

Mechanisms of eye-specific visual circuit development

Andrew D Huberman

Eye-specific visual connections are a prominent model system for exploring how precise circuits develop in the CNS and, in particular, for addressing the role of neural activity in synapse elimination and axon refinement. Recent experiments have identified the features of spontaneous retinal activity that mediate eye-specific retinogeniculate segregation, the synaptic events associated with this process, and the importance of axon guidance cues for organizing the overall layout of eye-specific maps. The classic model of ocular dominance column development, in which spontaneous retinal activity plays a crucial role, has also gained new support. Although many outstanding questions remain, the mechanisms that instruct eye-specific circuit development are becoming clear.

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Introduction

What mechanisms induce development of precise CNS circuitry? A classic model circuit for investigating this question is eye-specific visual connections: axons carrying visual information for the left and right eyes are segregated into non-overlapping domains in the lateral geniculate nucleus (LGN) and into ocular dominance columns (ODCs) in the visual cortex. The cellular events involved in eye-specific retinogeniculate refinement are well characterized: after an initial overlap phase, axons from the two eyes segregate by elaborating synapses and axon terminals in the same-eye territory and by eliminating synapses and axon terminals in opposite-eye territory [1,2]. Spontaneous retinal activity is known to be required for segregation to occur [3], but several important questions have remained unanswered: which features of spontaneous retinal activity are instructive for eye-specific segregation? What are the molecular mechanisms for eliminating weaker synapses and maintaining strong ones? What factors dictate the

overall layout of eye-specific maps? Similar questions exist regarding ODC development as well. In the past decade, however, even the basic cellular events associated with ODC development have become controversial as several high profile studies [4,5] challenged the idea that ODCs are sculpted by early retinal activity. Here, I review recent advances in our understanding of retinogeniculate and ODC development, and I suggest experiments that could further elucidate how these circuits form.

The role of patterned retinal activity in eye-specific retinogeniculate segregation

Neural activity mediates development of eye-specific retinogeniculate projections through competitive interactions involving the relative levels of retinal ganglion cell (RGC) spiking in the two eyes [3,6]. Hebbian models predict, however, that correlated firing — and not simply activity levels per se — of neighboring RGCs is crucial for eye-specific segregation [7]. In theory, retinal waves [8] induce patterns of RGC spiking optimal for Hebbian-based axonal refinement but, surprisingly, the first experiments to perturb retinal waves did not observe any accompanying disruptions to eye-specific segregation in the LGN [9]. Moreover, some mutant mice with altered retinal waves exhibit severe eye-specific retinogeniculate defects [10], and yet pharmacologically inducing waves in these mutants does not rescue segregation [11]. Thus, to elucidate which aspects of spontaneous retinal activity instruct eye-specific segregation, Feller and colleagues [12**] undertook a systematic analysis of RGC spiking patterns in different strains of mutant mice, each with differently altered retinal waves but with varying degrees of eye-specific segregation in the LGN. They found that high frequency correlated bursting (>10 Hz) of neighboring RGCs is a key parameter required for eye-specific segregation. They also found that the precise time-window for RGC firing is not crucial for segregation, provided that the degree of correlated firing among closely spaced RGCs remains relatively higher than the degree of correlation among distant RGCs. Their results suggest why in previous experiments where retinal waves were disrupted, the anticipated defects in retinogeniculate refinement were not observed [6,9]. They also suggest which types of synaptic plasticity can (and cannot) drive segregation. For instance, because low frequency (~ 1 Hz) RGC firing is not related to segregation [12**], it is unlikely that typical forms of long-term depression (LTD) mediate synaptic elimination in this system. By contrast, the importance of high frequency RGC bursts suggests that bursts trigger plasticity mechanisms that both stabilize same-eye inputs and eliminate opposite-eye inputs onto single LGN cells (i.e. heterosynaptic depression). Through the use

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Table of Contents Eye Volume 3 Muscular Mechanisms

1. Understanding the eBook Eye Volume 3 Muscular Mechanisms
 - The Rise of Digital Reading Eye Volume 3 Muscular Mechanisms
 - Advantages of eBooks Over Traditional Books
2. Identifying Eye Volume 3 Muscular Mechanisms
 - Exploring Different Genres
 - Considering Fiction vs. Non-Fiction
 - Determining Your Reading Goals
3. Choosing the Right eBook Platform
 - Popular eBook Platforms
 - Features to Look for in an Eye Volume 3 Muscular Mechanisms
 - User-Friendly Interface
4. Exploring eBook Recommendations from Eye Volume 3 Muscular Mechanisms
 - Personalized Recommendations
 - Eye Volume 3 Muscular Mechanisms User Reviews and Ratings
 - Eye Volume 3 Muscular Mechanisms and Bestseller Lists
5. Accessing Eye Volume 3 Muscular Mechanisms Free and Paid eBooks
 - Eye Volume 3 Muscular Mechanisms Public Domain eBooks

- Eye Volume 3 Muscular Mechanisms eBook Subscription Services
- Eye Volume 3 Muscular Mechanisms Budget-Friendly Options
- 6. Navigating Eye Volume 3 Muscular Mechanisms eBook Formats
 - ePub, PDF, MOBI, and More
 - Eye Volume 3 Muscular Mechanisms Compatibility with Devices
 - Eye Volume 3 Muscular Mechanisms Enhanced eBook Features
- 7. Enhancing Your Reading Experience
 - Adjustable Fonts and Text Sizes of Eye Volume 3 Muscular Mechanisms
 - Highlighting and Note-Taking Eye Volume 3 Muscular Mechanisms
 - Interactive Elements Eye Volume 3 Muscular Mechanisms
- 8. Staying Engaged with Eye Volume 3 Muscular Mechanisms
 - Joining Online Reading Communities
 - Participating in Virtual Book Clubs
 - Following Authors and Publishers Eye Volume 3 Muscular Mechanisms
- 9. Balancing eBooks and Physical Books Eye Volume 3 Muscular Mechanisms
 - Benefits of a Digital Library
 - Creating a Diverse Reading Collection Eye Volume 3 Muscular Mechanisms
- 10. Overcoming Reading Challenges
 - Dealing with Digital Eye Strain
 - Minimizing Distractions
 - Managing Screen Time
- 11. Cultivating a Reading Routine Eye Volume 3 Muscular Mechanisms
 - Setting Reading Goals Eye Volume 3 Muscular Mechanisms
 - Carving Out Dedicated Reading Time
- 12. Sourcing Reliable Information of Eye Volume 3 Muscular Mechanisms
 - Fact-Checking eBook Content of Eye Volume 3 Muscular Mechanisms
 - Distinguishing Credible Sources
- 13. Promoting Lifelong Learning
 - Utilizing eBooks for Skill Development
 - Exploring Educational eBooks

14. Embracing eBook Trends

- Integration of Multimedia Elements
- Interactive and Gamified eBooks

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