

Computational Maps in the Visual Cortex

Risto Miikkulainen
James A. Bednar
Yoonsuck Choe
Joseph Sirosh

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Risto Miikkulainen
Department of Computer Sciences
and Institute for Neuroscience
The University of Texas at Austin
Austin, TX 78712-0233
USA
<http://www.cs.utexas.edu/users/risto>

James A. Bednar
School of Informatics
The University of Edinburgh
5 Forrest Hill
Edinburgh, EH1 2QL UK
<http://homepages.inf.ed.ac.uk/jbednar>

Yoonsuck Choe
Department of Computer Science
Texas A&M University
College Station, TX 77843-3112
USA
<http://faculty.cs.tamu.edu/choe>

Joseph Sirosh
Fair, Isaac & Company, Inc.
San Diego, CA 92129
USA
<http://nn.cs.utexas.edu/keyword?sirosh>

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To our families

Foreword

Biological structures can be seen as collections of special devices coordinated by a matrix of organization. Devices are difficult to evolve and are meticulously conserved through the eons. Organization is a fluid medium capable of rapid adaptation. The brain carries organizational fluidity to the extreme. In its context, typical devices are ion channels, transmitters and receptors, signaling pathways, whole individual neurons or specific circuit patterns. The border line between what is to be called device and what a feat of organization is flowing, given that in time organized sub-systems solidify into devices. In spite of the neurosciences' traditional concentration on devices, their aiming point on the horizon must be to understand the principles by which the nervous system ties vast arrays of internal and external variables into one coherent purposeful functional whole — to understand the brain's mechanism of organization.

For that purpose a crucial methodology is *in silico* experimentation. Computer simulation is a convenient tool for testing functional ideas, a sharp weapon for distinguishing those that work from those that don't. To be sure, many alternatives can only be decided by direct experiment on the substrate, not by modeling. However, if a functional idea can be debunked as flawed once tried *in silico* it would be a waste to make it the subject of a decade of experimentation or discussion.

The venture of understanding the function and organization of the visual system illustrates this danger. Without much exaggeration it can be said that none of the academically formulated functional ideas could be shown to work on just any visual input. There is at present growing awareness that that is not due to lack of ingenuity but rather to a matter of principle: given the tremendous variability of the visual environment, no simple, intellectually coherent device can work in all situations. Object contours cannot be found solely by local contrast detection, the obvious direct mechanism, but only by coordination with other subsystems. The ambiguity plaguing the subsystems individually can be reduced only by global coordination between them. Thus, without understanding the phenomenon of organization we will not understand vision.

There is an even stronger reason to study organization. When trying to model brain function *in silico*, we have the tendency to first understand and solve the spe-

cific problem at hand in our own head and then create specific circuits and devices accordingly. This approach has long dominated the venture of artificial intelligence, and certainly also the field of computer vision. However, what may in the brain act like a fixed device may be an artifact of standardized experimental conditions and may in reality be the result of spontaneous organization. The devices (algorithms) in our computers are created by a separate process, in the mind of programmers. For the brain, there is no independent programmer (and evolution should not lightly be invoked as such). For the brain, there is no clear-cut separation between generation and execution of “algorithms.” The interdigitated processes of evolution, ontogenesis, learning, brain state organization and, in the case of man at least, culture and education, are autonomously organizing the brain’s functionality. The work of science will only have been done once we understand the principles of organization that not only coordinate subsystems but also create them. Only these principles are fixed, what they produce may to a large extent be due to accidents and circumstances.

This book is highly relevant to the goal of understanding organization. It summarizes and integrates an important body of work, accumulated over decades, aimed at describing and understanding the organization of the vertebrate visual system. Maps and columnar structures are a dominant theme of cortical organization. Due to an important wealth of experimental work on the substrate and in silico the mechanisms by which these structures are organized seem now before our eyes. The riddle of how less than 10^9 bits of genetic information are able to determine the arrangement of 10^{14} synaptic connections in ontogenesis is resolved by the demonstration that a relatively simple, genetically determined and controlled repertoire of cellular behavior is sufficient to understand the ontogenesis of regular connection patterns. The fundamental motivation behind hundreds of experimental studies of the ontogenesis of retinotopic connection patterns and also a sizable part of the work on cortical maps (on which this book concentrates) is the hope to elucidate the general mechanisms behind the development of the brain’s wiring patterns. This work has led to very clear-cut conclusions painting a convincing and coherent picture. There is a regrettable reluctance of neurobiology to broadcast such conclusions as the message of fundamental importance that they constitute, so that there is a mission still to be accomplished here. This book is an important step in that direction. It employs the tool of computer simulation to show the validity of the principles that have emerged, to teach them, to develop them further and prepare them for application to novel cases.

