THE NEW VISUAL NEUROSCIENCES

EDITED BY JOHN S. WERNER AND LEO M. CHALUPA

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Edited by John S. Werner and Leo M. Chalupa

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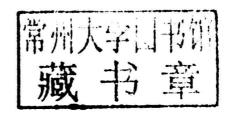
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THE NEW VISUAL NEUROSCIENCES

PREFACE

This book covers the extraordinary range of contemporary visual neuroscience, from molecules and cell assemblies to systems and therapy. Nowhere in the neurosciences has progress been so rapid as in the vision sciences. A book of this scope, which is even broader than the original *Visual Neurosciences* assembled 10 years ago, requires expert advice in many specialties even though the final product is intended for nonspecialists. We have been fortunate in enlisting the help of associate editors, authorities in various areas of vision science, with whom we have enjoyed a smooth working relationship through a variety of common bonds with the University of California at Davis. They reviewed chapters and solicited expertise from a large number of reviewers. We are grateful to all these colleagues for helping to bring this book to completion.

We thank Susan Garcia and Rieko Ringo for administrative support and for laboring long hours beyond their normal work day. We are also grateful to Laura Leming, Cameron Blount, and Grace Dell'Olio. In addition, the editorial staff at the MIT Press were not only cordial task masters, but reliable, supportive, and professional, especially Robert Prior, Susan Buckley, and Katherine Almeida. They provided valuable guidance at all stages. Finally, we thank the authors for adhering to tight deadlines in order to produce a book that is both up to date and of archival value, a work that we hope will inspire readers who are only beginning their quest in the visual neurosciences and those established scientists who wish to broaden the scope of their interests in *The New Visual Neurosciences*.

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1 A Decade of Progress and New Directions in the Visual Neurosciences

JOHN S. WERNER AND LEO M. CHALUPA

Even Charles Darwin was initially overwhelmed by the enormous variation among species in the manner in which the seemingly effortless task of vision is accomplished. In all species, vision begins with a cascade of molecular reactions in response to the absorption of electromagnetic radiation, but so varied are the "inimitable contrivances," wrote Darwin (1859), that the thought they "could have been formed by natural selection, seems, I freely confess, absurd to the highest possible degree" (p. 186). But Darwin overcame his own skepticism, perhaps aided by the realization that, despite a long evolutionary history, the eye is not perfect and is still subject to protracted processes of natural selection.

The visual system has attracted the curiosity of many other great scientists as well. In most cases, understanding vision was not only a challenge in its own right but also a test bed for larger fundamental principles. Isaac Newton (1704), for example, after working out the laws of motion and the planetary bodies and inventing the calculus, launched the modern era of vision science with his discovery of the nature of light. His insight that "the Rays to speak properly are not coloured" (p. 124) led to the realization that the proper understanding of vision is not to be found in the nature of light but in the nature of the visual pathways. He then went on to discover the partial decussation of the human visual pathways. One hundred years later another great physicist credited with unifying our understanding of electricity and magnetism, James Clerk Maxwell (1872), concluded from his experiments on color that vision science is "essentially a mental science" (p. 261). To the list of extraordinary scientists who facilitated the visual neurosciences, we could add the names of: Thomas Young, Jan Evangelista Purkinje, Charles Wheatstone, David Ferrier, Johannes Müller, Hermann von Helmholtz, Ewald Hering, Ernst Mach, and countless others.

The rapid growth of the vision sciences and the extraordinary interdisciplinary nature of the effort made it necessary to create anthologies even in the early twentieth century. The first and most important was

published in 1909 as Helmholtz's third edition of the Handbuch der physiologischen Optik (Helmholtz, 1909), which included not only his own writings from the first edition but also those of Gullstrand, von Kries, and Nagel. It would be many years later before edited volumes would follow, but they did so with increasing frequency as the field progressed and expanded in scope. Some that have shaped our own education include Graham's (1965) Vision and Visual Perception and the many volumes of The Handbook of Sensory Physiology (Autrum et al., 1971–1984). Other volumes integrated vision science with various areas of neuroscience such as the workshops held in Boulder, culminating in a series called, The Neurosciences (for example, Schmitt & Worden, 1979). The integration of visual neurophysiology and perception in a manner that could be accessible to students led to Visual Perception: The Neurophysiological Foundations (Spillmann & Werner, 1990). All of these volumes remain important, not just for their rich histories but for many gems lying in wait to be rediscovered and as brilliant examples of how to think about vision.

