Introduction to

Biological Signal Processing

and

Computational Neuroscience

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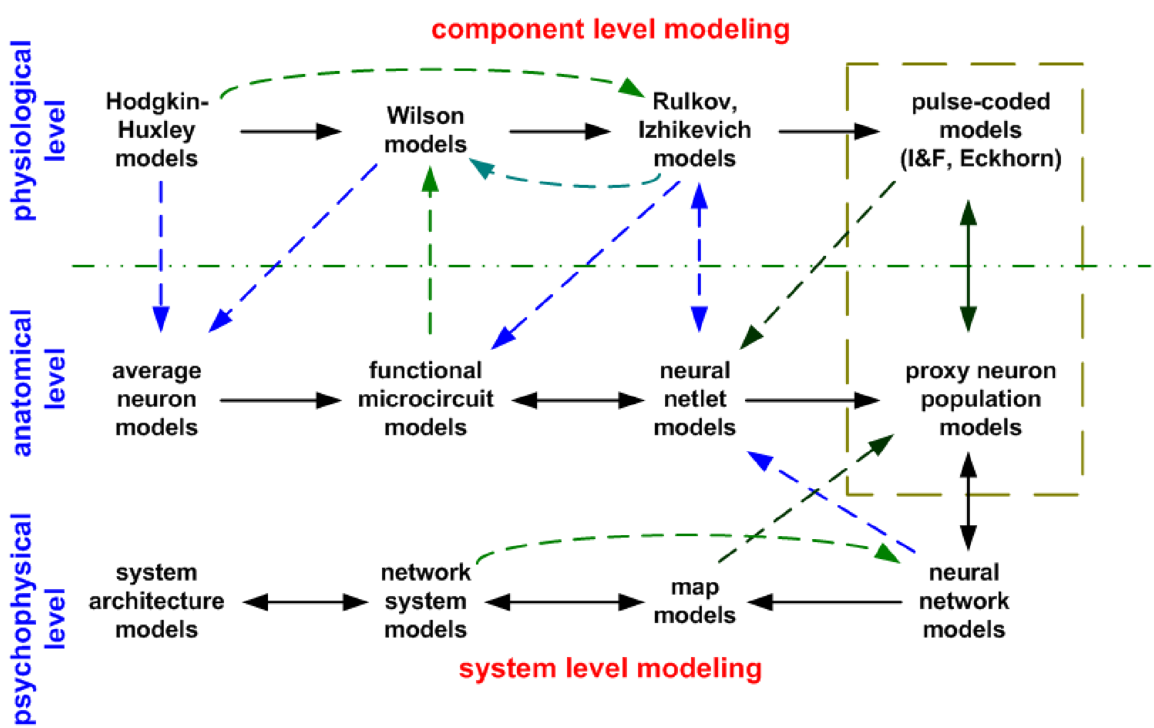

Preface

It is said by some that neuroscience is the science of the twenty-first century. This is a prediction with which the author of this textbook agrees. Neuroscience is a highly interdisciplinary science encompassing the biological, psychological, and mathematical dimensions involved in the study of the central nervous system. Additionally, it is a field that calls upon contributions from chemistry and biophysics. In a science with so many contributors from so many diverse specialty fields, it is crucial for students and researchers from the different disciplines to be able to communicate with one another and to understand at some basic level what colleagues from other disciplines do and what their findings imply globally for neuroscience. This book has been written with this in mind. It seeks to present to a broad audience the fundamentals of that mathematical wing of the science that has come to be called "computational neuroscience."

In manuscript form, this book has been used as the primary textbook for a first-year graduate level course in computational neuroscience and biological signal processing. The target audience in this course is made up of students coming from backgrounds in biology, psychology, mathematics, computer science, and engineering. From time to time, the course has even had students from philosophy and biochemistry in attendance. Typically these students are well-versed in their home disciplines but find themselves strangers in a strange land when the topics turn to arenas outside their home disciplines. This presents certain challenges for the instructor since the purpose of the course is to deliver to all of these students a non-trivial understanding of what it is that computational neuroscientists do, how they do it, and what their results mean within the broader context of neuroscience in general. The topics covered in the course and in this book are mathematical in character, and this book seeks to present these topics at a level as accessible to biologists as to mathematicians. For this reason, the book has been written in such a way that no more than a first-year course in basic calculus is required as a prerequisite. But the general topic also necessarily brings in elements of biology and psychology and these, too, must be made as accessible to the mathematician, physicist, computer scientist, and engineer as they are to the biologist and the psychologist. Thus, it discusses fundamental concepts and models that have emerged from biological neuroscience and psychological neuroscience without presupposing or requiring prior coursework in either field as a prerequisite for this material. The material presented here does presuppose some prior experience in computer programming at an introductory level but does not require knowledge of any one particular computer programming language. BASIC is as adequate a preparation for this material as any of the more advanced programming languages would be. Knowledge of MATLAB is ideal for this material.

Computational neuroscience is at root the art and science of modeling complex, nonlinear systems. The material presented here serves as a fundamental introduction to this topic. For almost all the author's students, the course is their first real exposure to nonlinear system theory, and for many of them it is their first exposure to system theory at any level. It is the nature of the modeling equations describing neuron and neural network models that these equations generally possess no known closed-form solution. The text is written in such a way as to turn this shortcoming into a virtue by focusing its attention on how to develop and set up model equations for computer solution. However, it does not presume any prior training in advanced numerical analysis methods. Instead, it uses the vehicle of the simple Euler approximation method, implicitly familiar to all freshman calculus students, to explain and develop the modeling techniques. The author's reasoning here is that of all the members of the target audience, only a fraction of the students will go on to actually specialize in computational neuroscience, and it can be presumed that these students will acquire more advanced training in numerical solution methods elsewhere in their studies.