Physics has found an ultimate receptacle and means of transmission of its results, in the form of mathematical descriptions and paradigmatic experiments. In distinction, biology still has to find the mode of knowledge formulation with which to capture the essence of the tremendous wealth of detailed results it has produced and is producing at a prodigious rate, a mode of formulation that makes it possible to close chapters and transmit conclusions to next generations of biologists. Theoretical biology is routinely applying mathematics to what I am calling here devices, but these individual mathematical formulations do not add up to a coherent canon, are rather as disparate as the devices to which they apply. There is, however, definite hope that a mathematical framework can be found for the phenomenon of organization. It has often been remarked that physics is deliberately studying the simple and that biol-

ogy by force is concerned with the complex. But then, what is irreducibly complex? Seen under the right perspective even complex matters may come under the sway of relatively simple conceptual frameworks. Where this is not possible there can be no science and art must reign. No doubt, there are domains of irreducible complexity, but I doubt that the mechanisms of organization form one. Meticulous study of paradigmatic cases is necessary to penetrate that domain, and the study of vision at the cortical level, the focus of a tremendous body of scientific work, is sure to play a central role here.

The eternal discussion of nature vs. nurture, of prenatal vs. postnatal organization, has taken a very interesting turn in the context of cortical map formation. As will be discussed in these pages, neither side can possibly win. The methods that life has chosen here give the intriguing feeling that they contain a message of great importance for organization in general, if only we found the right perspective. It all gives the impression that evolution, far from having labored to develop and genetically encode specific devices for specific purposes, is just lightly playing its usual games, that just new tunes are played on a long-existing piano, the behavioral repertoire of living cells. Ocularity stripes evidently are not a tremendously clever and hard-won trick of evolution to exploit some complex vision problem, but turn out to naturally result from the collision of two retinotopic mappings trying to carve out common territory. This message is forcefully brought home by the famous experiment of Constantine-Paton and Law, in which this situation was artificially created in a frog, promptly resulting in ocularity stripes on the tectum for the first time in the evolution of that frog.

All that organization is about is the coordination of subsystems under a purpose. It is interesting to see how the conclusions propagated in this book perfectly illustrate and concretize that general theme. The function of the primary cortices is not constructed in isolation, with afferents to be plugged in later, like a fully constructed computer to which peripherals are connected, but structuring the cortices is more of an exercise in adaptation to the periphery and to other subsystems. Purpose of a specific kind may be brought in by the prenatal simulation (within the retina, or in the pontine region, if the PGO hypothesis advanced here is correct) of biologically significant stimuli. Here, evolution has to labor and make it clear to the new-born human baby, for instance, that the face of the mother is a most interesting and important stimulus. But evolution does so in a parsimonious fashion, laying down a mere schema of the face, which together with filter properties of the immature visual system and simple behavioral patterns of the mother suffice to identify examples as soon as the eyes are open. A possibly very general principle of learning may lie here. In order to extract essential structure from the environment in learning, it is first necessary to identify and separate from the background what is biologically significant. The general principle to identify significant patterns might be based on schematic descriptions of significant structures in the learning brain and its ability to map them into the environment, schemas being defined by evolution (or as the result of previous learning). When a pattern has been recognized, it is separated from the background. The brain thus avoids being swamped by masses of irrelevant information. A likely

candidate mechanism for this separation is synchrony coding discussed here in the chapters on perceptual grouping.

It is my impression that the time is ripe for a major attack on the general problem of organization. Molecular biology and information technology are both hitting a serious complexity barrier. This can only be overcome by a shift of attention from the details of large systems to their organizing principles. Science can only conquer this domain with the help of insight gained on paradigmatic cases. The organization of visual cortex in perinatal ontogenesis may prove decisive in this role.

Bochum,
July 2004

Christoph von der Malsburg
Institut für Neuroinformatik, Ruhr-Universität Bochum;
Departments of Computer Science and Neurobiology,
University of Southern California

Preface

For several decades, the visual cortex has been the source of new theories and ideas about how the brain processes information. The visual cortex is easily accessible through a number of recording and imaging techniques and allows mapping high-level behavior relatively directly to neural mechanisms. It has also been the focal point in the emerging field of computational neuroscience. Several key ideas, such as input-driven self-organization, representing information on topographic maps, and temporal coding, originate from the mechanisms observed in the visual cortex. Understanding the computations in the visual cortex is therefore an important step toward a general computational brain theory.

Although computational theories of the visual cortex have existed for about 30 years, it has been difficult to test these theories experimentally and computationally. In the last 10 years or so the situation has finally started to change, for two reasons. First, it has become technically possible to measure how the visual cortex develops in response to external input, and how visual functions depend on low-level cortical mechanisms. Second, the available computational power has increased by several orders of magnitude. This technological confluence makes it possible for the first time to constrain and test precise computational models about how the visual cortex develops and functions, and why it has the organization it does. Computational models have gradually become an integral part of neuroscience theory.

The research in this area is far from unified. Several models exist to explain phenomena such as how ocular dominance and orientation preferences develop, how visual illusions and aftereffects arise, and how binding and segmentation take place, but it is not possible to see how they could function together in the visual cortex. Also, much of the research involves reimplementing ideas that have been around for several decades. There is no common overview of the field, nor is there a software framework on which future research could be based. This book is intended to fill these gaps: It presents a comprehensive, unified computational theory of the visual cortex as a laterally connected self-organizing map, it puts the theory in the context of past and current research in the area, and it is accompanied by a major software tool, *Topographica*, for modeling computational maps in the cortex in general.

