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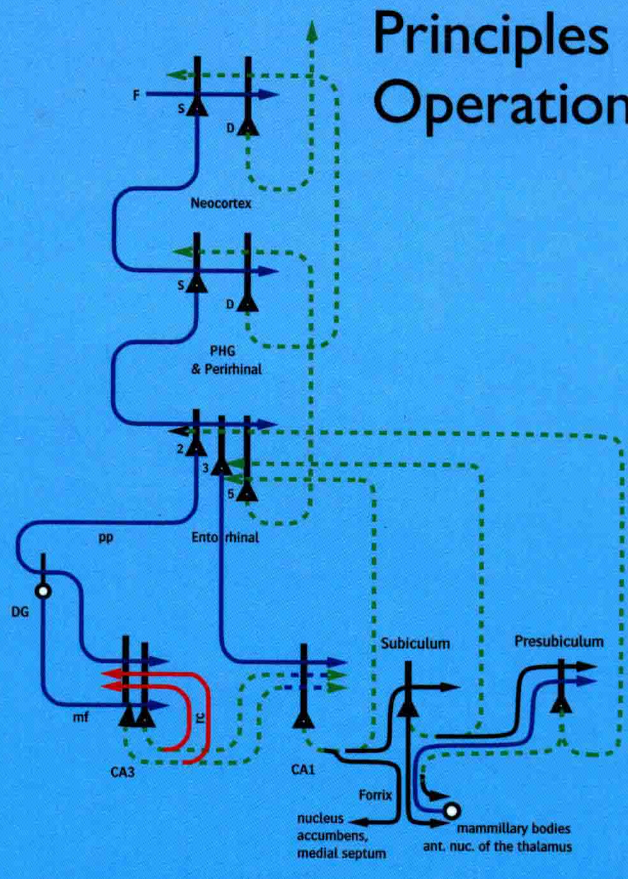
Principles of Operation



Cerebral Cortex
Principles of Operation

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Preface

The overall aim of this book is to provide insight into the principles of operation of the cerebral cortex. These are key to understanding how we, as humans, function.

There have been few previous attempts to set out some of the important principles of operation of the cortex, and this book is pioneering. I have asked some of the leading investigators in neuroscience about their views on this, and most have not had many well formulated answers or hypotheses. As clear hypotheses are needed in this most important area of 21st century science, how our brains work, I have formulated a set of hypotheses to guide thinking and future research. I present evidence for many of the hypotheses, but at the same time we must all recognise that hypotheses and theory in science are there to be tested, and hopefully refined rather than rejected. Nevertheless, such theories and hypotheses are essential to progress, and it is in this frame of reference that I present the theories, hypotheses, and ideas that I have produced and collected together.

This book focusses on the principles of operation of the cerebral cortex, because at this time it is possible to propose and describe many principles, and many are likely to stand the test of time, and provide a foundation I believe for further developments, even if some need to be changed. In this context, I have not attempted to produce an overall theory of operation of the cerebral cortex, because at this stage of our understanding, such a theory would be incorrect or incomplete. I believe though that many of the principles will be important, and that many will provide the foundations for more complete theories of the operation of the cerebral cortex.

Given that many different principles of operation of the cortex are proposed in this book, with often several principles in each Chapter, the reader may find it convenient to take one Chapter at a time, and think about the issues raised in each Chapter, as the overall enterprise is large. The Highlights sections provided at the end of each Chapter may be useful in helping the reader to appreciate the different principles being considered in each Chapter.

To understand how the cortex works, including how it functions in perception, memory, attention, decision-making, and cognitive functions, it is necessary to combine different approaches, including neural computation. Neurophysiology at the single neuron level is needed because this is the level at which information is exchanged between the computing elements of the brain. Evidence from the effects of brain damage, including that available from neuropsychology, is needed to help understand what different parts of the system do, and indeed what each part is necessary for. Neuroimaging is useful to indicate where in the human brain different processes take place, and to show which functions can be dissociated from each other. Knowledge of the biophysical and synaptic properties of neurons is essential to understand how the computing elements of the brain work, and therefore what the building blocks of biologically realistic computational models should be. Knowledge of the anatomical and functional architecture of the cortex is needed to show what types of neuronal network actually perform the computation. And finally the approach of neural computation is needed, as this is required to link together all the empirical evidence to produce an understanding of how the system actually works. This book utilizes evidence from all these disciplines to develop an understanding of how different types of memory, perception, attention, and decision-making are implemented by processing in the cerebral cortex.

I emphasize that to understand how memory, perception, attention, decision-making, cognitive functions, and actions are produced in the cortex, we are dealing with large-scale computational systems with interactions between the parts, and that this understanding requires analysis at the computational and global level of the operation of many neurons to perform together a useful function. Understanding at the molecular level is important for helping to understand how these large-scale computational processes are implemented in the brain, but will not by itself give any account of what computations are performed to implement these cognitive functions. Instead, understanding cognitive functions such as object recognition, memory recall, attention, and decision-making requires single neuron data to be closely linked to computational models of how the interactions between large numbers of neurons and many networks of neurons allow these cognitive problems to be solved. The single neuron level is important in this approach, for the single neurons can be thought of as the computational units of the system, and is the level at which the information is exchanged by the spiking activity between the computational elements of the brain. The single neuron level is therefore, because it is the level at which information is communicated between the computing elements of the brain, the fundamental level of information processing, and the level at which the information can be read out (by recording the spiking activity) in order to understand what information is being represented and processed in each brain area.

