

Contents

Series Foreword xiii

Acknowledgments xv

Preface xvii

1 Preliminary Material 1

1.1 Introduction 1

1.1.1 The Cell, the Circuit, and the Brain 1

1.1.2 Physics of Electrical Circuits 1

1.1.3 Mathematical Preliminaries 2

1.1.4 Writing Computer Code 4

1.2 The Neuron, the Circuit, and the Brain 4

1.2.1 The Cellular Level 4

1.2.2 The Circuit Level 7

1.2.3 The Regional Level 8

1.3 Physics of Electrical Circuits 11

1.3.1 Terms and Properties 11

1.3.2 Pumps, Reservoirs, and Pipes 12

1.3.3 Some Peculiarities of the Electrical Properties of Neurons 13

1.4 Mathematical Background 14

1.4.1 Ordinary Differential Equations 15

1.4.2 Vectors, Matrices, and Their Basic Operations 24

1.4.3 Probability and Bayes' Theorem 28

1.5 Introduction to Computing and MATLAB 36

1.5.1 Basic Commands 37

1.5.2 Arrays 38

1.5.3 Allocation of Memory 40

1.5.4 Using the Colon (:) Symbol 41

1.5.5 Saving Your Work 42

1.5.6 Plotting Graphs 42

1.5.7	Vector and Matrix Operations in MATLAB	43
1.5.8	Conditionals	44
1.5.9	Loops	46
1.5.10	Functions	47
1.5.11	Some Operations Useful for Modeling Neurons	48
1.5.12	Good Coding Practice	49
1.6	Solving Ordinary Differential Equations (ODEs)	51
1.6.1	Forward Euler Method	51
1.6.2	Simulating ODEs with MATLAB	52
1.6.3	Solving Coupled ODEs with Multiple Variables	54
1.6.4	Solving ODEs with Nested <code>for</code> Loops	55
1.6.5	Comparing Simulation Methods	55
1.6.6	Euler-Mayamara Method: Forward Euler with White Noise	56
2	The Neuron and Minimal Spiking Models	59
2.1	The Nernst Equilibrium Potential	59
2.2	An Equivalent Circuit Model of the Neural Membrane	62
2.2.1	Depolarization versus Hyperpolarization	65
2.3	The Leaky Integrate-and-Fire Model	66
2.3.1	Specific versus Absolute Properties of the Cell	68
2.3.2	Firing Rate as a Function of Current (<i>f-I</i> Curve) of the Leaky Integrate-and-Fire Model	69
2.4	Tutorial 2.1: The <i>f-I</i> Curve of the Leaky Integrate-and-Fire Neuron	70
2.5	Extensions of the Leaky Integrate-and-Fire Model	72
2.5.1	Refractory Period	72
2.5.2	Spike-Rate Adaptation (SRA)	74
2.6	Tutorial 2.2: Modeling the Refractory Period	76
2.7	Further Extensions of the Leaky Integrate-and-Fire Model	78
2.7.1	Exponential Leaky Integrate-and-Fire (ELIF) Model	78
2.7.2	Two-Variable Models: The Adaptive Exponential Leaky Integrate-and-Fire (AELIF) Neuron	79
2.7.3	Limitations of the LIF Formalism	81
2.8	Tutorial 2.3: Models Based on Extensions of the LIF Neuron	81
2.9	Appendix: Calculation of the Nernst Potential	86
3	Analysis of Individual Spike Trains	89
3.1	Responses of Single Neurons	89
3.1.1	Receptive Fields	89
3.1.2	Time-Varying Responses and the Peristimulus Time Histogram (PSTH)	92
3.1.3	Neurons as Linear Filters and the Linear-Nonlinear Model	93