For more than a decade, our research group at the University of Texas at Austin has worked on computational modeling of the visual cortex. Our perspective is to focus not only on the map-like structure of the cortex, but also take into account the dynamical processes that take place through lateral interaction and synchronization. It turns out that many developmental and functional phenomena depend on such processes, giving the model a unique explanatory power. This level of explanation is highly appropriate for understanding many visual processing phenomena; it is also a level where the theories are verifiable, leading to many predictions and proposals for future biological experiments. The book demonstrates how a number of phenomena follow from these principles, including columnar map organization and patchy connectivity, recovery from retinal and cortical injury, psychophysical phenomena such as tilt aftereffects and contour integration, and newborn preference for faces. Computational models are used to gain a precise understanding of existing data, and to make specific predictions for future experimental and theoretical research.

Our aim is to use the theory as a launching point to promote further research in this area. The principles of the models are described in detail, as are the techniques that make them work in practice, including parameter settings and scaling to different sizes and purposes. Most significantly, the book is accompanied by software, animations and demonstrations freely available on the Internet through <http://topographica.org>. *Topographica* is a general software tool for simulating cortical maps that allows neuroscientists to put together sophisticated computational experiments of their own design. As examples, the site contains specific models and demos described in this book. In this way, the book and the software are designed to complement each other, serving as a practical and a theoretical foundation for future research in computational neuroscience. Such a contribution, we believe, will significantly facilitate research in this area in the future.

The LISSOM project and the development of *Topographica* have benefited from the suggestions and contributions of many researchers, in fact too many to be listed here. We would especially like to thank Bill Geisler, Teuvo Kohonen, and Christoph von der Malsburg for substantial contributions of both ideas and critique over the years. Les Cohen, Larry Cormack, Joydeep Ghosh, Ben Kuipers, Bruce McCormick, Ray Mooney, Bruce Porter, Eyal Seidemann, Peter Stone, Chris Williams, and David Willshaw provided inspiration and guidance as doctoral committee members and as colleagues. Many research ideas were refined in discussions with Mike Arbib, Tony Bell, David Brainard, Dan Butts, Cara Cashon, Dmitri Chklovskii, Gary Cottrell, Jack Cowan, Michael Crair, Yang Dan, Peter Dayan, Scania de Schonen, Eizaburo Doi, Dawei Dong, Shimon Edelman, Steven Eglen, James Elder, Jeff Elman, Jerry Feldman, David Field, Peter Fox, Uli Frauenfelder, Nigel Goddard, Geoff Goodhill, Anatoli Gorchetnikov, Steve Grossberg, Seung Kee Han, Seong-Whan Lee, Mike Hasselmo, Robert Hecht-Nielsen, Mike Hines, Geoff Hinton, David Horn, Fred Howell, Patrik Hoyer, Aapo Hyvärinen, Risto Ilmoniemi, Masumi Ishikawa, Naoum Issa, Mark Johnson, George Kalarickal, Pentti Kanerva, Sami Kaski, Krista Lagus, Pat Langley, Daniel Lee, Soo-Young Lee, Christian Lehmann, Ping Li, Jyh-Charn Liu, Xiuwen Liu, Jay McClelland, Brian MacWhinney, Gary Marcus, Denis Mareschal, Vinod Menon, Ken Miller, Klaus Obermayer, Erkki Oja, Bruno Ol-

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Risto Miikkulainen
James A. Bednar
Yoonsuck Choe
Joseph Sirosh

Contents

Foreword	vii
Preface	xi
List of Figures	xxv
List of Tables	xxxix

Part I FOUNDATIONS

1 Introduction	3
1.1 Input-Driven Self-Organization	4
1.2 Constructing Visual Function	7
1.3 Perceptual Grouping	8
1.4 Approach	10
1.5 Guide for the Reader	13
2 Biological Background	15
2.1 Visual System Organization	15
2.1.1 Early Visual Processing	16
2.1.2 Primary Visual Cortex	18
2.1.3 Face and Object Processing	20
2.1.4 Input-Driven Self-Organization	22
2.2 Lateral Connections	23
2.2.1 Organization	23
2.2.2 Development	25
2.2.3 Computational and Functional Hypotheses	26
2.3 Genetic Versus Environmental Factors in Development	28
2.3.1 Bias/Variance Tradeoff	29
2.3.2 Combining Genetic and Environmental Information	30
2.3.3 Retinal Waves	31

