The NEURON Book

CARNEVALE and HINES

The authoritative reference on NEURON, the simulation environment for modeling biological neurons and neural networks that enjoys wide use in the experimental and computational neuroscience communities. This book will show you how to use NEURON to construct and apply empirically based models. Written primarily for neuroscience investigators, teachers, and students, it assumes no previous knowledge of computer programming or numerical methods. Readers with a background in the physical sciences or mathematics, who have some knowledge about brain cells and circuits and are interested in computational modeling, will also find it helpful. The NEURON Book covers material that ranges from the inner workings of this program to practical considerations involved in specifying the anatomical and biophysical properties that are to be represented in models. It uses a problem-solving approach, with many working examples that readers can try for themselves.

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Michael L. Hines is a Research Scientist in the Department of Computer Science at Yale University. He created NEURON in collaboration with John W. Moore at Duke University, Durham NC, and is the principal investigator and chief software architect on the project that continues to support and extend it.

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It is some systematized exhibition of the whale in his broad genera, that
I would now fain put before you. Yet is it no easy task. The classification of the
constituents of a chaos, nothing less is here essayed.

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Preface

I promise nothing complete; because any human thing supposed to be complete, must for that very reason infallibly be faulty.

Who should read this book?

This book is about how to use the NEURON simulation environment to construct and apply empirically based models of neurons and neural networks. It is written primarily for neuroscience investigators, teachers, and students, but readers with a background in the physical sciences or mathematics who have some knowledge about brain cells and circuits and are interested in computational modeling will also find it helpful. The emphasis is on the most productive use of NEURON as a means for testing hypotheses that are founded on experimental observations, and for exploring ideas that may lead to the design of new experiments. Therefore the book uses a problem-solving approach, with many working examples that readers can try for themselves.

What this book is, and is not, about

Formulating a *conceptual model* is an attempt to capture the essential features that underlie some particular function. This necessarily involves simplification and abstraction of real-world complexities. Even so, one may not necessarily understand all implications of the conceptual model. To evaluate a conceptual model it is often necessary to devise a hypothesis or test in which the behavior of the model is compared against a prediction. *Computational models* are useful for performing such tests. The conceptual model and the hypothesis should determine what is included in a computational model and what is left out. This book is not about how to come up with conceptual models or hypotheses, but instead focuses on how to use NEURON to create and use computational models as a means for evaluating conceptual models.

What to read, and why?

Chapter 1 conveys a basic idea of NEURON's primary domain of application by guiding the reader through the construction and use of a model neuron. This exercise is based entirely on NEURON's graphical user interface (GUI), and requires no programming ability or prior experience with NEURON whatsoever.

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Chapter 2 considers the role of computational modeling in neuroscience research from a general perspective. Chapters 3 and 4 focus on aspects of applied mathematics and numerical methods that are particularly relevant to computational neuroscience. Chapter 5 discusses the concepts and strategies that are used in NEURON to simplify the task of representing neurons, which (at least at the level of synapses and cells) are distributed and continuous in space and time, in a digital computer, where neither time nor numeric values are continuous. Chapter 6 returns to the topic of model construction, emphasizing the use of programming.

Chapters 7 and 8 provide "inside information" about NEURON's standard run and initialization systems, so that readers can make best use of their features and customize them to meet special modeling needs. Chapter 9 shows how to use the NMODL programming language to add new biophysical mechanisms to NEURON. This theme continues in Chapter 10, which starts with mechanisms of communication between cells (gap junctions, graded and spike-triggered synaptic transmission), and moves on to models of artificial spiking neurons (e.g. integrate and fire cells). The first half of Chapter 11 is a tutorial on NEURON's GUI tools for creating simple network models, and the second half shows how to use the combined strength of the GUI and `hoc` programming to create more complex networks.

Chapter 12 discusses the elementary features of the `hoc` programming language itself. Chapter 13 describes the object-oriented extensions that have been added to `hoc`. These extensions have greatly facilitated construction of NEURON's GUI tools, and they can also be very helpful in many other complex programming tasks such as creating and managing network models. Chapter 14 presents an example of how to use object-oriented programming to increase the functionality of NEURON.

Appendix 1 presents a mathematical analysis of the IntFire4 artificial spiking cell mechanism, proving a result that is used to achieve computational efficiency. Appendix 2 summarizes the commands for NEURON's built-in text editor.

Typeface conventions

This book uses special typefaces to distinguish two different sets of keywords – code and GUI – from each other and from words with the same spelling that are not being used as keywords. Ordinary program code is printed with a `courier typeface`. Optional code, or items that are generic placeholders that the reader should substitute with his or her own specific entries, are indicated by *`slanted courier`* (not really italic, is it?). Samples of command-line usage employ **`bold courier`** to signify user input. GUI keywords, which are the labels that appear in NEURON's graphical interface, are presented with a sans-serif typeface.

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Acknowledgments

First and foremost, we want to thank our mentor and colleague John W. Moore for his vision, support, encouragement, and active participation in the development of NEURON, without which neither it nor this book would exist. Through his research and teaching, he was introducing students to "computational neuroscience" long before that glorious term was invented. NEURON had its beginnings in John's laboratory at Duke University almost three decades ago, when he and one of the authors (MLH) started their collaboration to develop simulation software for neuroscience research. Users of NEURON on the Macintosh owe John a particular debt. He continues to participate in the development and dissemination of NEURON, concentrating most recently on educational applications in collaboration with Ann Stuart (Moore and Stuart 2004).

The list of others who have added in one way or another to the development of NEURON is far too long for this short preface. Zach Mainen, Alain Destexhe, Bill Lytton, Terry Sejnowski, and Gordon Shepherd deserve special mention for many contributions, both direct and indirect, that range from specific enhancements to the program, to fostering the wider acceptance of computational approaches in general, and NEURON in particular, by the neuroscience community at large. We also thank the countless NEURON users whose questions and suggestions continue to help guide the evolution of this software and its documentation. The development of NEURON and this book has been made possible by support from the National Institutes of Health and the National Science Foundation. We are sure that our readers will recognize the epigrams from Herman Melville's *Moby Dick* that are scattered throughout this book, as well as the (mis)quotation from *The Treasure of the Sierra Madre* (book by B. Traven, screenplay by John Huston). We hope that everyone else will forgive any omission and remind us, gently, in time for the second edition.

Finally, we thank our wives and children for their encouragement and patience while we completed this book.

REFERENCE

Moore, J.W. and Stuart, A.E. *Neurons in Action: Computer Simulations with NeuroLab.* Sunderland, MA: Sinauer Associates, 2004.

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