3.1.4	Spike-Triggered Average	96
3.1.5	White-Noise Stimuli for Receptive Field Generation	96
3.1.6	Spatiotemporal Receptive Fields	98
3.2	Tutorial 3.1: Generating Receptive Fields with Spike-Triggered Averages	100
3.3	Spike-Train Statistics	104
3.3.1	Coefficient of Variation (CV) of Interspike Intervals	105
3.3.2	Fano Factor	107
3.3.3	The Homogeneous Poisson Process: A Random Point Process for Artificial Spike Trains	108
3.3.4	Comments on Analyses and Use of Dummy Data	109
3.4	Tutorial 3.2: Statistical Properties of Simulated Spike Trains	110
3.5	Receiver-Operating Characteristic (ROC)	113
3.5.1	Producing the ROC Curve	113
3.5.2	Optimal Position of the Threshold	115
3.5.3	Uncovering the Underlying Distributions from Binary Responses: Recollection versus Familiarity	118
3.6	Tutorial 3.3: Receiver-Operating Characteristic of a Noisy Neuron	121
3.7	Appendix A: The Poisson Process	123
3.7.1	The Poisson Distribution	123
3.7.2	Expected Value of the Mean of a Poisson Process	125
3.7.3	Fano Factor of the Poisson Process	125
3.7.4	The Coefficient of Variation (CV) of the ISI Distribution of a Poisson Process	126
3.7.5	Selecting from a Probability Distribution: Generating ISIs for the Poisson Process	127
3.8	Appendix B: Stimulus Discriminability	128
3.8.1	Optimal Value of Threshold	129
3.8.2	Calculating the Probability of an Error	130
3.8.3	Generating a Z-Score from a Probability	130
4	Conductance-Based Models	133
4.1	Introduction to the Hodgkin-Huxley Model	133
4.1.1	Positive versus Negative Feedback	134
4.1.2	Voltage Clamp versus Current Clamp	136
4.2	Simulation of the Hodgkin-Huxley Model	137
4.2.1	Two-State Systems	138
4.2.2	Full Set of Dynamical Equations for the Hodgkin-Huxley Model	139
4.2.3	Dynamical Behavior of the Hodgkin-Huxley Model: A Type-II Neuron	140
4.3	Tutorial 4.1: The Hodgkin-Huxley Model as an Oscillator	147
4.4	The Connor-Stevens Model: A Type-I Model	150

4.5	Calcium Currents and Bursting	154
4.5.1	Thalamic Rebound and the T-Type Calcium Channel	155
4.6	Tutorial 4.2: Postinhibitory Rebound	156
4.7	Modeling Multiple Compartments	159
4.7.1	The Pinsky-Rinzel Model of an Intrinsic Burster	160
4.7.2	Simulating the Pinsky-Rinzel Model	160
4.7.3	A Note on Multicompartmental Modeling with Specific Conductances versus Absolute Conductances	163
4.7.4	Model Complexity	166
4.8	Hyperpolarization-Activated Currents (I_h) and Pacemaker Control	166
4.9	Dendritic Computation	168
4.10	Tutorial 4.3: A Two-Compartment Model of an Intrinsically Bursting Neuron	170
5	Connections between Neurons	173
5.1	The Synapse	173
5.1.1	Electrical Synapses	173
5.1.2	Chemical Synapses	174
5.2	Modeling Synaptic Transmission through Chemical Synapses	179
5.2.1	Spike-Induced Transmission	179
5.2.2	Graded Release	181
5.3	Dynamical Synapses	182
5.3.1	Short-Term Synaptic Depression	183
5.3.2	Short-Term Synaptic Facilitation	183
5.3.3	Modeling Dynamical Synapses	184
5.4	Tutorial 5.1: Synaptic Responses to Changes in Inputs	185
5.5	The Connectivity Matrix	187
5.5.1	General Types of Connectivity Matrices	189
5.5.2	Cortical Connections: Sparseness and Structure	190
5.5.3	Motifs	191
5.6	Tutorial 5.2: Detecting Circuit Structure and Nonrandom Features within a Connectivity Matrix	193
5.7	Oscillations and Multistability in Small Circuits	196
5.8	Central Pattern Generators	197
5.8.1	The Half-Center Oscillator	199
5.8.2	The Triphasic Rhythm	199
5.8.3	Phase Response Curves	200
5.9	Tutorial 5.3: Bistability and Oscillations from Two LIF Neurons	203
5.10	Appendix: Synaptic Input Produced by a Poisson Process	205
5.10.1	Synaptic Saturation	205
5.10.2	Synaptic Depression	208

- 5.10.3 Synaptic Facilitation 209
- 5.10.4 Notes on Combining Mechanisms 209

6 Firing-Rate Models and Network Dynamics 211

- 6.1 Firing-Rate Models 211
- 6.2 Simulating a Firing-Rate Model 213
 - 6.2.1 Meaning of a Unit and Dale's Principle 216
- 6.3 Recurrent Feedback and Bistability 217
 - 6.3.1 Bistability from Positive Feedback 217
 - 6.3.2 Limiting the Maximum Firing Rate Reached 221
 - 6.3.3 Dynamics of Synaptic Response 222
 - 6.3.4 Dynamics of Synaptic Depression and Facilitation 223
 - 6.3.5 Integration and Parametric Memory 225
- 6.4 Tutorial 6.1: Bistability and Oscillations in a Firing-Rate Model with Feedback 227
- 6.5 Decision-Making Circuits 229
 - 6.5.1 Decisions by Integration of Evidence 232
 - 6.5.2 Decision-Making Performance 233
 - 6.5.3 Decisions as State Transitions 235
 - 6.5.4 Biasing Decisions 235
- 6.6 Tutorial 6.2: Dynamics of a Decision-Making Circuit in Two Modes of Operation 236
- 6.7 Oscillations from Excitatory and Inhibitory Feedback 238
- 6.8 Tutorial 6.3: Frequency of an Excitatory-Inhibitory Coupled Unit Oscillator and PING 242
- 6.9 Orientation Selectivity and Contrast Invariance 245
 - 6.9.1 Ring Models 246
- 6.10 Ring Attractors for Spatial Memory and Head Direction 250
 - 6.10.1 Dynamics of the Ring Attractor 252
- 6.11 Tutorial 6.4: Orientation Selectivity in a Ring Model 254

