

ELECTRICAL DYNAMICS OF THE DENDRITIC SPACE

The authors explain how the whole dendritic arborization contributes to the generation of various output discharges and elucidate the mechanisms of the transfer function of all dendritic sites. Their alternative approach to conventional models introduces the notion of a functional dendritic space, and they have concentrated on a detailed spatial description of the electrical states at all dendritic sites when the dendrites operate. By analyzing the electrical dendritic space in which all the signals are processed, the authors provide tools to explore the spatial dimension of the transient events well known by electrophysiologists. They demonstrate the mechanisms by which the operating dendrites decide how, *in fine*, the distributed synaptic inputs generate various final output discharges. Their approach reveals the mechanisms by which individual dendritic geometry determines the sequence of action potentials that is the neuronal code. An accompanying NeuronViewer allows readers to monitor the simulation of operating dendritic arborization.

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Contents

<i>Preface</i>	<i>page ix</i>
1 Definition of the neuron	1
1.1 The biologist	1
1.2 The physicist	8
1.3 The physicist and the biologist	9
References	10
2 3D geometry of dendritic arborizations	13
2.1 Brief historical background	13
2.2 Single neuron labelling	15
2.3 Dendritic quantification	17
2.4 Data quality and morphological noise	22
2.5 Models of neurons	25
References	31
3 Basics in bioelectricity	37
3.1 Ions as carriers of current	37
3.2 Selective ion permeability of neuronal membrane	38
3.3 Ion pumps	39
3.4 Ion channels	40
3.5 Voltage dependence of membrane conductance	41
3.6 Effective equilibrium potential of multicomponent ion current	41
3.7 Membrane capacitance and capacitive current	42
3.8 External sources	43
3.9 Local current–voltage (I – V) relations	43
Reference	46
4 Cable theory and dendrites	47
4.1 Dendrites as electrical cables	47
4.2 The cable equation	49
4.3 Additional conditions required for solution	53

vi	<i>Contents</i>	
	4.4 Input–output (point-to-point) relations in dendritic cables	56
	References	57
5	Voltage transfer over dendrites	59
	5.1 Dendritic cables in the steady state	59
	5.2 Voltage transients in dendritic cables	62
6	Current transfer over dendrites	65
	6.1 Charge transfer ratio	65
	6.2 Somatopetal current transfer and somatofugal voltage spread	66
	6.3 Current transfer ratio for passive paths at different boundary conditions	71
	6.4 Local electro-geometrical coupling in non-uniform paths	72
	6.5 Current transfer from distributed dendritic sources	75
	References	76
7	Electrical structure of an artificial dendritic path	77
	7.1 Electrical structure of passive paths with single-site inputs	79
	7.2 Electrical structure of paths with distributed tonic inputs	81
	References	94
8	Electrical structure of a bifurcation	95
	8.1 Theory for different configurations	95
	8.2 Electrical structure of passive branching paths with single-site inputs	100
	8.3 Electrical structure of a bifurcation receiving distributed tonic inputs	102
	8.4 Recapitulation and conclusions	111
	References	112
9	Geography of the dendritic space	113
	9.1 Dendritic arborization in 3D and 2D representations	114
	9.2 Distinct 3D dendritic landscapes	118
	9.3 Digitized dendritic arborizations	121
	References	125
10	Electrical structures of biological dendrites	127
	10.1 Geometry of an example dendrite	127
	10.2 Passive dendrite with single-site inputs	129
	10.3 Dendrites with distributed inputs	130
	10.4 Reconfigurations of passive electrical structures	136
	References	139
11	Electrical structure of the whole arborization	141
	11.1 Organization of the spatial electrical profiles	141
	11.2 Robustness of the electrical bundles	150
	11.3 Dynamic reconfigurations of the whole electrical structure	152

<i>Contents</i>		vii
11.4	Spatial aspects of reconfigured electrical structure	156
11.5	Complexity of the whole arborization and its electrical domains	159
	References	160
12	Electrical structures in 3D dendritic space	161
12.1	The 3D electrical structures of Purkinje neurons	162
12.2	The 3D electrical structure of pyramidal neurons	164
12.3	The 3D electrical structures of motoneurons	164
12.4	High-efficiency domain of the motoneuronal arborizations in 3D	166
12.5	Bistable dendritic field	168
	References	171
13	Dendritic space as a coder of the temporal output patterns	173
13.1	Terminology to describe the repertoire of neuronal discharges	173
13.2	Geometry-induced features of Purkinje cell discharges	174
13.3	Geometry-dependent repertoire of pyramidal cell activity	189
13.4	Some general rules	193
	References	194
14	Concluding remarks	197
14.1	Impact for interpretation of neuronal discharges	199
14.2	The dancing dendrites	200
14.3	Speculation for the future	200
	References	202
	<i>Index</i>	205
	<i>Colour plate section is between pages 116–17.</i>	

Preface

Dear Reader,

We invite you to travel in space with us! This will be a very peculiar space: the dendritic space of neurons that is *the cosmos for neuroscientists*. It is mysterious and practically unexplored like the outer space we glimpse at in the sky. Curiously, we can further extend this analogy: the tools of astronomy can be turned from the sky to the microscope stage to explore shining brain stars, the neurons radiating their dendrites into the surrounding space. This was performed in the pioneering work by Paul Gogan and co-workers using a modified astronomical camera to image the microstructure of the dendritic membrane during the excitation of single live neurons in culture (see references in Chapter 14). The explorers of the dendritic space still have to invent the appropriate spacecrafts and technologies. As in cosmology, experimentation is limited, and mathematical and computer models are the only way of gaining insight into the nature of the dendritic space. The itinerary of our travel relies on these tools.