2.3.4	Ponto-Geniculo-Occipital Waves	32
2.4	Temporal Coding	33
2.4.1	Binding Through Synchronization	33
2.4.2	Experimental Evidence	34
2.4.3	Modes of Synchronization	36
2.5	Conclusion	36
3	Computational Foundations	39
3.1	Computational Units	39
3.1.1	Compartmental Models	40
3.1.2	Coupled Oscillators	42
3.1.3	Integrate-and-Fire Neurons	43
3.1.4	Firing-Rate Neurons	45
3.2	Temporal Coding	46
3.3	Adaptation	48
3.4	Self-Organizing Maps	50
3.4.1	Variations of Map Models	50
3.4.2	Architecture and Computations	53
3.4.3	Self-Organizing Process	55
3.5	Knowledge Representation in Maps	57
3.5.1	Principal Surfaces	59
3.5.2	Folding	62
3.6	Conclusion	63
<hr/>		
Part II INPUT-DRIVEN SELF-ORGANIZATION		
<hr/>		
4	LISSOM: A Computational Map Model of V1	67
4.1	Motivation: Cortical Maps	67
4.2	The LISSOM Architecture	68
4.2.1	Overview	68
4.2.2	Connections to the LGN	70
4.2.3	Connections in the Cortex	72
4.3	Response Generation	73
4.3.1	Retinal Activation	73
4.3.2	LGN Activation	73
4.3.3	Cortical Activation	75
4.4	Learning	76
4.4.1	Weight Adaptation	76
4.4.2	Connection Death	77
4.4.3	Parameter Adaptation	77
4.5	Self-Organizing Process	78
4.5.1	Method	78
4.5.2	Afferent Connections	78
4.5.3	Lateral Connections	79

4.5.4	Differences Between LISSOM and SOM	80
4.6	Conclusion	82
5	Development of Maps and Connections	85
5.1	Biological Background	85
5.1.1	Quantitative Descriptions of Maps and Connections	86
5.1.2	Experimental Manipulation of Maps	87
5.1.3	Interactions Between Multiple Maps	88
5.2	Computational Models	91
5.2.1	Non-Incremental Models	91
5.2.2	Incremental Models with Fixed Lateral Connections	93
5.2.3	Incremental Models with Modifiable Lateral Connections	94
5.3	Orientation Maps	95
5.3.1	Method	95
5.3.2	Receptive Fields and Orientation Maps	97
5.3.3	Analysis of the Orientation Maps	99
5.3.4	Lateral Connections	101
5.3.5	Effect of Input Types	104
5.4	Ocular Dominance Maps	106
5.4.1	Method	106
5.4.2	Normal Ocular Dominance Maps	107
5.4.3	Strabismic Ocular Dominance Maps	109
5.4.4	Effect of Input Disparity	111
5.5	Direction Selectivity Maps	113
5.5.1	Method	113
5.5.2	Direction Maps	115
5.5.3	Effect of Input Speed	119
5.6	Combined Maps of Multiple Features	119
5.6.1	Method	121
5.6.2	Combined Orientation / Ocular Dominance Maps	122
5.6.3	Combined Orientation / Ocular Dominance / Direction Maps	124
5.6.4	Effect of Input Types	124
5.7	Discussion	130
5.8	Conclusion	132
6	Understanding Plasticity	133
6.1	Biological and Computational Background	133
6.1.1	Reorganization After Retinal Lesions	133
6.1.2	Reorganization After Cortical Lesions	135
6.1.3	Computational Models	137
6.2	The Reduced LISSOM Model	138
6.2.1	Method of Self-Organization	138
6.2.2	Orientation Maps with and without the LGN	140
6.2.3	The Role of ON/OFF Channels	140
6.2.4	Methods for Modeling Plasticity	142

6.3	Retinal Lesions	142
6.3.1	Reorganization of the Map	142
6.3.2	Dynamic Receptive Fields	145
6.4	Cortical Lesions	146
6.4.1	Reorganization of the Map	147
6.4.2	Limits of Reorganization	151
6.4.3	Medical Implications	151
6.5	Discussion	152
6.6	Conclusion	153
7	Understanding Visual Performance: The Tilt Aftereffect	155
7.1	Psychophysical and Computational Background	155
7.1.1	Psychophysical Data	155
7.1.2	Theoretical Explanations	158
7.1.3	Computational Models	159
7.2	Method	160
7.2.1	Quantifying the Perceived Orientation	161
7.2.2	Measuring the Tilt Aftereffect	162
7.3	Results	164
7.3.1	Magnitude Versus Orientation Difference	164
7.3.2	Magnitude over Time	165
7.4	Analysis	166
7.4.1	Afferent and Lateral Contributions	166
7.4.2	Mechanisms	167
7.5	Discussion	170
7.6	Conclusion	171
<hr/>		
Part III CONSTRUCTING VISUAL FUNCTION		
<hr/>		
8	HLISSOM: A Hierarchical Model	175
8.1	Motivation: Synergy of Nature and Nurture	175
8.2	The Hierarchical Architecture	178
8.2.1	Brainstem Input Area	178
8.2.2	Face-Selective Area	178
8.2.3	Afferent Normalization	180
8.3	Inputs, Activation and Learning	181
8.4	Effect of Input Sequence and Initial Organization	184
8.5	Conclusion	185
9	Understanding Low-Level Development: Orientation Maps	189
9.1	Biological Motivation	189
9.2	Prenatal Development	190
9.2.1	Method	191
9.2.2	Map Organization	192

