Computational Maps in the Visual Cortex

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With 177 Figures, 47 in Full Color

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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 subsystems 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 specific 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 biology 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,
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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 Gorchetchnikov, 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 Olshausen, Remus Osan, Larry Parsons, Jim Reggia, Pamela Reinagel, Helge Ritter, Adrian Roberts, Eytan Ruppin, Terry Sejnowski, Lokendra Shastri, Harel Shouval, Hava Siegelmann, Michael Stryker, Mriganka Sur, John Taylor, Simon Thorpe, Dave Touretzky, David van Essen, Rufin VanRullen, Thomas Wachtler, DeLiang Wang, Mike Weliky, and Len White. Several former and current members of the University of Texas Neural Networks Research Group contributed to the design and implementation of the models and experiments, including Gautam Agarwal, Justine Blackmore, Judah De Paula, Igor Farkas, Andrea Haessly, Stefanie Jegelka, Amol Kelkar, Jeff Provost, Joe Reisinger, Yaron Silberman, Yiu Fai Sit, Tal Tversky, and Vinod Valsalam.

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