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Mathematical Foundations of Neuroscience

 Springer

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Preface

One can say that the field of computational neuroscience started with the 1952 paper of Hodgkin and Huxley in which they describe, through nonlinear partial differential equations, the genesis of the action potential in the giant axon of the squid. These equations and the methods that arose from this combination of modeling and experiments have since formed the basis for nearly every subsequent model for active cells. The Hodgkin–Huxley model and a host of simplified equations that are derived from it have inspired the development of new and beautiful mathematics. Dynamical systems and computational methods are now being used to study activity patterns in a variety of neuronal systems. It is becoming increasingly recognized, by both experimentalists and theoreticians, that issues raised in neuroscience and the mathematical analysis of neuronal models provide unique interdisciplinary collaborative research and educational opportunities.

This book is motivated by a perceived need for an overview of how dynamical systems and computational analysis have been used in understanding the types of models that come out of neuroscience. Our hope is that this will help to stimulate an increasing number of collaborations between mathematicians and other theoreticians, looking for interesting and relevant problems in applied mathematics and dynamical systems, and neuroscientists, looking for new ways to think about the biological mechanisms underlying experimental data.

The book arose out of several courses that the authors have taught. One of these is a graduate course in computational neuroscience that has students from the disciplines of psychology, mathematics, computer science, physics, and neuroscience. Of course, teaching a course to students with such diverse backgrounds presents many challenges. However, the course provides many opportunities to encourage students, who may not normally interact with each other, to collaborate on exercises and projects. Throughout the book are many exercises that involve both computation and analysis. All of the exercises are motivated by issues that arise from the biology.

We have attempted to provide a comprehensive introduction to the vocabulary of neuroscience for mathematicians who are just becoming interested in the field, but who have struggled with the biological details. Anyone who wants to work in computational neuroscience should learn these details as this is the only way one can be sure that the analysis and modeling is actually saying something useful to

biologists. We highly recommend the reader study this material in more detail by consulting one of the many excellent books devoted primarily to neuroscience. Such books include those by Kandel et al. [144] and Johnston and Wu [139].

We have also tried to provide background material on dynamical systems theory, including phase plane methods, oscillations, singular perturbations, and bifurcation analysis. An excellent way to learn this material is by using it, together with computer simulations, to analyze interesting, concrete examples. The only prerequisites are a basic knowledge of calculus, knowledge of a little linear algebra (matrices, eigenvalues), and understanding of some basic theory of ordinary differential equations. Much of the mathematics is at the level of Strogatz [255].

The book is organized from the bottom up. The first part of the book is concerned with properties of a single neuron. We start with the biophysics of the cell membrane, add active ion channels, introduce cable theory, and then derive the Hodgkin–Huxley model. Chapter 2 is concerned with the basic properties of dendrites. We then introduce dynamical systems theory, using a simple neuron model to illustrate the basic concepts. We return to the biology in Chap. 4, where we discuss the variety of ion channels which have been found in neurons. Chapters 5 and 6 are devoted to bursting oscillations and propagating action potentials, respectively. Here, we use many of the dynamical systems techniques to describe mechanisms underlying these behaviors. The second part of the book is concerned with neuronal networks. In Chap. 7, we describe synaptic channels, which are the primary way that neurons communicate with each other. Chapters 8 and 9 discuss two different approaches for studying networks. First, we assume weak coupling and use phase-response methods. We then demonstrate how one can analyze firing patterns in neuronal networks using fast/slow analysis. In Chap. 10, we discuss the role of noise in neuron models. Here, we briefly introduce the reader to the mathematical theory of stochastic differential equations. Finally, in Chaps. 11 and 12 we discuss firing rate models and spatially distributed networks.

There is far more material in this book than could be covered in a one-semester course. Furthermore, some of the material is quite advanced. A course in computational neuroscience slanted toward mechanisms and dynamics could easily be made out of the first five chapters along with Chap. 7. These chapters would cover most of the basics of single-cell modeling as well as introduce students to dynamical systems. The remainder of such a course could include selections from Chaps. 8–12. For example, Chap. 11 contains firing rate models, with many applications provided in Sect. 11.3. Parts of Chap. 12 could comprise the remainder of the course.

For more mathematically inclined students, the elementary dynamics chapter (Chap. 3) could be skipped and the more technical chapters could be emphasized. There is lovely nonlinear dynamics in Chaps. 5, 6, 8, and 9, which along with the earlier chapters could form the core of a mathematical neuroscience course.

There are several recent books that cover some of the same material as in the present volume. *Theoretical Neuroscience* by Dayan and Abbott [53] has a broader range of topics than our book; however, it does not go very deeply into the mathematical analysis of neurons and networks, nor does it emphasize the dynamical systems approach. A much more similar book is *Dynamical Systems*

in Neuroscience by Izhikevich [136]. This book emphasizes the same approach as we take here; however, the main emphasis of *Dynamical Systems in Neuroscience* is on single-neuron behavior. We cover a good deal of single-neuron biophysics, but include a much larger proportion of theory on systems neuroscience and applications to networks. There are many specific models and equations in this text. The forms of these models and their parameters are available at <http://www.math.pitt.edu/~bard/bardware/neurobook/allodes.html>.

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– David H. Terman, The Ohio State University, 2009

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