In Heinke, D., & Mavritsaki, E., Editors, (in press). Computational Modelling in Behavioural Neuroscience: Closing the gap between neurophysiology and behaviour. Psychology Press, London.

## **Preface**

Behavioural neuroscience is mainly concerned with understanding of how neurophysiological processes, such as chemical processes in synapses or chemo-electrical processes in axonal spikes, ultimately lead to human behaviour. There are numerous empirical approaches to this issue, e.g. experiments with stroke patients (neuropsychology), fMRI-experiments, EEG-experiments, etc. Classically behavioural neuroscience theorises about such experimental evidence in a qualitative way. More recently, however, there has been an increasing development of mathematical and computational models of experimental results. In general, these models are more clearly defined and more detailed than their qualitative counter parts. The aim of this book is to give an overview of the state-of-the-art of computational modelling in behavioural neuroscience.

In general, these computational models consist of networks of processing units ("neurons"). The operations of these neurons are based upon evidence from neurophysiological processes, whilst at the same time allowing whole-system behaviour to emerge from the network of such neurons. Such models can be set up so that they are consistent with both single neuron and whole-system levels of operation, allowing physiological results to be meshed with behavioural data, i. a. closing the gap between neurophysiology and human behaviour.

Apart from this very general definition of computational models in behavioural neuroscience, there is considerable diversity between models with respect to the methodology of designing a model, the degree to which neurophysiological processes are taken into account and the way data (behavioural, electrophysiological, etc) constrain a model. In 15 chapters this book presents examples of this diversity and, in doing this, it covers the state-of-art of computational modelling in behavioural neuroscience.

The book is formed from talks given at the third Behavioural Brain Sciences Symposium, held at the Behavioural Brain Sciences Centre, University of Birmingham, UK, in May 2007. We were delighted to host such a distinguished set of contributors and we hope both the meeting and the chapters that have emerged will contribute to the progress of understanding how human behaviour relates to neurophysiological processes in general and, more specifically, to the advancement of computational modelling as part of this particular scientific quest.

In the following paragraphs we summarize the content of each chapter. The summaries are written for researchers working in the area of behavioural neuroscience who may not be not familiar with computational modelling. Thus, apart from stating the main implication of a chapter, we point out the human behaviour considered by each chapter and the particular neurophysiological processes taken into account by each model. We hope these introductions will make it easier for non-experts in computational modelling to read the chapters, allowing them to pick and chose chapters relevant for their own area of interest.

We have organized the chapters in an order reflecting differences in the way neurophysiological processes are taken into account in the models. The approaches to modelling can be roughly grouped into two types according to the way the 'processing units' – the neurons in the systems - operate: "spiking neurons" and "rate-coded neurons". Generally, spiking neurons can be seen as taking more neurophysiological details into account than do rate-coded neurons. Even though, at first glance, it may be seen as preferable to use the more detailed approach, there are also many reasons why the rate-coded approach is more suitable, as discussed in Chapter 15. The models presented in the first two chapters utilize spiking neuron models. In contrast, Chapter 3 – 5 advocate that modellers move between the degrees of abstraction during the design process. Finally, the models in Chapter 6 – 12 are based on rate-coded neuron models. Chapter 13 and 14 take a more general approach to understanding the brain which do not easily fit into those three categories.

In Chapter 1 Graham and Cutsuridis present a model of the microcircuity in the CA1 region of the mammalian hippocampus, which covers a broad range of neurophysiological details including the properties of pyramidal cells, bistratified cells, basket cells, exo-axonic cells and oriens-lacunosum-moleculare cells. The result is a multi-compartment model with AMPA, NMDA, GABA-A and GABA-B synapses. With this computer model, Graham and Cutsuridis support the hypothesis that the CA1 region coordinates both the storage of new information and the retrieval of old information, and the authors highlight the specific roles of the different neuron types in the solution of this problem.

In Chapter 2 Thorpe summarizes the implications of his "temporal coding hypothesis". Central to this hypothesis is that perceptual information is coded by the order in which neurons within a population fire ("order code"). He argues that such a single-spike based code can explain the speed with which humans can process complex visual scenes. Interestingly, together with Spike-Time Dependent Plasticity (STDP) this approach can implement unsupervised learning of face features.

In Chapter 3 Deco and Rolls present another example where processes on the cellular level, as modelled by integrate-and-fire neurons (one compartment, point-like neurons), are important for the understanding of whole-system behaviour. In their chapter they demonstrate that stochastic processes on the cellular level are intrinsically linked with probabilistic behaviour in decision-making, as expressed by the Weber's law. In addition, their chapter suggests that using rate-coded neurons (mean-field approach) to design the model first, and then employing a veridical transformation of the model to the spiking-level, can be accomplished to simulate real neuronal behaviour.

In Chapter 4 Humphreys, Mavritsaki, Allen, Heinke and Deco applied Deco and Rolls's mathematical framework to simulate data on human search over time as well as space, the Search over Time and Space (sSoTS) model. In a first series of simulations they show that behavioural deficits of stroke patients can be linked to lesions in the posterior parietal cortex and reduced levels of neurotransmitters. In a second study Humphreys et al. demonstrate that sSoTS can be used to decompose complex neural circuits found in fMRI studies of human attention, separating circuits concerned with inhibition attention function from those concerned with top-down enhancement.