With its focus on how the brain and especially how the cortex works at the computational neuroscience level, this book is distinct from the many excellent books on neuroscience that describe much evidence about brain structure and function, but do not aim to provide an understanding of how the brain works at the computational level. This book aims to forge an understanding of how some key brain systems may operate at the computational level, so that we can understand how the cortex actually performs some of its complex and necessarily computational functions in memory, perception, attention, decision-making, cognitive functions, and actions.

A test of whether one's understanding is correct is to simulate the processing on a computer, and to show whether the simulation can perform the tasks of cortical systems, and whether the simulation has similar properties to the real cortex. The approach of neural computation leads to a precise definition of how the computation is performed, and to precise and quantitative tests of the theories produced. How memory systems in the cortex work is a paradigm example of this approach, because memory-like operations which involve altered functionality as a result of synaptic modification are at the heart of how many computations in the cortex are performed. It happens that attention and decision-making can be understood in terms of interactions between and fundamental operations in memory systems in the cortex, and therefore it is natural to treat these areas of cognitive neuroscience in this book. The same fundamental concepts based on the operation of neuronal circuitry can be applied to all these functions, as is shown in this book.

One of the distinctive properties of this book is that it links the neural computation approach not only firmly to neuronal neurophysiology, which provides much of the primary data about how the cortex operates, but also to psychophysical studies (for example of attention); to neuropsychological studies of patients with brain damage; and to functional magnetic resonance imaging (fMRI) (and other neuroimaging) approaches. The empirical evidence that is brought to bear is largely from non-human primates and from humans, because of the considerable similarity of their cortical systems.

In this book, I have not attempted to produce a single computational theory of how the cortex operates. Instead, I have highlighted many different principles of cortical function, most of which are likely to be building blocks of how our cortex operates. The reason for this approach is that many of the principles may well be correct, and useful in understanding how the cortex operates, but some might turn out not to be useful or correct. The aim of this *book is therefore to propose some of the fundamental principles of operation of the cerebral cortex, many or most of which will provide a foundation for understanding the operation of the cortex, rather than to produce a single theory of operation of the cortex, which might be disproved if any one of its elements was found to be weak.*

The overall aims of the book are developed further, and the plan of the book is described, in Chapter 1, Section 1.1. Some of the main Principles of Operation of the Cerebral Cortex that I describe can be found in the titles of Chapters 2–22; but in practice, most Chapters include several Principles of Operation, which will appear in the Highlights to each Chapter. Section 26.5 may be useful in addition to the Highlights, for Section 26.5 draws together in a synthesis some of the Principles of Operation of the Cerebral Cortex that are described in the book. Further evidence on how these principles are relevant to the operation of different cortical areas and systems and operate together is provided in Chapters 24–25. In these Chapters, the operation of two major cortical systems, those involved in memory and in visual object recognition, are considered to illustrate how the principles are combined to implement two different key cortical functions. The Appendices provide some of the more formal and quantitative properties of the operation of neuronal systems, and are provided because they provide a route to a deeper understanding on the principles, and to enable the presentation in earlier Chapters to be at a readily approachable level. The Appendices describe many of the building blocks of the neurocomputational approach, and are designed to be useful for teaching. Appendix D describes Matlab software that has been made available with this book to provide simple demonstrations of the operation of some key neuronal networks related to cortical function. The programs are available at http://www.oxcns.org.

Part of the material described in the book reflects work performed in collaboration with many colleagues, whose tremendous contributions are warmly appreciated. The contributions of many will be evident from the references cited in the text. Especial appreciation is due to Gustavo Deco, Simon M. Stringer, and Alessandro Treves who have contributed greatly in an always interesting and fruitful research collaboration on computational aspects of brain function, and to many neurophysiology and functional neuroimaging colleagues who have contributed to the empirical discoveries that provide the foundation to which the computational neuroscience must always be closely linked, and whose names are cited throughout the text. Much of the work described would not have been possible without financial support from a number of sources, particularly the Medical Research Council of the UK, the Human Frontier Science Program, the Wellcome Trust, and the James S. McDonnell Foundation. I am also grateful to many colleagues who I have consulted while writing this book, including Joel Price (Washington University School of Medicine), and Donald Wilson (New York University). Dr Patrick Mills is warmly thanked for his comments on the text. Section 24.3.12 on *ars memoriae* is warmly dedicated to my colleagues at Corpus Christi College, Oxford. The book was typeset by the author using LaTeXand WinEdt.

The cover includes part of the picture *Pandora* painted in 1896 by J. W. Waterhouse. The metaphor is to look inside the system of the mind and the brain, in order to understand how the brain functions, and thereby better to understand and treat its disorders. The cover also includes an image of the dendritic morphology of excitatory neurons in S1 whisker barrel cortex (Fig. 1.14) (adapted from Marcel Oberlaender, Christiaan P.J. de Kock, Randy M. Bruno, Alejandro Ramirez, Hanno S. Meyer, Vincent J. Dercksen, Moritz Helmstaedter and Bert Sakmann, Cell type-specific three-dimensional structure of thalamocortical circuits in a column of rat vibrissal cortex, Cerebral Cortex, 2012, Vol. 22, issue 10, pp. 2375–2391, by permission of Oxford University Press). The cover also includes a diagram of the computational circuitry of the hippocampus by the author (Fig. 24.1). The aim of these second two images is to highlight the importance of moving from the anatomy of the cortex using all the approaches available including neuronal network models that address and incorporate neurophysiological discoveries to lead to an understanding of how the cortex operates computationally.

Updates to and .pdfs of many of the publications cited in this book are available at http://www.oxcns.org. Updates and corrections to the text and notes are also available at http://www.oxcns.org.

I dedicate this work to the overlapping group: my family, friends, and colleagues – in salutem praesentium, in memoriam absentium.

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