, and was shown to be true. When a new environment is added that requires protective structures, the aggregates exhibit morphogenesis by evolving mechanisms for growing shells in a precise manner.

After obtaining each of these objectives, it is possible to review the hypothesis of this thesis as well:

It is useful to evolve hierarchical visually guided neural network agents for the purpose of investigating complex interactions.

In this thesis, a population of visually guided neural network agents was evolved in order to explore numerous hypotheses. In the course of the thesis, these agents became increasingly hierarchical as the model was expanded. In addition, in every chapter a complex interactions analysis was conducted for the experiments that took place.

By performing the complex interactions analysis, it was possible to discover new findings that relate to biological complex systems. At the same time, this investigation also enabled the demonstration that incorporating hierarchical complexity into model design increases the understanding of the modelled phenomena, and allowed the exploration of several computational and biological hypotheses (which resulted in multiple contributions). To conclude, this thesis has provided clear and unambiguous evidence that it is useful to evolve hierarchical visually guided neural network agents.

9.5 Thesis contributions

This thesis makes a number of novel contributions to the fields of computer science (evolutionary computation, artificial life), complex systems, neuroscience and evolutionary biology.

Mechanisms and methods

1. Creation of Mosaic World, a hierarchical complex system model that can be used to investigate complex interactions and numerous additional computational and biological hypotheses.

2. Creation of the complex interactions analysis, a novel form of analysis of complex systems.

3. Creation of the visual brain, a 3D modular feed-forward artificial neural network for control of agents by visual guidance.

4. Definition of E_{total}, a novel method for measurement of the evolvability of agents in artificial life simulations.

Analyses

5. Detailed analysis of multiple complex interactions that take place within a hierarchical complex system model (Mosaic World), focusing on: Gene→gene, receptor→environment, critter→environment, control network→module, critter→aggregate and critter→critter.

6. Analysis of agent evolvability as affected by the usage of five different types of structural mutations in the evolutionary process.

7. Demonstration that agents controlled by modular neural networks are fitter than agents that are controlled by non-modular neural networks and that the improvement in fitness occurred through specialisation of modules.

8. Demonstration that members of aggregates of artificial agents differentiate in order that the aggregate become more efficient.

9. Demonstration that usage of modularity encourages the formation of specialised modules

that are assigned for different tasks.

Artificial life and biology

10. Demonstration that evolved computational visual systems resemble biological systems in the sense that both evolve in order to detect behaviourally significant visual elements regardless of the physical appearance of these elements (e.g. visual systems evolve to identify specific food items both in nature and in Mosaic World).

11. Demonstration that evolved computational visual systems resemble biological systems in the sense that both evolve specific visual adaptations in order to be able to successfully function in visually challenging environments.

12. Empirical support for a biological theory suggesting that colour vision evolved as a method of dealing with ambiguous stimuli.

13. Demonstration that artificial agents can evolve the computational equivalent of colour vision.

14. Demonstration that artificial agents evolve different behavioural strategies for environments of different levels of difficulty, and that the behavioural strategies of evolved artificial agents under harsh conditions (hunger, scarcity of resources) parallel the behavioural strategies of certain insects and animals in nature under equivalent conditions.

15. Empirical support for the theory suggesting that the mechanisms of gene duplication affect functional specialisation (specifically, in this case it is shown that such mechanisms affect the utilisation of specialised modules).

16. Empirical support for three biological theories regarding the emergence of multicellular life on primordial earth, specifically:
    (a) Predation is a sufficient condition to cause the emergence of multicellularity.
    (b) Accidental aggregation, without any explicit immediate advantages, is a sufficient condition to cause the emergence of multicellularity.
    (c) Member differentiation is important to multicellular organisms.

17. Demonstration that environmental variation can affect the morphology of evolved aggregates.

18. Demonstration that different types of life-like ecosystems can evolve in an artificial life environment.

9.6 Future work

Considering the fact that the work in this thesis spanned multiple fields and subfields, it is possible to extend this work in many different ways.

