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978-1-107-06083-8 - Neuronal Dynamics: From Single Neurons to Networks and Models of Cognition
Wulfram Gerstner, Werner M. Kistler, Richard Naud and Liam Paninski
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NEURONAL DYNAMICS

What happens in our brain when we make a decision? What triggers a neuron to send out a signal? What is the neural code?

This textbook for advanced undergraduate and beginning graduate students provides a thorough and up-to-date introduction to the fields of computational and theoretical neuroscience. It covers classical topics, including the Hodgkin–Huxley equations and Hopfield model, as well as modern developments in the field such as Generalized Linear Models and decision theory. Concepts are introduced using clear step-by-step explanations suitable for readers with only a basic knowledge of differential equations and probabilities, and richly illustrated by figures and worked-out examples.

End-of-chapter summaries and classroom-tested exercises make the book ideal for courses or for self-study. The authors also give pointers to the literature and an extensive bibliography, which will prove invaluable to readers interested in further study.

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Preface

This textbook for advanced undergraduate and beginning graduate students provides a systematic introduction into the fields of neuron modeling, neuronal dynamics, neural coding, and neural networks. It can be used as a text for introductory courses on Computational and Theoretical Neuroscience or as main text for a more focused course on Neural Dynamics and Neural Modeling at the graduate level. The book is also a useful resource for researchers and students who want to learn how different models of neurons and descriptions of neural activity are related to each other.

All mathematical concepts are introduced the pedestrian way: step by step. All chapters are richly illustrated by figures and worked examples. Each chapter closes with a short summary and a series of mathematical Exercises. On the authors' webpage Python source code is provided for numerical simulations that illustrate the main ideas and models of the chapter (http://lcn.epfl.ch/~gerstner/NeuronalDynamics.html).

The book is organized into four parts with a total of 20 chapters. Part I provides a general introduction to the foundations of computational neuroscience and its mathematical tools. It covers classic material such as the Hodgkin–Huxley model, ion channels and dendrites, or phase plane analysis of two-dimensional systems of differential equations. A special focus is put on the firing threshold for the generation of action potentials, in the Hodgkin–Huxley models, as well as in reduced two-dimensional neuron models such as the Morris–Lecar model.

Part II focuses on simplified models for the dynamics of a *single* neuron. It covers nonlinear integrate-and-fire models with and without adaptation, in particular the quadratic and exponential integrate-and-fire model, as well as the Izhikevich model and adaptive exponential integrate-and-fire model. The question of noise in the neural dynamics is posed and two classic descriptions of noise are presented. First, stochasticity arising from random spike arrival: this approach leads to a noise term in the differential equation of the voltage, and can be formulated as a Langevin equation. Second, intrinsic stochasticity of neurons leading to an "escape" across the firing threshold even when the neuron is in the subthreshold regime: this approach leads to the framework of a Generalized Linear Model which is systematically introduced and discussed in applications of neuronal coding and decoding. The relation between the neuron models of Part II and biological data is highlighted and systematic parameter optimization algorithms are presented.

Part III takes the simplified models derived in Part II and builds networks out of these. The collective properties of the network dynamics are described in terms of equations for the population activity also called the population firing rate. The conditions under which population activity can be described by a standard rate model are identified.

Part IV makes the link from dynamics to cognition. The population activity equations are used for an analysis of famous paradigms of computational and cognitive neuroscience, such as the neural activity during decision making or memory retrieval. In Part IV we also sketch the theory of learning in relation to synaptic plasticity. The book closes with a fascinating application of the principles of neuronal dynamics to help patients suffering from Parkinson's disease.

A small fraction of the text of the present book is based on *Spiking Neuron Models* (Cambridge University Press) which was first published in 2002 and has been reprinted several times since then. In the meantime, the field has changed and we felt that a simple update of *Spiking Neuron Models* for a second edition would not be enough to give credit to the developments that have occurred.

Scientifically, the scope of *Spiking Neuron Models* was limited in several respects. First, it mainly focused on *linear* integrate-and-fire models, and mentioned their nonlinear counterparts only in passing. In the present book, nonlinear integrate-and-fire models are treated in a full chapter. Second, adaptation was neglected in the treatment 10 years ago – mainly because population equations for adaptive neurons were not yet available. In the present book, adaptive integrate-and-fire models are covered at length in a separate chapter and the population activity equations for adaptive neurons are derived. Third, while the Spike Response Model with escape noise has always contained all the features of a Generalized Linear Model (GLM), by the year 2002 the theory of GLMs had not yet found its way into the field of neuroscience and was therefore simply absent from the original book. Given the phenomenal rise of GLMs in neuroscience, the theory of GLMs for fitting neuronal data is given a prominent role in this book. Finally, during teaching we always felt the need to show famous applications of the principles of neuronal dynamics, such as retrieval of contents from associative memories or decision dynamics and the neuroscience of free will. The present book covers these topics.

On a more general level, we felt that it would be useful to have a book that is, from the beginning, designed as a textbook rather than a monograph. Therefore, the present book makes the link to experimental data more visible, has more explanatory text, and, last but not least, provides a series of exercises that have already been tested in the classroom over several years.

We hope that this book will be useful for students and researchers alike.

Wulfram Gerstner, Werner Kistler, Richard Naud, Liam Paninski

Advice to the reader

Each chapter starts with a specific question and gives first intuitive answers in the first section. As the chapter proceeds, the material gets more advanced, and the presentation becomes more technical. For a first reading of the book, it is possible to read only the first section, or first two sections, of each chapter and just glance at the subsequent sections.

More specific advice depends on the background. For example, readers who are new to the field of computational neuroscience are advised to spend enough time with the classic material of Part I, before they move on to Parts II and IV. The expert reader may skip Part I completely and start directly with Part II.

In Part III, the main ideas are exposed in Chapters 12 and 15, which present the foundations for the rate models in Part IV. The more technical chapters and sections of Part III can be skipped at a first reading, but are necessary for a thorough understanding of the current developments in the field of computational neuroscience.

Part IV contains applications of neuronal dynamics to questions of cognition and can be read in any arbitrary order.

Sections marked by an asterisk (∗) are mathematically more advanced and can be omitted during a first reading of the book.

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The writing of the text was a joint work of the four authors. Werner Kistler and Wulfram Gerstner were the authors of *Spiking Neuron Models* from which several sections survived. Liam Paninski was mainly involved in writing Chapters 9–11 of the present book and gave valuable input to other chapters of Part II. Richard Naud contributed to writing Chapters 1–11 and 14 with a leading role in some of these, made valuable comments and suggestions for all other chapters, and was responsible for all the figures. Wulfram Gerstner wrote the first drafts of Parts III and IV and contributed text to all other chapters.

Wulfram Gerstner, Werner Kistler, Richard Naud, Liam Paninski