9.2.3	Effect of Training-Pattern Variations	192
9.3	Postnatal Development	194
9.3.1	Method	194
9.3.2	Map Organization	195
9.3.3	Effect of Visual Environment	197
9.4	Prenatal and Postnatal Contributions	199
9.4.1	Method	199
9.4.2	Effect of Training-Regime Variations	199
9.5	Discussion	201
9.6	Conclusion	202
10	Understanding High-Level Development: Face Detection	203
10.1	Psychophysical and Computational Background	203
10.1.1	Psychophysical Data	203
10.1.2	Computational Models of Face Processing	206
10.1.3	Theoretical Models of Newborn Face Preferences	208
10.2	Prenatal Development	213
10.2.1	Training Method	213
10.2.2	V1 and Face-Selective Area Organization	216
10.2.3	Testing Method	217
10.2.4	Responses to Schematic Patterns	218
10.2.5	Responses to Natural Images	221
10.2.6	Effect of Training-Pattern Shape	225
10.3	Postnatal Development	227
10.3.1	Initial Trained and Naïve Networks	227
10.3.2	Training and Testing Methods	228
10.3.3	Prenatally Established Bias for Learning Faces	230
10.3.4	Decline in Response to Schematics	231
10.3.5	Mother Preferences	233
10.4	Discussion	233
10.5	Conclusion	238

Part IV PERCEPTUAL GROUPING

11	PGLISSOM: A Perceptual Grouping Model	241
11.1	Motivation: Temporal Coding	241
11.2	The Self-Organization and Grouping Architecture	243
11.3	Spiking Unit Model	244
11.3.1	Leaky Synapse	244
11.3.2	Activation	246
11.3.3	Threshold Mechanism	246
11.4	Learning	247
11.5	Self-Organizing Process	249
11.5.1	Method	249

11.5.2	Receptive Fields and Orientation Maps	249
11.5.3	Lateral Connections	252
11.6	Conclusion	255
12	Temporal Coding	257
12.1	Method	257
12.2	Binding Through Synchronization	258
12.2.1	Effect of Synaptic Decay Rate	258
12.2.2	Effect of Connection Range	261
12.3	Segmentation Through Desynchronization	263
12.3.1	Effect of Connection Types	263
12.3.2	Effect of Noise	263
12.4	Robustness Against Variation and Noise	265
12.4.1	Robustness Against Size Differences	265
12.4.2	Overcoming Noise with Strong Excitation	268
12.4.3	Overcoming Noise with a Long Refractory Period	269
12.5	Discussion	270
12.6	Conclusion	271
13	Understanding Perceptual Grouping: Contour Integration	273
13.1	Psychophysical and Computational Background	273
13.1.1	Psychophysical Data	273
13.1.2	Computational Models	278
13.2	Contour Integration and Segmentation	280
13.2.1	Method	280
13.2.2	Contour Integration	282
13.2.3	The Role of Lateral Connections	284
13.2.4	Contour Segmentation	286
13.3	Contour Completion and Illusory Contours	288
13.3.1	Method	288
13.3.2	Contour Completion	289
13.3.3	Afferent and Lateral Contributions	290
13.3.4	Completion of Illusory Contours	292
13.3.5	Salience of Closed Versus Open Contours	294
13.4	Influence of Input Distribution on Anatomy and Performance	295
13.4.1	Method	295
13.4.2	Differences in Connection Patterns	296
13.4.3	Differences in Contour Integration	299
13.5	Discussion	299
13.6	Conclusion	304

Part V EVALUATION AND FUTURE DIRECTIONS

14 Computations in Visual Maps	307
14.1 Visual Coding in the Cortex	307
14.2 Visual Coding in LISSOM	309
14.2.1 Method	309
14.2.2 Sparse, Redundancy-Reduced Representations	311
14.2.3 The Role of Self-Organized Lateral Connections	311
14.3 Visual Coding for High-Level Tasks	314
14.3.1 The Handwritten Digit Recognition Task	314
14.3.2 Method	315
14.3.3 Forming Map Representations	318
14.3.4 Recognizing Map Representations	319
14.4 Discussion	319
14.5 Conclusion	324
15 Scaling LISSOM simulations	325
15.1 Parameter Scaling Approach	325
15.2 Scaling Equations	326
15.2.1 Scaling the Area	326
15.2.2 Scaling Retinal Density	327
15.2.3 Scaling Cortical Density	330
15.3 Forming Large Maps: The GLISSOM Approach	332
15.4 GLISSOM Scaling	332
15.4.1 Weight Interpolation Algorithm	333
15.4.2 Method	336
15.4.3 Comparing LISSOM and GLISSOM Maps	337
15.5 Scaling to Cortical Dimensions	339
15.6 Discussion	342
15.7 Conclusion	343
16 Discussion: Biological Assumptions and Predictions	345
16.1 Self-Organization	345
16.1.1 Recurrent Lateral Interactions	346
16.1.2 Adapting Lateral Connections	346
16.1.3 Normalization of Connections	348
16.1.4 The Role of Excitatory and Inhibitory Lateral Connections	349
16.1.5 Connection Death	352
16.1.6 Parameter Adaptation	353
16.2 Genetically Driven Development	354
16.2.1 Self-Organization of V1	354
16.2.2 Self-Organization of Higher Levels	355
16.2.3 Evolving Complex Systems	357
16.3 Temporal Coding	358

