Color and the Cone Mosaic

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Abstract

Compensation of the eye's aberrations with adaptive optics allows high resolution images and identification of individual cones in the living human eye. Such images, combined with psychophysical measures in the same eyes, reveal the effect of the trichromatic cone mosaic on color and spatial vision. Perhaps the most striking conclusion from this work is how little impact the topography of the mosaic has on vision, illustrating the brain's cleverness in concealing variations in cone topography from our visual experience. Application of adaptive optics imaging of the cone mosaics of color blind eyes in conjunction molecular genetics has revealed a new cause for color blindness. Finally, adaptive optics can also be used to probe single cones in the human eye with tiny flashes of light. This produces a striking variation of color experience from flash to flash that calls for a revision of prevailing models of human color processing.

Adaptive Optics Imaging of the Trichromatic Cone Mosaic

By compensating for all the significant monochromatic aberrations in the eye's cornea and lens, adaptive optics can provide microscopic views of the living retina with increased transverse resolution, high enough to resolve single cone photoreceptors [1]. One of the first demonstrations of the scientific value of retinal imaging with adaptive optics was its use in identifying the photopigment in single human cones *in vivo* [2]. It has been known for nearly 200 years that human color vision depends on three fundamental channels in the retina, the short wavelength (S), middle wavelength (M), and long wavelength (L) cones, but the packing arrangement and relative numbers of two of the three cone classes (the L and M cones) remained unclear. With adaptive optics, we succeeded in classifying large numbers of living human foveal cones by comparing images of the photoreceptor mosaic when the photopigment was fully bleached with those when the photopigment was selectively bleached with different wavelengths of light. Heidi Hofer subsequently improved this method and increased the number of eyes that were characterized [3]. The images obtained with this method show an essentially random, or nearly random, packing arrangement of the cones as well as the large variation from eye to eye in the ratio of L to M cones in the normal retina. The retinas imaged to date span a 45-fold range of L to M cone ratio. One of the striking findings from this work was that color appearance does not vary with L to M ratio [4, 5].

Pokorny and Smith [6] had previously suggested that experience with the chromatic environment rather than cone numerosity establishes the subjective boundaries between hues. Neitz et al. [5] described experimental support for this view, showing that the color boundary between red and green, unique yellow, can undergo modification over a period of many days of exposure to an altered chromatic environment.

Imaging the Color Blind Mosaic

Adaptive optics has also provided a valuable new tool for understanding the origins of color blindness [7]. Dichromatic color vision results from the functional loss of one cone class, however, one of the central questions has been whether individuals with this form of red-green color-blindness have lost one population of cones or whether they have normal numbers of cones filled with either of two instead of three pigments. Evidence has accumulated favoring the latter view in which the photopigment in one class of cone is replaced, but the issue had not been resolved directly. Joe Carroll, working with the adaptive optics system at Rochester, obtained images of the mosaics of many dichromats, most of which had normal numbers of cones (though they had only two instead of three different pigments filling them). However, some dichromats show a striking departure from this rule. For example, a dichromat was imaged who has the genes for all three photopigments, but a novel mutation in one of those genes. His mosaic is randomly peppered with gaps, corresponding to a loss of 30% of the cones in his retina. This finding suggested that previous models of dichromacy do not hold for all subjects. One of the intriguing aspects this patient is that his visual acuity is normal (20/16) despite the loss of 30% of his cones. This result highlights the insensitivity of conventional clinical tests of retinal disease, and points to the role that adaptive optics may eventually play in the early detection of diseases that produce the dropout of photoreceptors or perhaps other neurons such as the ganglion cells which are damaged by glaucoma.

Microstimulation of Single Cones

Adaptive optics has also provided an opportunity to explore the color appearance produced by stimulating individual cones or small groups of cones with tiny, brief flashes of monochromatic light [8]. It has been known since Holmgren [9] that the color appearance of such stimuli fluctuates from flash to flash, presumably depending on the specific photoreceptors that are excited by each flash. Adaptive optics allows us to make much more compact light distributions on the retina, enhancing these color fluctuations and making them easier to study in the laboratory. Hofer et al [8] could explain the variation in color appearance with a model in which different cones containing the same photopigment produce different chromatic sensations when stimulated. These experiments showed that the color sensation produced by stimulating a cone depends on the circuitry each cone feeds rather than simply on the photopigment the cone contains.

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Author Biography

Williams completed his Ph.D. at UCSD in 1979 and a postdoc at Bell Laboratories in 1980. He is currently William G. Allyn Professor of Medical Optics and Director of the Center for Visual Science at the University of Rochester. Williams develops optical technology to explore the limits of spatial and color vision. Awards include the OSA Edgar G. Tillyer Award in 1998 and the Association for Research in Vision and Ophthalmology's Friedenwald Award in 2006.