We start with a brief historical background to the dendritic problem and describe the origin of the structural data used for further morphometric and computer simulation studies of the dendritic arborizations (Chapters 1 and 2). Chapter 3 describes basic bioelectricity with emphasis on space. We show how charge carriers are separated in space and thus electric fields and currents are created across the neuronal membrane. An important generalization is that, despite multiplicity and diversity of channel types, the number of different types of current–voltage relations is restricted to three. Chapter 4 recapitulates the cable theory of the dendritic transfer properties with special focus on the terms of the cable equation which determine the electrical communication across the membrane and along the dendritic membrane. This issue is further developed in Chapters 5 and 6, specifying the voltage and current transfer along the dendrites. We highlight that the transfer maps provide an informative representation of the dendritic electrical structure. Chapters 7 and 8 explain how the electrical structures of an artificial dendritic path and of a branch bifurcation

are built and how they indicate electrical relations in different dimensions of the dendritic space that are the proximal-to-distal and the path-to-path relations. Next the critical role of metrical asymmetry of the dendritic branches becomes obvious. Chapter 9 navigates in the dendritic space of biological neurons and introduces our library of reconstructed cells providing specific examples of metrical asymmetry of complex dendritic arborizations. Chapter 10 explores the electrical structures of single biological dendrites as the basic elements for constructing the whole arborization. Here electrical features related to elementary structural heterogeneities present in random combinations in the biological dendrites are noticeable. The electrical structures of the whole reconstructed dendritic arborizations of different types of neurons are analyzed and classified in Chapters 11 and 12. Relations of the electrical structures related to size, complexity and asymmetry of the arborizations are explored. Finally, Chapter 13 considers the consequences of morphological and electrical structures of the dendritic arborizations for the generation of output discharge patterns. These spatial–temporal patterns indicate some new emerging rules by which the dendrites govern the whole cell activity.

This book results from more than 15 years of cooperation between French and Ukrainian laboratories: the Unit of Cellular Neurocybernetics of the CNRS in Marseille and the Laboratory of Biophysics and Bioelectronics, Dnipropetrovsk National University and Dnipropetrovsk Division of the International Center for Molecular Physiology, National Academy of Sciences of the Ukraine. It originated in the form of seminars, lectures, published papers and notes for students. We have benefited from innumerable discussions with students and colleagues. To acknowledge all of them personally is impossible but we wish to thank first our collaborators who have co-authored our published articles and who were directly involved in various aspects of our work at different periods between 1993 and 2007. This book would have never happened without them.

In the French team, we are specially grateful to Dr. Cesira Batini and Dr. Ginette Bossavit. We should like to pay tribute to Paul Gogan who initiated the quantification of dendritic geometry. His vision was far in advance of the impact of computer science in biology. He had foreseen what could be done by introducing high computational technology in our neurobiological laboratory. His knowledge of electrophysiology, his wide scientific background and his generous participation in our work make him an essential person to thank. We would also like to thank the technicians, secretaries, programmers and photographers of our laboratories for their generous assistance and invaluable help.

In the Ukrainian team, Yuri Ivanov, Irina Kopysova and Vladimir Sarana valuably participated at earlier stages of our joint work on the dendritic processing. We especially acknowledge the contribution of Dr. Iryna Kulagina, who is the co-author of most of the results presented in this book, some of which have already

Preface

xi

been published, as well as unpublished data in Chapter 13. Her thorough and creative work provided novel dynamic electrical maps of the dendritic space which look sunny and bear clear landmarks of the determinative role of geometry in spatial–temporal electrical phenomena in the dendrites. We appreciate the creative contribution by Valery Kukushka who developed the NeuronViewer, a tool for interactively displaying spatial–temporal dendritic activity described in Chapter 13. NeuronViewer is available at Cambridge University Press site (URL . . .). Scientific cooperation between our teams was efficiently supported by the French Embassy in Ukraine and we are deeply grateful for that.

We want to thank our friends and colleagues Dr. Elska Jankowska, Dr. John Lagnado, Dr. Bob Liberman, Dr. Hans Lüscher and Dr. Gerta Vrbova for reading some parts of the manuscript and for their comments, criticisms and encouragement.

Finally and importantly, we regret that we can only provide an incomplete picture of dendritic spatial processing, but we are happy to open this space for younger generations of researchers.