Ten years ago we assembled summaries of all areas of visual neuroscience from leaders in the field who covered the state of the art, which had by then expanded to include molecular processes, extraclassical receptive fields, and excitement about extrastriate cortex, which together with striate cortex was understood to include more than one-third of the primate brain and promised to link visual cognition to visual neurophysiology. The state of our understanding of these processes was summarized in two edited volumes called The Visual Neurosciences (Chalupa & Werner, 2004). It provided a comprehensive set of reviews of the field by leading international authorities in language intended for nonexperts and beginning graduate students. We could not have anticipated that, in only one decade, many of these areas would advance so fast and so far as to require much more than an update, because there is so much that is new.

The New Visual Neurosciences is a comprehensive review of the vast progress of the past decade. Most of the

authors are new, and a few chapters are updated, but many cover entirely new topics. The chapters in the previous volume should be consulted along with this one, as they contain an essential body of information that is only partially repeated here.

Chapters 2-15 of the section on Retinal Mechanisms and Processes describe how photoreceptor signals are processed in the retina and compressed for transmission to other brain areas by some 1 million optic nerve fibers. Much of what is known about the structure of cells in the retina is owed to the Golgi stain so effectively exploited by Ramón y Cajal (1892/1972), but remarkable new techniques described in this section such as optogenetics, targeted fluorescent markers, and transsynaptic viral labeling are revolutionizing our understanding of anatomical organization and are aided further by connectomics and multielectrode arrays that permit ensembles of cellular interactions and outputs to be discovered, quantified, and manipulated at a level that is without precedent. Topics included here that were not covered in the first edition of this book include: connectomics, gap junctions, retinal feature detection, correlated activity, intrinsically photosensitive ganglion cells, and postreceptoral adaptation.

Central mechanisms of vision encompass chapters 16-32, divided into sections on Organization of Visual Pathways, Subcortical Processing, and Processing in Primary Visual Cortex. They collectively provide an up-to-date account of our understanding of the functional organization of neural pathways that interconnect visual areas in the brain, the circuit mechanisms responsible for the generation of emergent receptive-field properties, and the influence of brain state and behavior on visual processing in early visual areas. Our understanding of these topics has grown since the discovery of what is now known as the classical receptive field (Barlow, 1953; Kuffler, 1953). The effort has benefited tremendously from the increasing use of alert monkeys for studying early visual processing as well as the addition of the genetically modifiable mouse as a major model system for understanding vision. Specific topics included here that were not covered in the first edition of this book include cortical connectomics, the role of inhibition and other identified local circuits for visual processing, the dynamic properties of neural circuits for vision, and feedback from cortex to lateral geniculate nucleus. Indeed, all of these areas are shaped by feedback from other areas, cortical and subcortical, making it possible for top-down influences to shape our visual perception by attention and prior learning.

The sections on *Brightness and Color* (chapters 33–41), *Pattern, Surface, and Shape* (chapters 42–47), *Objects and Scenes* (chapters 48–52), and *Time, Motion, and Depth*

(chapters 53–58) highlight the extension of analyses of visual coding to higher stages of visual processing and to more ecologically relevant contexts where analyses of the properties of natural images continue to play an important role. This can be seen in the way subjects such as color and brightness constancy have changed to the newly added sections in this volume on topics such as face and scene perception. This myriad of visual recognition tasks is normally taken for granted but still can be accomplished to only a limited extent by artificial vision systems. More than half of the chapters in the pattern, object, scene, and motion sections are new to this work. The remaining chapters are complete revisions, focusing entirely on the last 10 years of research. The first edition provides a basic foundation that is not repeated in the new chapters. The revised and new chapters fill in crucial advances, linking low-level pattern and texture analysis to surface representation, object recognition, and, finally, scene processing. Entirely new subfields are represented in the new book, for example, on time perception. The chapters cover a wider range of techniques including psychophysics, functional imaging, and brain stimulation, and they introduce new avenues of investigation on midlevel vision and spatiotemporal perception.

A comprehensive coverage of all forms of Eye Movements is provided by chapters 59–68. Natural vision is an active and dynamic process that depends on eye movements to stabilize the image of objects on the retina and to direct the eyes to regions of high visual salience. These operations are carried out by complex subcortical and cortical circuits, and the dialogues between eye movements and sensory systems are essential in disambiguating signals generated by the motion of the eye itself from those present in the external world. The opening chapter of this section reviews the role of eye movements in natural behavior. Subsequent chapters describe the eye's orbital mechanics and the circuitry underlying eye movements and target selection. The final chapter reviews the neurology of eye movements and how models of the eye movement circuitry and cellular neurophysiology are being used to diagnose and treat eye movement disorders.

