

Two chapters focus on cellular functions of Wnt signaling, each with examples from different tissues and organisms. Gretchen Dollar and Sergei Sokol describe how Wnts control cellular polarity, including such well-studied events as apical-basal polarization, planar cell polarity, cell movement and asymmetric division. Each topic is introduced with sufficient background information, followed by genetic and biochemical evidence of Wnt pathway functions in the process. The common themes aid a reader in drawing parallels with their favorite system, and allow predictions for how Wnts might act in unstudied cell types. Almut Köhler, Alexandra Schambony and Doris Wedlich focus specifically on cell migration, using examples from mouse gastrulation, the nervous system, and formation of eye and heart fields. Similarities appear between single-cell and tissue-level migratory regulation, and classical embryological models, such as *Xenopus* gastrulation, are juxtaposed with newer topics, providing a comprehensive overview. Although it is not surprising that non-canonical Wnt signaling can affect cell migration in a variety of systems, this chapter also leaves the reader with the important idea that canonical signaling can regulate migration at the level of gene expression.

Finally, two chapters discuss Wnt signaling functions in specific tissue types. Elizabeth Heeg-Truesdell and Carole LaBonne review multiple stages of neural crest development, providing evidence for regulation by Wnts at each step from crest induction to cellular differentiation. This chapter creates perhaps the clearest overview of how a single class of extracellular signals, through multiple downstream pathways, are used reiteratively throughout the development of one cell type. This is a fundamental concept in developmental biology, as is the idea that Wnts are likely to act in concert with other signals at all these steps. Néstor Masckauchán and Jan Kitajewski focus on Wnt pathways in angiogenesis, which is a relatively new direction of research that has uncovered known and novel members of the signaling cascade using genetic approaches. Most of the initial work has centered on diseases of the retinal vasculature, which have provided a good model for ligand and receptor activity in the growth and regression of vessels. These findings have led to the search for additional functions for Wnt signaling in angiogenesis, with obvious clinical implications. Together, these chapters illustrate the forward movement in the field towards translational research

using Wnt pathway modulation to treat developmental disorders and disease.

With all the data accumulated from hundreds of studies, one purpose of these chapters is to help separate the wheat from the chaff. A good chapter should not only summarize the data, but also act as a filter through the expertise of the author to help interpret the current state of the field. Is a finding significant, or is it a one-off observation? How do we interpret studies with directly contradictory conclusions? Some of the chapters are more successful at addressing these questions, offering interpretations of discrepancies in the literature and suggesting general themes. In other chapters, every finding is presented with equal weight, leaving it up to the reader to judge their importance. However, it is nice to

see more-recent research directions represented in this book, such as angiogenesis and cell polarity, even if the significance of some of these studies is less clear at this point.

Overall, this book is akin to an encyclopedia without alphabetization. Most facts that a reader might want to know are in there somewhere, it's just a matter of finding them (although the index is helpful). Because of this, one might be better served by reading through the entire volume, rather than searching for specific information in individual chapters. Editors of review compilations are limited by their ability to recruit authors with expertise, and Dr Sokol has brought together a first-rate group, possibly at the expense of a more-standardized selection of topics. The perfect book would have both.

## Through the eye of a book... on the eye

Carol Mason

Department of Pathology and Cell Biology, and Neuroscience, College of Physicians and Surgeons, Columbia University, 14-509 P&S building, 630 W. 168th Street, New York, NY 10032, USA  
E-mail: cam4@columbia.edu

doi:10.1242/dev.007419

### Retinal Development

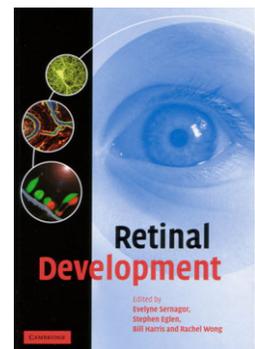
Edited by Evelyne Sernagor, Stephen Eglén, Bill Harris and Rachel Wong

Cambridge University Press (2006) 383 pages  
ISBN 10: 0-521-83798-7  
£75/\$130 (hardback)

The retina is perhaps our most intricate and well-studied sensory structure. It receives visual information from the outside world and interprets this information as color, shape and movement, and then transmits it to visual centers in the brain in the form of coded impulses. The embryonic and early postnatal retina has long been a rich setting for studying the basics of neural development – from cell genesis through axon guidance, synaptic interactions and the role of activity in the innervation of targets – perhaps more so than any other model sensory system. However, until now, a reference resource in the form of a review collection that guides the reader through the state-of-the-art approaches for studying retinal development has not been available. Especially daunting for the developmental biologist is the recent outpouring of molecular, genetic, functional and structural

data on the mature and diseased retina that have been published in a wide range of vision and neuroscience journals. Finding information on the developing eye, or information that bridges basic findings on retinal development to retinal disease, is not an easy task. As such, the book *Retinal Development* is especially welcome and is also a delightful read.

The editors of this fine collection of articles aim to tell the story of how the retina develops and to make this information accessible to developmental biologists, as well as to those interested in the causes of retinal disease. Although by now a little out of date, as is true of most books that are a collection of articles (most references are from 2004 and earlier), the volume serves as a ready reference to themes in retinal development, and points the way to topics now in the current literature. This book bears the stamp of the editors, all distinguished vision scientists who have worked on the developing retina from functional (Evelyne Sernagor and Stephen Eglén) and cell and molecular (Bill Harris and Rachel Wong) viewpoints, and bears



their characteristically clear and articulate style. The summaries, prose and style of the book are rich and consistent, and the index detailed. The editors must have taken to task their authors and guided them with a firm hand as each chapter has the same informative format; each has a developmental component, and brings the topic of a chapter back to the morphological and molecular beginnings of a particular cell type or developmental phase. Each chapter also brings to the fore a broad view of a particular topic, and not simply the purview or opinions of its authors.