The pedagogical form of the material contained in this book is modern system theory, sometimes known synonymously as state-variable theory. Computational neuroscience and biological signal processing is inherently suited to this form of mathematics, and this mathematical form lends itself quite well to setting up the modeling equations for subsequent computer solution. It has the additional advantage of not requiring more advanced methods in applied mathematics, a background well beyond the usual preparatory training received by biologists and psychologists. The book presumes no prior preparation in the theory of state variables. The necessary mathematics is introduced and developed *en route,* as it were, and always within the specific context of the modeling problems at hand.

This book is about *quantitative* modeling of biological and psychological phenomena. While the development of models is fundamental in all sciences, it is a peculiar aspect of higher education in America that modeling itself, as a topic, generally receives very little treatment within any of the usual disciplines. This lack of treatment oftentimes makes modeling look more like an art than a science. However, to be useful to science, a model maker must be conscious of *what* he or she is modeling and, more importantly, what the *limits* of the proposed model are, the *assumptions* that have gone into the model, and the *way* in which the model is and can be linked to the experimental data by which the predictions of the model will ultimately be tested. A corollary to the latter is the on-going requirement that a useful theoretical model *must* have predictive power and not merely serve as a glorified curve fit that simply parrots back what the experimentalist already knows. To accomplish this, the book contains as a core topic the subject of making the transition from experimental facts won in the laboratory to the precise, quantitative implications of these facts for theoretical neuroscience. Toward that end, the book discusses such topics as "what is a model?" and "how may model *systems* be linked one to another along the successive levels of scientific reduction leading from psychology to biology in pursuit of our understanding of the brain?"

The scope of neuroscience is vast. It runs the spectrum from behaviors observable by psychologists all the way down to the molecules studied by biologists and biochemists. In the opinion of the author, the final goal of neuroscience is to understand the central nervous system from one end of this spectrum to the other, and this cannot be said to be accomplished until our theories at all levels can be linked up and down across what he likes to call "the ladder of scientific reduction and model order reduction." If a particular scientific discipline is viewed as one rung on the ladder of scientific reduction, it is not enough that we eventually develop only a system of different rungs. The ladder must have rails as well, else the knowledge won by one discipline can only float disconnected from the knowledge won by another discipline. In the author's view, the science of "constructing the rungs" is the real central mission of computational neuroscience.

As one rises up from the level of molecules and cells toward the level of psychological phenomena, it is crucial that we have and develop methods for addressing the catastrophic increase in the cost of computing our models that otherwise takes place. The gulf of abstraction between cell-level modeling and neural network modeling is vast. Models that are perfectly adequate for describing the membrane response of a neuron are hopelessly inadequate, computationally, for describing brain or spinal cord function (much less for describing the neurological implications of behavior). A central theme recurring throughout this book is the theme of what is required of a modeler for producing a unified science of the brain and mind. To the author's best knowledge, this is a subject generally left out of today's existing textbooks on theoretical and computational neuroscience.

The book is laid out to progress from the level of basic neuron modeling all the way up to the modeling of complex neural network systems. It spans the science from the basic membrane and Hodgkin-Huxley models on the biological end of the spectrum and progresses all the way to adaptive resonance theory on the side of modeling complex central systems. Part I of this book (chapters 2 through 6) will be of primary interest to the student of biological neuroscience. Part II of this book (chapters 8 and 9, 11 through 18) will be of primary interest to neural network theorists and psychologists. Chapter 7 of this book is a transition chapter, the point where the focus passes smoothly from the modeling of biological function to the modeling of psychological function. Chapter 10 is a chapter likely to be of primary interest to the mathematician; it discusses an intriguing hypothesis, suggested by findings coming out of developmental psychology, regarding the possibility that neurological structure may be linked at a fundamental level to the most fundamental structures found in pure mathematics. The material in chapter 10 is, of course, very speculative. However, it does present a new way of possibly exploring the long-standing problem in theoretical neuroscience known as "the problem of the neural code."

Neuroscience generally, and theoretical neuroscience in particular, finds itself these days calling more and more upon considerations that only a few years ago were confined to the hallways of philosophy departments. Indeed, one very encouraging development that has occurred over the past two decades has been the more active role being played by philosophers in neuroscience. While this textbook is not a philosophy book, chapters 7, 10, part of 12, and 13 include topics of a somewhat philosophical flavor as these considerations are of direct significance to neuroscience.

This book also presents for the first time to a wide audience a new modeling schema, developed in the author's laboratory, for linking the modeling of biochemical processes to the traditional Hodgkin-Huxley-like models of the neuron. This new modeling schema, named the Linvill model, provides a new approach for tying the actions of metabotropic processes and metabotropic signal processing to end effects registered at the cell level in neurons and glia.

The book contains numerous exercises. The student is encourage to do these exercises to gain practice at the mechanics of constructing computer models. In the author's course, students are also required to undertake a semester-long term project modeling some biological or psychological neural system. The exercises will provide valuable experience in carrying out the term project research project.

Finally, the author strongly believes that neuroscience and the engineering field of artificial neural network research each have much to gain from the other. It has long been a claim by artificial neural network theorists working on various engineering applications that their artificial systems are "inspired by biology." Brain science can and, indeed, should contribute to these engineering endeavors. At the same time, he also believes that discoveries made by engineering researchers hold great potential to repay the favor, particularly on the side of large-scale brain systems, provided the artificial neural network theorists aspire to take more than merely "inspiration" from neuroscience. There are opportunities for wider-ranging interdisciplinary collaborations, and this book does not hesitate to point some of these out along the way.

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