Modular brains

Although modular brains were demonstrated to exhibit superior performance in comparison to the standard non-modular brains, the implementation of modularity used is partial. This limitation not only prevented thoroughly examining the fitness increase that can be obtained through modularity, but is also likely to have limited the functional specialisation that was used by evolution.

It is possible to extend this model by (a) removing the 8 module limit and (b) extending the control hierarchy, that is, allow a module to act as a control network to its own subordinate modules (and these modules can also act as control networks).

It is quite likely to assume that this will increase the usefulness of this mechanism, and additional insights about the breakdown of the task and the specialisations of the subordinate modules may be found as well. It is particularly interesting to see whether further task breakdowns across modules and levels will be apparent when this mechanism is used.

The beginning of development

By chapter 8, Mosaic World exhibited some of the elements of development: growth, differentiation, and to some extent, morphogenesis. Originally it was aimed to implicitly evolve more developmental mechanisms. Initial steps were taken to achieving this goal, but the investigation required more time that was available, and the results were not of sufficient quality and interest to be included in this thesis. Two aspects of development were partially explored.

Pattern formation

Although the work in this thesis undeniably demonstrated that morphogenesis can be implicitly evolved, it would have been very interesting to see whether specific and precise morphologies can be induced to evolve implicitly as well. This can be of use to developmental biology, by examining the conditions that are necessary for pattern formation to take place, and to computer science, since it could enable the construction of precise structures.

This can be accomplished by assigning explicit advantages to specific shapes that are evolved in several different ways:

(a) By providing energy advantages to aggregates of a specific form: e.g. cube-like aggregates are fitter, or aggregates that are very narrow and long. These energy advantages can decrease the cost of aggregate metabolic activities.

(b) By enabling sexual reproduction of aggregates that evolve compatible shapes. Specifically, by predefining the shape of one species of aggregates, it would be possible to encourage other species of aggregates to evolve compatible shape in order to mate with it.

Cell signalling

This aspect of development can be studied by examining the conditions that cause cells in an aggregate (individual critters) to communicate information to other cells. This could be of interest both to developmental biology and to computer science (by demonstrating that evolved members are able to cooperate by sharing information in order to achieve an overall goal).

Simulation of cell signalling can be achieved by enabling internal communications within aggregates, which can be achieved in several different ways:

(a) By enabling critters to change their transmittance (colour) in real time, it would be possible for critters to relay information to other critters. The mechanism for transmittance detection is already in place.

(b) By incorporating a chemical diffusion network into the aggregate system, which may be used in the same way. This would require mechanisms for creation of a chemical, as well as mechanisms of detection of the chemical.

Both mechanisms would require that communication between members would be necessary or advantageous.

Complex interactions

In order to expand the investigation of complex interactions, the model's hierarchical complexity needs to be further increased. Although this can be potentially accomplished in several ways, one way in particular seems like an appropriate choice: the creation of multiple societies within Mosaic World. By treating Mosaic World's ecosystem as a society, creating multiple societies (each a complete and separate ecosystem), and enabling communication and interaction between societies, it will be possible to investigate the interactions that take place between different societies, and also compare the interactions that take place within several societies.

This setting can be used to investigate several different premises. For example, investigating the evolution of society: under what conditions a society manages to successfully stabilise? And how similar is it to its parent society? Alternatively, it is possible to investigate the evolution of language: by implementing a simple and evolvable form of communication and watching how members of a society communicate, and the difficulties of communication between members of different societies, some interesting insights about the evolution of language and communication may be obtained.

Evolvability

It is possible to examine the effect of different crossover operators using the evolvability measure defined in chapter 4. By incorporating the same principles believed to affect evolvability, it is likely that different types of crossover operators that have a positive effect on critter evolvability will be found. Specifically, these crossover operators can incorporate the same principles that were explored in chapter 4: gradual changes, structural duplication, and adaptive evolution.

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