16.3.1	Synchrony as a Perceptual Representation	358
16.3.2	Interpretation of Temporal Codes	359
16.3.3	The Role of the Different Layers	360
16.4	Predictions	362
16.4.1	Cortical Organization	362
16.4.2	Patterns of Lateral Connections	363
16.4.3	Tilt Aftereffects	365
16.4.4	Plasticity	365
16.4.5	Internal Pattern Generation	366
16.4.6	Face Processing	368
16.4.7	Synchronization	368
16.4.8	Perceptual Grouping	370
16.4.9	Sparse Coding	372
16.5	Conclusion	373
17	Future Work: Computational Directions	375
17.1	Extensions to the LISSOM Mechanisms	375
17.1.1	Threshold Adaptation	375
17.1.2	Push–Pull Afferent Connections	376
17.1.3	Modeling Substructure Within Columns	377
17.1.4	Phase-Invariant Responses	378
17.1.5	Time-Lagged Activation	379
17.2	Modeling New Phenomena with LISSOM	379
17.2.1	Spatial Frequency, Color, and Disparity in V1	380
17.2.2	Differences between Species	381
17.2.3	Prenatal and Early Postnatal Development of V1	382
17.2.4	Postnatal Internally Generated Patterns	383
17.2.5	Tilt Illusions	384
17.2.6	Other Visual Aftereffects	385
17.2.7	Hyperacuity	386
17.2.8	Grouping with Natural Input	386
17.2.9	Scaling up to Large Networks	387
17.2.10	Foveated Input and Eye Movements	388
17.2.11	Scaling up to Cortical Hierarchy	389
17.2.12	Line-End-Induced Illusory Contours and Occluded Objects	390
17.2.13	Feedback from Higher Levels	391
17.2.14	High-Level Influence on Perceptual Grouping	393
17.2.15	Multi-Modal Integration	394
17.3	New Research Directions	396
17.3.1	Theoretical Analysis of Visual Computations	396
17.3.2	Genetically Specified Pattern Associations	397
17.3.3	Embodied, Situated Perception	399
17.3.4	Building Artificial Vision Systems	400
17.3.5	Constructing Complex Systems	401
17.4	The <i>Topographica</i> Cortical Map Simulator	403

17.4.1	Overview	403
17.4.2	Scope and Design	404
17.4.3	Implementation	405
17.4.4	Further Development	406
17.5	Conclusion	406
18	Conclusion	409
18.1	Contributions	409
18.2	Conclusion	412

Appendices

A	LISSOM Simulation Specifications	415
A.1	Generalized Activation Equation	415
A.2	Default Parameters	416
A.3	Choosing Parameters for New Simulations	419
A.4	Retinotopic Maps	422
A.5	Orientation Maps	422
A.6	Ocular Dominance Maps	423
A.7	Direction Maps	424
A.8	Combined Orientation / Ocular Dominance Maps	424
A.9	Combined Orientation / Ocular Dominance / Direction Maps	424
B	Reduced LISSOM Simulation Specifications	427
B.1	Plasticity	427
B.2	Tilt Aftereffect	428
B.3	Scaling	428
C	HLISSOM Simulation Specifications	429
C.1	V1 Only	429
C.2	Face-Selective Area Only	430
C.3	Combined V1 and Face-Selective Area	432
D	PGLISSOM Simulation Specifications	435
D.1	Self-Organization	435
D.2	Grouping	437
D.3	Synchronization	438
E	SOM Simulation Specifications	439
F	Visual Coding Simulation Specifications	441
F.1	Sparse Coding and Reconstruction	441
F.2	Handwritten Digit Recognition	442

G	Calculating Feature Maps	445
G.1	Preference Map Algorithms	445
G.2	Retinotopic Maps	449
G.3	Orientation Maps	449
G.4	Ocular Dominance Maps	449
G.5	Direction Maps	450
G.6	Orientation Gradients	450
References		451
Author Index		503
Subject Index		523

List of Figures

1.1	Columnar organization of the primary visual cortex	5
1.2	Spontaneous activity in the retina	7
1.3	Perceptual grouping tasks	9
1.4	Basic LISSOM model of the primary visual cortex	11
2.1	Human visual pathways (top view)	16
2.2	Receptive field types in retina, LGN and V1	17
2.3	Measuring cortical maps	19
2.4	Orientation map in the macaque	20
2.5	Hierarchical organization of feature preferences in the macaque	21
2.6	Long-range lateral connections in the macaque	24
2.7	Lateral connections in the tree shrew orientation map	25
2.8	Spontaneous activity in the cat PGO pathway	32
2.9	Solving the superposition catastrophe through temporal coding	34
2.10	Synchronization of one and two input objects in the cat	35
3.1	Computational abstractions of neurons and networks	41
3.2	Perceptual grouping through temporal coding	47
3.3	General architecture of self-organizing map models of the primary visual cortex	51
3.4	Training a self-organizing map with Gaussian activity patterns	55
3.5	Self-organization of weight vectors	56
3.6	Self-organization of a retinotopic map	58
3.7	Magnification of dense input areas	59
3.8	Principal components of data distributions	60
3.9	Approximating nonlinear distributions with principal curves and folding	61
3.10	Three-dimensional model of ocular dominance	63
4.1	Architecture of the basic LISSOM model	69
4.2	Afferent weights of ON and OFF neurons in the LGN	71