7 An Introduction to Dynamical Systems 257

- 7.1 What Is a Dynamical System? 257
- 7.2 Single Variable Behavior and Fixed Points 258
 - 7.2.1 Bifurcations 258
 - 7.2.2 Requirement for Oscillations 260
- 7.3 Models with Two Variables 261
 - 7.3.1 Nullclines and Phase-Plane Analysis 262
 - 7.3.2 The Inhibition-Stabilized Network 264
 - 7.3.3 How Inhibitory Feedback to Inhibitory Neurons Impacts Stability of States 267
- 7.4 Tutorial 7.1: The Inhibition-Stabilized Circuit 267

7.5	Attractor State Itinerancy	269
7.5.1	Bistable Percepts	269
7.5.2	Noise-Driven Transitions in a Bistable System	270
7.6	Quasistability and Relaxation Oscillators: The FitzHugh-Nagumo Model	271
7.7	Heteroclinic Sequences	275
7.8	Chaos	275
7.8.1	Chaotic Systems and Lack of Predictability	277
7.8.2	Examples of Chaotic Neural Circuits	279
7.9	Criticality	282
7.9.1	Power-Law Distributions	283
7.9.2	Requirements for Criticality	284
7.9.3	A Simplified Avalanche Model with a Subset of the Features of Criticality	287
7.10	Tutorial 7.2: Diverse Dynamical Systems from Similar Circuit Architectures	288
7.11	Appendix: Proof of the Scaling Relationship for Avalanche Sizes	290
8	Learning and Synaptic Plasticity	293
8.1	Hebbian Plasticity	293
8.1.1	Modeling Hebbian Plasticity	296
8.2	Tutorial 8.1: Pattern Completion and Pattern Separation via Hebbian Learning	297
8.3	Spike-Timing Dependent Plasticity (STDP)	300
8.3.1	Model of STDP	302
8.3.2	Synaptic Competition via STDP	304
8.3.3	Sequence Learning via STDP	305
8.3.4	Triplet STDP	305
8.3.5	A Note on Spike-Timing Dependent Plasticity	308
8.3.6	Mechanisms of Spike-Timing Dependent Synaptic Plasticity	309
8.4	More Detailed Empirical Models of Synaptic Plasticity	309
8.5	Tutorial 8.2: Competition via STDP	311
8.6	Homeostasis	313
8.6.1	Firing-Rate Homeostasis	314
8.6.2	Homeostasis of Synaptic Inputs	316
8.6.3	Homeostasis of Intrinsic Properties	317
8.7	Supervised Learning	319
8.7.1	Conditioning	321
8.7.2	Reward Prediction Errors and Reinforcement Learning	322
8.7.3	The Weather-Prediction Task	324
8.7.4	Calculations Required in the Weather-Prediction Task	325
8.8	Tutorial 8.3: Learning the Weather-Prediction Task in a Neural Circuit	326
8.9	Eyeblink Conditioning	329
8.10	Tutorial 8.4: A Model of Eyeblink Conditioning	331

8.11	Appendix A: Rate-Dependent Plasticity via STDP between Uncorrelated Poisson Spike Trains	335
8.12	Appendix B: Rate-Dependence of Triplet STDP between Uncorrelated Poisson Spike Trains	336
9	Analysis of Population Data	339
9.1	Principal Component Analysis (PCA)	340
9.1.1	PCA for Sorting of Spikes	341
9.1.2	PCA for Analysis of Firing Rates	342
9.1.3	PCA in Practice	342
9.1.4	The Procedure of PCA	345
9.2	Tutorial 9.1: Principal Component Analysis of Firing-Rate Trajectories	346
9.3	Single-Trial versus Trial-Averaged Analyses	348
9.4	Change-Point Detection	349
9.4.1	Computational Note	351
9.5	Hidden Markov Modeling (HMM)	351
9.6	Tutorial 9.2: Change-Point Detection for a Poisson Process	355
9.7	Decoding Position from Multiple Place Fields	357
9.8	Appendix A: How PCA Works: Choosing a Direction to Maximize the Variance of the Projected Data	362
9.8.1	Carrying out PCA without a Built-in Function	364
9.9	Appendix B: Determining the Probability of Change Points for a Poisson Process	366
9.9.1	Optimal Rate	366
9.9.2	Evaluating the Change Point, Method 1	367
9.9.3	Evaluating the Change Point, Method 2	367
	References	369
	Index	381