Chapter 13

Inert Absorbing and Reflecting Pigments

By

W. R. A. Muntz, Falmer, Brighton (Great Britain)

With 16 Figures

Contents

I. Introduction .......................................................... 530

II. Pre-Retinal Absorption ................................................ 530
  A. Spectral Characteristics of Lens, Cornea, and Vitreous in Vertebrates ........................................ 530
     1. Early Work .................................................. 530
     2. Spectrophotometric Data ................................... 531
     3. Fluorescence ................................................ 536
     4. Function of Yellow Lenses and Corneas .................. 537
  B. Invertebrate Corneas ............................................. 538

III. Absorption at the Retinal Level ................................. 540
  A. Oil Droplets .................................................... 540
     1. Introduction ............................................... 540
     2. Spectrophotometric Data ................................... 540
     3. Distribution in the Retina ................................ 543
     4. Phylogenetic Distribution .................................. 544
     5. Development ................................................ 547
     6. Effect on Spectral Sensitivity ............................. 547
     7. Theories of Oil-Droplet Function ......................... 549
        a) Role in Colour Vision .................................... 549
        b) Other Theories ......................................... 552
  B. Blood Vessels ..................................................... 553
  C. The Macular Pigment ............................................ 553
  D. Photopigments and Photoproducts ............................... 554

IV. Absorption and Reflection Behind the Retina .................. 556
  A. Introduction .................................................... 556
  B. Melanin ........................................................ 556
  C. The Tapetum ..................................................... 556
     1. The Tapetum Fibrosum ...................................... 556
     2. The Tapetum Cellulosum .................................... 557
     3. Choroidal Tapeta .......................................... 558
     4. Retinal Tapeta .............................................. 559
     5. Invertebrate Tapeta ........................................ 559

V. Summary .................................................................... 560

References .................................................................... 561

E. W. Abrahamson et al., *Photochemistry of Vision*

© Springer-Verlag, Berlin · Heidelberg 1972
I. Introduction

One of the most striking early correlations between physiology and behaviour was König's (1894) demonstration that human scotopic spectral sensitivity resembled the spectral absorptive characteristics (difference spectrum) of a pigment — visual purple, or rhodopsin — that he extracted from the human retina. Later comparisons between such functions (e.g. Hecht and Williams, 1922; Dartnall and Goodeve, 1937; Wald, 1938; Crescitelli and Dartnall, 1953; Dartnall, 1953; Wald and Brown, 1958; Weale, 1961; Dartnall, 1961) have amply confirmed König's hypothesis. No one today doubts that the photosensitive pigments in retinal receptors mediate vision, and the sophisticated comparisons that are now possible serve rather to give some insight into the nature of the visual process.

Spectral sensitivity can be defined as the spectral variation of the reciprocal of the relative numbers of quanta in stimuli that evoke equal responses. These numbers must, of course, refer to the stimuli that reach the visual pigment. The quantal intensities measured are those incident on the cornea, and hence allowance must be made for the substantial losses by absorption in pre-retinal media (e.g. cornea, lens, and humours) and for the (usually small) gains by reflectance and fluorescence of surfaces lying behind the retina. The correlation between human scotopic sensitivity and human visual pigment has improved as each of these effects has been measured and allowed for, until, today, the two sets of measurements agree within the limits of experimental accuracy.

The success of the comparison in the human case has led to numerous other attempts to correlate visual pigment absorbance spectra and measures of spectral sensitivity. These have included, for example, attempts by Wald (1949) and Granit (1955) to identify the pigments underlying scotopic and photopic vision in a variety of animals, as well as attempts to unravel the workings of the retina by hypothesising interactions between receptors that are assumed to contain various visual pigments (e.g. Rushton, 1959).

Work of this type requires a knowledge of the absorption characteristics of all the structures in the eye lying between the photosensitive pigments and the light. It also requires a knowledge of any fluorescence and scattering that may occur, and of any reflecting structures in the eye, such as a tapetum. The purpose of the present chapter is to review the data that are at present available on these questions. This subject was reviewed by Walls and Judd in 1933 (summarised in Walls 1942), and, in general, work previous to that date will not be covered in this chapter.

II. Pre-Retinal Absorption

A. Spectral Characteristics of Lens, Cornea, and Vitreous in Vertebrates

1. Early Work

It has long been known that the lens and cornea of some vertebrates are yellow in colour. Walls and Judd (1933) presented a comprehensive review of the