In this edition several chapters investigate how visual information is integrated with other sensory systems as well as the motor system in order to generate visually guided movements. How the parietal lobe and other traditionally considered multisensory cortical areas are involved in complex processing is now covered in chapters related to visual-auditory interactions and visually guided movements. These chapters are embedded with related chapters that comprise the section on *Cortical Mechanisms of Attention, Cognition, and Multimodal*

Integration (chapters 69–78). The last decade has seen an explosion of work in the cognitive neurosciences, spurred largely by advances in methods that measure ongoing activity in the human and nonhuman primate brain during complex awake behaviors. Leaders in the field describe signature accomplishments in understanding of how extrasensory processing and multimodal integration contribute to visual perception in the earliest stages of sensory processing and the control mechanisms that support these changes.

Invertebrate Vision (chapters 79-85) was not included in the previous edition, but it has an important place in our description of neural mechanisms mediating vision. Because of the relatively small numbers of neurons in their visual pathways (compared to vertebrates) and the relative ease with which their electrophysiological responses can be recorded (by virtue of their large size, especially at the peripheral levels of the visual pathways), invertebrates have spearheaded our understanding of a number of fundamental principles of visual processing. Examples include the first investigations of phototransduction and photoreceptor physiology—in the horseshoe crab, Limulus (Fuortes, 1959), the first discovery of lateral inhibition and of its role in sharpening visual contours as described perceptually by Mach—again in Limulus (Hartline & Ratliff, 1957), and the first quantitative characterization of visual motion detection—in the beetle Chlorophanus (Hassenstein & Reichardt, 1956). Invertebrates continue to fascinate and challenge, with chapters from this volume elucidating, for example, the perception of polarized light (a domain of vision that lies entirely outside our own) and its use in navigation and the color vision of mantis shrimps, which possess over a dozen spectral classes of photoreceptors. This section is closely linked with the following section on Theoretical Perspectives.

Theoretical Perspectives (chapters 86-89) presents some of the prevailing theories regarding the evolution of the visual system and the principles that underlie its function. The opening chapter in this section describes the features of the primate visual system that distinguish it from those of other mammals, and it provides a possible account for how these features evolved and how they became diversified as an adaptation to variations in ecological niche and primate lifestyles. Two related theoretical frameworks are provided in chapters on the neural computations underlying visual perception. One attempts to account for aspects of neural coding and representation in terms of their relation to natural scene statistics, and the other attempts to show how visual systems learn and exploit these statistics for inferential computations. There is much new work on these topics since the last edition that is emphasized in both

chapters. An issue that has been a subject of much theoretical speculation and debate in visual neuroscience is the role that neural oscillations play in information processing. The past decade has seen a resurgence of interest and study on this topic, and the final chapter in this section provides an up-to-date account of the latest experimental and theoretical developments.

Chapters 90-100, Molecular and Developmental Processes, describe visual system development from retina to visual cortex. These chapters cover the wide range of events that constitute neural development, from prenatal events such as neurogenesis and neuronal migration through molecular specification of cell types, formation of connections, development of functional properties, and activity-dependent plasticity. Many of these topics were covered in the first edition, but the dramatically increased depth of the science included here illustrates the significant advances over the past 10 years in this field in understanding the molecular mechanisms that mediate the development of the visual system. New molecular and genetic techniques have revealed unexpected complexity in cell types within the retina and equally complex mechanisms to specify the proper connections among those cell types. The standardization of the mouse visual system for studying development and plasticity has pushed the field forward, allowing major advances in determining the learning rules that govern activity-dependent plasticity as well as in identifying central molecular pathways that mediate this plasticity. Combining the now widespread availability of knockout mice with cutting-edge genomic and imaging techniques has also provided critical insight into how projections find their targets at multiple levels within the visual system. These advances have identified many classes of new molecules involved in visual system development, including immune molecules and glial-derived factors. Finally, these accomplishments in understanding the rules that regulate visual system development have facilitated truly remarkable and groundbreaking advances in understanding and promoting optic nerve regeneration, reviewed here.

The final section of the book, Translational Visual Neuroscience (chapters 101-112) is closely related to the preceding section on development. The previous edition did not cover applied research, but progress in the field now requires a separate translational section. Its inclusion here is because of the amazing scientific progress in novel treatment modalities, many of which are made possible only by building on equally remarkable progress in basic science that has directed these new understandings to attack ocular disease. Disease processes begin at the molecular level and be addressed sometimes by controlling