4.3	Initial V1 afferent and lateral weights	72
4.4	Example input and response	74
4.5	Neuron activation function $\sigma(s)$	75
4.6	Self-organized V1 afferent weights	79
4.7	Self-organized afferent and lateral weights across V1	80
4.8	Self-organization of the retinotopic map	81
4.9	Self-organized V1 lateral weights	82
5.1	Fourier spectrum and gradient of the macaque orientation map	86
5.2	Normal vs. strabismic cat ocular dominance maps and lateral connections	88
5.3	Combined OR/OD map in the macaque	89
5.4	Spatiotemporal receptive fields, direction maps, and combined OR/DR maps in animals	90
5.5	Initial V1 afferent and lateral weights	96
5.6	Example input and response	97
5.7	Self-organized V1 afferent and lateral weights	98
5.8	Self-organized afferent and lateral weights across V1	99
5.9	Self-organization of the orientation map	100
5.10	Fourier spectrum and gradient of the orientation map	101
5.11	Retinotopic organization of the orientation map	102
5.12	Long-range lateral connections in the orientation map	103
5.13	Effect of training patterns on orientation maps	105
5.14	LISSOM model of ocular dominance	107
5.15	Self-organization of afferent weights into OD receptive fields	108
5.16	Self-organized ocular dominance map	108
5.17	Long-range lateral connections in the ocular dominance map	109
5.18	Ocular dominance and long-range lateral connections in the strabismic ocular dominance map	110
5.19	Effect of disparity on ocular dominance maps	112
5.20	LISSOM model of orientation and direction selectivity	114
5.21	Self-organization of afferent weights into spatiotemporal RFs	115
5.22	Self-organized OR/DR map	116
5.23	Combined OR/DR map	117
5.24	Long-range lateral connections in the combined OR/DR map	118
5.25	Effect of input speed on direction maps	120
5.26	LISSOM model of orientation, ocular dominance, and direction selectivity	121
5.27	Self-organized OR/OD map	123
5.28	Long-range lateral connections in the combined OR/OD map	125
5.29	Combined OR/OD/DR map trained with Gaussians	126
5.30	Example natural image input for training the OR/OD/DR map	127
5.31	Combined OR/OD/DR map trained with natural images	128
5.32	Effect of training patterns on OR/OD/DR maps	129

6.1	Reorganization of receptive fields after a retinal lesion	134
6.2	Reorganization of receptive fields after a cortical lesion.....	136
6.3	Architecture of the reduced LISSOM model	138
6.4	Effect of ON/OFF channels on orientation maps	139
6.5	Role of ON/OFF channels in processing various kinds of inputs....	141
6.6	Retinal activation and V1 response before and after a retinal scotoma	143
6.7	Reorganization of the orientation map after a retinal scotoma	144
6.8	Dynamic RF expansion and perceptual shift after a retinal scotoma .	146
6.9	Retinal activation and V1 response before and after a cortical lesion	147
6.10	Cortical response after a cortical lesion	148
6.11	Reorganization of lateral inhibitory weights after a cortical lesion ..	149
6.12	Reorganization of the orientation map after a cortical lesion	150
7.1	Demonstration of the tilt aftereffect	156
7.2	Tilt aftereffect in human subjects	157
7.3	Measuring perceived orientation as vector sum	161
7.4	Cortical response and perceived orientation	163
7.5	Tilt aftereffect in humans and in LISSOM	164
7.6	Tilt aftereffect over time in humans and in LISSOM	165
7.7	Components of the tilt aftereffect due to each weight type.....	167
7.8	Changes in lateral inhibitory weights due to adaptation	168
7.9	Cortical response during adaptation and during direct and indirect tilt aftereffect	169
8.1	Architecture of the HLISSOM model	179
8.2	Effect of afferent normalization on V1 responses	181
8.3	Effect of afferent normalization on V1 neuron tuning	182
8.4	Internally generated and environmental input patterns	183
8.5	Effect of different input streams and initial organizations on the self-organizing process	186
9.1	Effect of internally generated prenatal training patterns on orientation maps	193
9.2	Prenatal orientation maps in animals and in HLISSOM	194
9.3	Effect of environmental postnatal training patterns on orientation maps	196
9.4	Postnatal orientation maps in animals and in HLISSOM	197
9.5	Distribution of orientation preferences in animals and in HLISSOM	198
9.6	Effect of prenatal and postnatal training on orientation maps	200
10.1	Measuring newborn face preferences	205
10.2	Face preferences in newborns	206
10.3	Face preferences in young infants	207
10.4	Self-organization of the scaled-up orientation map	215
10.5	Self-organization of the FSA map	216