The book begins with several chapters on 'how a patch of ectoderm becomes committed to become the complex sensory structure that the retina is'. The most remarkable of these, the first chapter by Michael Zuber and Harris, is on the formation of the eye field in the early embryo. Retinal neurons must then be generated and must migrate and become organized into layers, as described in the chapters by David Rapaport and by Leanne Godinho and Brian Link, which highlight how these events differ from those of the more widely studied cortical neurons. A refreshing aspect of the book is that it moves effortlessly up and down the phylogenetic scale, from zebrafish models to primates, and from early eye development through to more traditionally covered topics, such as retinal mosaics (by Eglen and Lucia Galli-Resta), programmed cell death (Rafael Linden and Ben Reese) and optic nerve formation (David Sretavan). As discussed below, these excellent chapters are capped off by considerations of the role of early neural activity in synaptogenesis (Sernagor) and on the onset of light responses (Sernagor and Leo Chalupa).

Far from being a dull review of what is known on these topics, the chapters in this book offer a blend of information on many different aspects of a given cell type or process that would be difficult to parse from a search in PubMed. A favorite chapter of mine is by Michalis Agathocleous and Harris on cell determination – how the different cell classes are formed and to what extent cell cycle progression affects this process. Vital nuggets of information are offered in these comparative reviews; for example, in the chapter by Jennie Close and Tom Reh, which emphasizes that the ciliary margin zone of frogs and fish is a continual source of progenitors or stem cells. As one who has searched for information about this specialized rim of the retina, I found a single figure and page packed with information on this structure that was enlightening. Likewise,

fascinating information on the mosaic organization of the retina can be found in the chapter by Eglen and Galli-Resta, and in the chapters by James Fadool and John Dowling and by Jeff Mumm and Christian Lohmann, on how cells and their dendrites are 'tiled' during early development.

A second goal of the editors was to highlight how the incredibly rapid development of techniques drives discovery, and, as is the case with imaging, how this progress can reveal detail never achieved before about developmental processes and cell organization. Several chapters describe studies that have been fuelled by advances in imaging of the retina in transgenic fish and mice, in which specific classes of cells have been labeled with fluorescent markers, an advance over the capricious Golgi method. Agathocleous and Harris discuss the monitoring of the activities of living,

---

**The editors of this fine collection of articles aim to tell the story of how the retina develops and to make this information accessible to developmental biologists and to those interested in retinal disease**

---

twitching neurons, and of retinal precursors that divide, migrate and visibly turn on a specification gene. Mumm and Lohmann chronicle the laying down of dendritic fields in the plane of the retina and the refinement of the lamination of dendritic arbors in the vertical plane of intrinsic retinal cells during retinal development. Always magical to witness, these studies are much needed if we are to understand how such neural circuitry arises in all its complexity.

During later development, even before the eyes open, intrinsic electrical activity is generated in retinal neurons and spreads across the retinal sheet. There is much debate about how this activity is generated, from which cells, and about which processes might require it. Also under debate is how this activity might direct the formation of the eye-specific connections of the long axons of retinal ganglion cells with their targets. A couple of chapters help to explain the context for, and the findings that contribute to, this debate. For example, the chapter by Sernagor describes how to make

sense of electrophysiological recordings from dozens of retinal cells and how to interpret synaptogenesis, whereas a companion chapter by Sernagor and Chalupa explains how to distinguish between retinal waves and the earliest light responses in the retina, and discusses how the plasticity of retinal ganglion cells is due to these modes of activities.

Some chapters, such as the one on glial cells in the retina, are wonderfully detailed. The chapter by Kathleen Zahs and Manuel Esguerra reviews everything you might want to know about the development, cell relationships and physiology of the Mueller glia, which, like the Bergmann glia of the cerebellum, remain radial throughout adulthood. Meanwhile, the chapter by Close and Reh outlines the developmental potential of radial glia, which can act as neural progenitors, and of retinal pigment epithelial cells, which can not only regenerate, but differentiate into new tissue containing the proper types and organization of retinal cells. These chapters are essential reading for those interested in stem cells.

Will clinical researchers working on the developmental origins of glaucoma or on adult macular degeneration refer to this volume? Most likely, yes. They should find David Sretavan's chapter on the developmental and molecular aspects of optic nerve formation of interest; the optic nerve is the primary site of damage in glaucoma, secondarily causing retrograde damage and the death of retinal ganglion cells. The chapter by Fadool and Dowling is of clinical relevance as it lays out the advantages of zebrafish as a model genetic system for identifying candidate disease genes through large-scale mutagenesis screens for factors that affect retinal cell development. Seth Blackshaw's chapter describes his herculean efforts at gene discovery in the retina. He points out the pluses and minuses of the different gene profiling techniques, and lists some of the developmentally relevant and cell-specific genes that have been identified. The chapters by Rachael Pearson on neurotrophins and neurotransmitters, and by Linden and Reese on cell death, describe growth factors that delay apoptosis in genetically determined retinal dystrophies. Some of these themes are hidden in chapters with basic science-sounding titles.

Although this book is aimed at the specialist, it will make good reading for graduate students and postdocs who are starting out on a project on the retina or visual system. My recommendation is: keep an eye out for it for your lab.