Chromatic Topography of the Retina

INTRODUCTION

Color vision is both initiated and limited by the responses of retinal cone photoreceptors. It is well established that in primates there are three main classes of cone—long-, middle-, and short-wavelength sensitive (L, M, and S, respectively)—each maximally sensitive to a different region of the visible spectrum. The fact that just three classes of cone sample the visible spectrum restricts the spectral information available for visual processing and leads to the trichromacy of human vision. Furthermore, these three cone types are confined to a two-dimensional surface, or mosaic, on the retina—a configuration that imposes additional constraints on the ability of cones in their dual role to provide both spatial and color vision. The packing arrangement and the relative proportions of the cones are properties of the retinal cone mosaic that are still not well understood. There is evidence that individual differences in these topographic features occur in the human population and that the arrangement and proportion of the photoreceptors also vary across species, both within the primates and across other mammals. Consideration of individual differences in the architecture of the photoreceptor mosaic both within and across species is beginning to provide insight into the relationship between the chromatic topography of the retina and visual capacity. Current experiments are providing the foundation for a complete understanding of the neural circuits for color vision and how they function. They are also laying the groundwork for understanding the biological mechanisms that position the cones in the retinal mosaic during development and how the neural circuits might adjust to compensate for large biases in the cone ratios.

Recent advances in experimental techniques, together with more-traditional assessment methods, are now providing a clearer picture of the chromatic topography of the retina. New techniques include direct imaging, using adaptive optics, of living human photoreceptors; estimation of cone proportions by analysis of gene expression in photoreceptor cells; and physiological mapping of the primate retina. The goal of this March special feature is to present, in one forum, a series of papers that represent the diversity of experimental approaches that have been brought to bear on understanding the chromatic topography of the retina and its implications. These approaches include techniques of optics, psychophysics, anatomy, physiology, and molecular biology. The 16 papers presented herein have been segregated into three broad categories: distribution and proportion of L and M cones (six papers), distribution of S cones and their pathways (three papers), and processing of photoreceptor signals and consequences of topography (seven papers). The papers concerning the L and M cones are separated from the S cone papers because primate color vision depends on two parallel subsystems. One system is phylogenetically ancient, and it compares the outputs of the S cones with those that absorb in the medium-to-long wavelengths. The other system compares outputs among the L and M cones; it has evolved very recently and is found only in primates and in humans. The papers in the third category emphasize the implications of chromatic topography at higher levels of chromatic processing.

In the first category, Carroll *et al.* estimate the proportion of L:M cones, using the electroretinogram; Krauskopf considers estimates of the relative contributions of L and M cones in psychophysical measurements; and Kremers *et al.* compare estimates of the cone proportions from measurements, using both psychophysics and the electroretinogram. Hagstrom *et al.* employ a molecular biology approach to examine the ratio of L:M cones in the human retina, and Deeb *et al.* bring molecular biology to bear on the issues of the L:M cone ratio in macaques. In the final paper of the first group, Dobkins *et al.* examine differences in the L:M ratio between macaques and humans.

In the second category of papers, Martin *et al.* study the distribution of the S cones in the primate retina, and Szél *et al.* examine the distribution of S cones in subprimate species, paying special attention to the pattern of S cone photopigment expression during development. In the final paper of the second group, Ahnelt *et al.* consider issues of connectivity of S cones with second-order neurons.

Dacey *et al.* begin the third group of papers with an examination of the physiology of L and M cone inputs to horizontal cells that connect with cones in the primate retina. Calkins considers the representation of cone signals as they are processed through the neural layers of the primate retina. The paper by Brainard *et al.* brings us back to human physiology. They examine electroretinograms and psychophysical measures for two male observers who were found to have dramatically different L:M cone proportions by direct imaging through adaptive optics. In the next paper, Otake and Cicerone examine issues of L:M cone ratio and consequences for processing of chromatic signals. Using a similar approach, Volbrecht *et al.* consider the implications of the S cone mosaic and rods for color signals in the retina. The arrangement of the cones and the implications for vision have long been a topic of interest. In their paper, Hsu *et al.* show that, when one considers the electrical coupling between the cones, patchiness of L and M cones may provide stronger chromatic signals than a regular array of alternating L and M cones. In the final paper of the feature, Volbrecht *et al.* use a psychophysical approach to examine the spatial summation of the human cone signals in the human retina.

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