SPIKING NEURON MODELS
Single Neurons, Populations, Plasticity

Neurons in the brain communicate by short electrical pulses, the so-called action potentials or spikes. How can we understand the process of spike generation? How can we understand information transmission by neurons? What happens if thousands of neurons are coupled together in a seemingly random network? How does the network connectivity determine the activity patterns? And, vice versa, how does the spike activity influence the connectivity pattern? These questions are addressed in this introductory text aimed at those taking courses in computational neuroscience, theoretical biology, neuronal modeling, biophysics, or neural networks. The authors focus on phenomenological approaches so that beginners can get to grips with the theoretical concepts before confronting the wealth of detail in biological systems. The book is in three Parts dealing, in order, with neurons and connections, collective behavior in networks, and synaptic plasticity and its role in learning, memory, and development. Each chapter ends with a literature survey, and a comprehensive bibliography is included. As such the book will also introduce readers to current research.

The approach will be suitable for students of physics, mathematics, or computer science with an interest in biology; but it will also be useful for biologists who are interested in mathematical modeling. A large number of worked examples are embedded in the text, which is profusely illustrated. There are no mathematical prerequisites beyond what the audience would meet as undergraduates: more advanced techniques are introduced in an elementary, concrete fashion when needed.

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Single Neurons, Populations, Plasticity

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CAMBRIDGE
UNIVERSITY PRESS

PUBLISHED BY THE PRESS SYNDICATE OF THE UNIVERSITY OF CAMBRIDGE
The Pitt Building, Trumpington Street, Cambridge, United Kingdom

CAMBRIDGE UNIVERSITY PRESS
The Edinburgh Building, Cambridge CB2 2RU, UK
40 West 20th Street, New York, NY 10011-4211, USA
477 Williamstown Road, Port Melbourne, VIC 3207, Australia
Ruiz de Alarcón 13, 28014, Madrid, Spain
Dock House, The Waterfront, Cape Town 8001, South Africa

http://www.cambridge.org

First published 2002

Printed in the United Kingdom at the University Press, Cambridge

Typeface Times 11/14pt. *System* LaTeX 2_ε [DBD]

A catalogue record of this book is available from the British Library

ISBN 0 521 81384 0 hardback
ISBN 0 521 89079 9 paperback

Cambridge University Press
0521813840 - Spiking Neuron Models: Single Neurons, Populations, Plasticity
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Preface

The task of understanding the principles of information processing in the brain poses, apart from numerous experimental questions, challenging theoretical problems on all levels from molecules to behavior. This books concentrates on modeling approaches at the level of neurons and small populations of neurons, since we think that this is an appropriate level to address fundamental questions of neuronal coding, signal transmission, or synaptic plasticity. In this text we concentrate on theoretical concepts and phenomenological models derived from them. We think of a neuron primarily as a dynamic element that emits output pulses whenever the excitation exceeds some threshold. The resulting sequence of pulses or "spikes" contains all the information that is transmitted from one neuron to the next. In order to understand signal transmission and signal processing in neuronal systems, we need an understanding of their basic elements, i.e., the neurons, which is the topic of Part I. New phenomena emerge when several neurons are coupled. Part II introduces network concepts, in particular pattern formation, collective excitations, and rapid signal transmission between neuronal populations. Learning concepts presented in Part III are based on spike-time-dependent synaptic plasticity.

We wrote this book as an introduction to spiking neuron models for advanced undergraduate or graduate students. It can be used either as the main text for a course that focuses on neuronal dynamics, or as part of a larger course in computational neuroscience, theoretical biology, neuronal modeling, biophysics, or neural networks. For a one-semester course on neuronal modeling, we usually teach one chapter per week focusing on the first sections of each chapter for lectures and give the remainder as reading assignments. Many of the examples can be adapted to become exercises or projects for students. While writing the book we had in mind students of physics, mathematics, or computer science with an interest in biology; but it might also be useful for students of biology who are interested in mathematical modeling. All the necessary mathematical concepts are introduced

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in an elementary fashion and we have provided many illustrative figures which complement the mathematical analysis and help the reader picture what is going on. No prior knowledge beyond undergraduate mathematics should be necessary to read the book. An asterisk (*) marks those sections that have a more mathematical focus. These sections can be skipped at a first reading.

We have also tried to keep the book self-contained with respect to the underlying neurobiology. The fundamentals of neuronal excitation and synaptic signal transmission are briefly introduced in Chapter 1 together with an outlook on the principal topics of the book, viz., formal spiking neuron models and the problem of neuronal coding. In Chapter 2 we review biophysical models (such as Hodgkin–Huxley) of neuronal dynamics and models of dendritic integration based on the cable equation. These are the starting point for a systematic reduction to neuronal models with a reduced complexity that are open to an analytical treatment. Whereas Chapter 3 is dedicated to two-dimensional differential equations as a description of neuronal dynamics, Chapter 4 introduces formal spiking neuron models, namely the integrate-and-fire model and the Spike Response Model. These formal neuron models are the foundation for all the following chapters. Part I on "Single Neuron Models" is rounded off by Chapter 5 which gives an overview of spike-train statistics and illustrates how noise can be implemented in spiking neuron models.

The step from single-neuron models to networks of neurons is taken in Chapter 6 where equations for the macroscopic dynamics of large populations of neurons are derived. Based on these equations phenomena such as signal transmission and coding (Chapter 7), oscillations and synchrony (Chapter 8), and pattern formation in spatially structured networks (Chapter 9) can be investigated. Up to this point, only networks with a fixed synaptic connectivity have been discussed. The third part of the book, finally, deals with synaptic plasticity and its role in development, learning, and memory. In Chapter 10, principles of Hebbian plasticity are presented and various models of synaptic plasticity are described that are more or less directly inspired by neurobiological findings. Equations that relate the synaptic weight dynamics to the statistical properties of neuronal spike activity are derived in Chapter 11. Last but not least, Chapter 12 presents an – admittedly personal – choice of illustrative applications of spike-timing-dependent synaptic plasticity to fundamental problems of neuronal coding.

While the book contains material which is now considered as standard for courses of the type mentioned earlier, it also provides a bridge to current research which has developed over the last few years. In most chapters, the reader will find some sections which either report recent results or shed new light on well-known models. The viewpoint taken in the presentation of the material is of course highly subjective and a bias towards our own research is obvious. Nevertheless, we hope that the book will find the interest of students and researchers in the field.

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Lausanne, November 2001

Acknowledgments

This book would not have been possible without the help of our friends and colleagues who made many valuable comments and spotted numerous mistakes. In particular, we would like to thank Silvio Borer, Nicolas Brunel, Stefano Fusi, Evan Haskell, Andreas Herz, Renaud Jolivet, Maurizio Mattia, Jean-Pascal Pfister, Hans-Ekkehard Plesser, Marc van Rossum, Walter Senn, and Arnaud Tonnelier for a careful reading of the text. We owe special thanks to Leo van Hemmen who encouraged us to write a book on our joint work. Even though the scope of the text has changed over the years, the original initiative is due to him. Finally, we thank all the students who attended tutorials or classes taught by us and whose critical comments helped us to organize our thoughts.

W.G. and W.K.