10.6	Response to schematic images by Goren et al. (1975) and Johnson et al. (1991)	220
10.7	Response to schematic images by Valenza et al. (1996) and Simion et al. (1998a)	221
10.8	Spurious responses to the inverted three-dot pattern	222
10.9	Response to natural images	223
10.10	Response variation with size and viewpoint	224
10.11	Effect of training patterns on face preferences	226
10.12	Initial afferent weights across prenatally trained and naïve FSA networks	228
10.13	Face and object images in postnatal training	229
10.14	Example postnatal training presentations	230
10.15	Prenatally established bias for learning faces	231
10.16	Postnatal decline in response to schematic images	232
10.17	Mother preferences based on both internal and external features . . .	234
11.1	Architecture of the PGLISSOM model	243
11.2	The leaky integrator neuron model	245
11.3	Self-organized afferent weights and retinotopic organization	250
11.4	Self-organized orientation map	251
11.5	Long-range lateral connections in GMAP	253
11.6	Activating neurons with collinear and cocircular RFs	254
11.7	Distribution of lateral connections in animals and in PGLISSOM . .	254
12.1	Synchronized and desynchronized modes of firing	259
12.2	Effect of connection type and decay rate on synchronization	261
12.3	Effect of excitatory connection range on synchronization	262
12.4	Binding and segmentation with different connection types	264
12.5	Effect of noise on desynchronization	266
12.6	Effect of relative input size on synchronization	267
12.7	Overcoming noise with strong excitation	268
12.8	Overcoming noise with a long refractory period	269
13.1	Demonstration of contour integration	274
13.2	Association fields for contour integration	275
13.3	Edge-induced vs. line-end-induced illusory contours	276
13.4	Contour completion across edge inducers	279
13.5	Measuring local response as multi-unit activity	281
13.6	Contour integration process with varying degrees of orientation jitter	283
13.7	Contour integration performance in humans and in PGLISSOM . . .	284
13.8	Quantifying the spatial relationship between two receptive fields . . .	285
13.9	Edge cooccurrence in nature and long-range lateral connections in PGLISSOM	286
13.10	Contour segmentation process	287
13.11	Contour segmentation performance	288

13.12	Contour completion process	289
13.13	Afferent contribution in contour completion	290
13.14	Contour completion process with different kinds of connections . . .	291
13.15	Contour completion performance with different kinds of connections	291
13.16	Contour completion process in the illusory triangle	292
13.17	Salience of complete vs. incomplete illusory triangles	293
13.18	Contour completion performance in the illusory triangle	293
13.19	Contour completion performance in closed vs. open contours	295
13.20	Orientation selectivity in SMAP with different input distributions . .	297
13.21	Lateral excitatory connections in GMAP with different input frequencies	298
13.22	Lateral excitatory connections in GMAP with different curvature ranges	298
13.23	Contour integration process with different input frequencies	300
13.24	Contour integration process with different curvature ranges	301
13.25	Contour integration performance with different input distributions . .	302
14.1	Self-organized vs. isotropic lateral connections	310
14.2	Sparse, redundancy-reduced coding with self-organized lateral connections	312
14.3	Architecture of the handwritten digit recognition system	315
14.4	Handwritten digit examples	316
14.5	Self-organized SOM afferent weights	320
14.6	Self-organized LISSOM afferent and lateral weights	321
14.7	SOM activity patterns	322
14.8	LISSOM activity patterns	323
15.1	Scaling retinal and cortical area	328
15.2	Scaling retinal density	329
15.3	Scaling cortical density	331
15.4	Training time and memory usage in LISSOM vs. GLISSOM	333
15.5	Weight interpolation in GLISSOM	334
15.6	Scaling cortical density in GLISSOM	336
15.7	Self-organization of LISSOM and GLISSOM orientation maps	338
15.8	Accuracy of the final GLISSOM map as a function of the initial network size	338
15.9	Orientation maps in LISSOM and GLISSOM	339
15.10	Simulation time and memory usage in LISSOM vs. GLISSOM	340
16.1	Local microcircuit for lateral interactions	351
17.1	High-level influence on illusory contour perception	393
17.2	Example <i>Topographica</i> model	404
17.3	Example <i>Topographica</i> screenshot	407
A.1	Mapping between neural sheets in LISSOM	421

List of Tables

A.1	Parameters for the LISSOM reference simulation	417
A.2	Defaults for constant parameters	419
A.3	Default parameter change schedule	420
C.1	Defaults for FSA simulations	430
C.2	Parameters for different types of face training patterns	431
C.3	Parameter change schedule for postnatal FSA simulations	431
C.4	Parameter change schedule for combined V1 and FSA simulations . .	432
D.1	Defaults for PGLISSOM simulations	436
D.2	Parameter change schedule for PGLISSOM simulations	437
E.1	Defaults for SOM simulations	440

Part I

FOUNDATIONS