In Chapter 5 Heinke, Mavritsaki, Backhaus and Kreyling present new versions of the Selective Attention for Identification model (SAIM). In general, SAIM implements translation-invariant object identification in multiple object scenes. In a approach analogous to Deco and Roll's method, they demonstrate that the initial structure of

SAIM, based on rate-coded neurons, can be used to guide the design of a new model utilizing spiking neurons. In addition they argue that a modelling approach for "bridging the gap" should not only include neurological processes, but also should be able to deal with ecologically valid stimuli. To show that SAIM can satisfy this requirement, Heinke et al. present an extension of SAIM that can select and recognize objects in naturalistic scenes.

In Chapter 6 Gurney proposes a similar top-down approach to modelling albeit within a Marrian framework (see also Chapter 15). He illustrates this approach with a summary of his modelling work on the Basal Ganglia which presents results from several levels of abstraction, ranging from conductance based models of individual neurons, through spiking neuronal networks, to systems level models with rate codes and embodied (robotic) models in a naturalistic environment.

So far, the first two chapters focused on spiking neurons and the following four chapters used a mix of models to close the gap between human behaviour and neurophysiology. In following chapters the modelling work is based on rate-coded neuron models.

In Chapter 7, Zhaoping, May and Koene summarize simulation results from a physiological-plausible model of V1 supporting Zhaoping et al. 's "V1 saliency hypothesis". Central to this hypothesis is that processes in V1 can explain input-driven target detection ("odd-one out") in visual search tasks, e.g. the detection of a red-vertical bar among red-horizontal and green-vertical bars. In addition, Zhaoping et al. present empirical support for V1 representing the saliency of stimuli. It should be noted that Zhaoping et al. consider their model as an alternative approach to the standard saliency-based approach (see Chapter 13 for an example).

In Chapter 8 Thomas Trappenberg shows that a simple dynamic neural field model can link a broad range of behavioural findings with physiological measurements in the brain, e.g. a motion discrimination task. Trappenberg points out that because this model is so successful, it is safe to argue that it captures principal mechanisms which are important for "brain-style information processing".

In Chapter 9 John Bullinaria presents a model for the origin of modularity in the brain by using a standard Multi-Layer Perceptron. The structure of the network is modified by an evolutionary algorithm and each generation is trained with a standard backpropagation algorithm to solve complex pattern discrimination tasks. Within this framework Bullinaria demonstrates that modularity emerges from a combination of behavioural requirements, e.g. pattern discrimination, and neurophysiological constraints (e.g. the size of the brain, the length of connections, etc.).

In Chapter 10 Ward and Ward present results from their "research tool" termed "minimally cognitive agent". This tool models the performance of a visual agent (VA) as part of a perception-action cycle situated in a simple simulated environment. A VA consists of continuous-time recurrent network trained by a genetic algorithm to perform a specific task, such as catching two falling balls. In the first part of their chapter Ward and Ward summarize their earlier results with the VA approach on selective attention and the implications of the results for the neurophysiology of selective attention (e.g. for the need for "reactive inhibition" in order to switch attention). In the second part of the chapter, Ward and Ward present new results of simulations with multiple VAs leading to speculation that the organisation of the brain can be described as multiple VAs acting in concert.

Emilio Kropff (Chapter 11) presents a new learning rule for an autoassociative memory which is optimal for storing correlated patterns. He argues that the storage of

correlated patterns is behaviourally particularly relevant since semantic information must be represented in correlated patterns (e.g. as expressed in feature norms).

In Chapter 12 Mozer and Wilder present a new theory to unify exogenous and endogenous attentional control. Central to their theory is the assumption that attentional control operates on two dimensions: the spatial scale of operation (local vs. global) and the degree of task focus (low vs. high). For instance, if the task is to search for a person with a red coat in street scenes, the attentional control setting is "local spatial scale" and "high degree of task focus". Mozer and Wilder integrate their attentional control system into a standard saliency-based computer model by means of associative mapping. Their results show this approach can successfully simulate a broad range of data from visual search tasks.

Chapter 13 (Friston, Stephan and Kiebel) presents an abstract, mathematical and approach to understanding the brain. Friston et al. argue that the brain's function and structure can be understood in terms of one simple principle, the minimisation of "free-energy". From this principled stance, they derive a broad range of conclusions concerning perception, action and learning. For instance, actions aim to minimize surprising exchanges with the environment, whereas perception serves to infer the causes of sensory inputs. As to the structure of the brain, Friston et al. conclude from the free-energy principle that the brain's hierarchical structure can be interpreted as an attempt to represent causal hierarchies in the environment.

In Chapter 14 Aaron Sloman combines the standpoints of philosophy and artificial intelligence with theoretical psychology and summarizes several decades of research into the functions of vision in humans and other animals. This paper focuses almost entirely on what needs to be explained rather than presenting a computational model. However, from this survey, Sloman derives a list of requirements that future computational models will need to take into account.

The final chapter (Chapter 15) is somewhat unusual. In this chapter Dietmar Heinke presents the minutes of discussions at the meeting. In this way the chapter gives an overview of the methodologies and approaches represented in this volume while (hopefully) conveying some of the excitement of the discussions that took place.

Taken together, the content of this book gives an overview of the computational methods currently used in the field and how these methods intend to bridge the gap between behaviour and neurophysiology.

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