Studies of Brain Function

Eberhart Zrenner

Neurophysiological Aspects of Color Vision in Primates

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Comparative Studies on Simian Retinal Ganglion Cells and the Human Visual System

With 71 Figures

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To my wife Claudia,
*to Christoph Daniel Frederik * 5.2.1981,*
and his grandparents

Preface

"To explain all nature is too difficult a task for any one man or even for any one age. 'Tis much better to do a little with certainty, and leave the rest for others that come after you, than to explain all things . . ."
Sir Isaac Newton (1642–1727)

This book describes and discusses some new aspects of color vision in primates which have emerged from a series of experiments conducted over the past 8 years both on single ganglion cells in monkey retina and on the visually evoked cortical potential in man: corresponding psychophysical mechanisms of human perception will be considered as well. An attempt will be made to better understand the basic mechanisms of color vision using a more comprehensive approach which takes into account new mechanisms found in single cells and relates them to those found valid for the entire visual system. The processing of color signals was followed up from the retina to the visual cortex and to the perceptual centers, as far as the available techniques permitted.

Since the neurophysiological link between the physiological function of neurons and visual perceptions is still missing, it cannot be my intention to speculate on the neuronal basis of certain perceptions. However, in several cases the reverse approach was taken, namely to detect in the perceptive phenomena the action of the neuronal mechanisms of single cells, which beyond any doubt contribute to building up such perceptions as simultaneous color contrast, flicker-induced colors, brightness enhancement, transient tritanopia, and many others. Attention is also given to review articles and publications which enable the reader to gain information about matters which at first sight are not directly related to color vision but are crucial to the understanding of some mechanisms described here.

Since the primary object of this book is color vision, mechanisms subserving spatial resolution as well as light and dark adaptation will only be discussed as far as they interrelate with color vision. The well-known psychophysical and electrophysiological data on trichromatic color vision are touched upon only briefly; the reader interested in gaining a broader view of the subject is therefore referred to the following sample of comprehensive books, chapters, reviews and articles, which have appeared over the last 25 years: Judd (1943), Pitt (1944), Boynton (1960), Trendelenburg (1961), Linksz (1964), MacNichol (1964), Schober (1964), Graham (1965), Jung (1965, 1973, 1978), De Valois and Abramov (1966), Wyszecki and Stiles (1967), Baumann (1968), Le Grand (1968), Sheppard (1968), Creutzfeld and Sakmann (1969), Wright (1969), Ripps and Weale (1969), Brindley (1970), Cornsweet (1970), Motokawa (1970), Abramov (1972), Rushton (1972a), Walraven (1972), Daw (1973), MacNichol et al. (1973), Rodieck (1973), Davson and Graham (1974), De Valois and De Valois (1975), Davson (1976), Scheibner (1976a,b), Hurvich (1977, 1981a,b), Verriest and Frey (1977), Baumgartner et al. (1978), Stiles (1978), Wasserman (1978), Boynton (1979), Dodt (1979), Robinson (1980), Gouras and Zrenner (1981b), Mollon (1982).

Nevertheless, the attempt is made in the introduction (Chap. 1) to summarize the pertinent information contained in these publications, including some historical backgrounds.

The questions raised by the newly discovered (or less known) mechanisms in single simian ganglion cells and visually evoked cortical potentials will, however, be described in depth. It is to be hoped that they can provide the basis for a more comprehensive understanding of the processes involved in primate color vision.

For a survey of the data and concepts presented in the following, the reader is referred to the summary at the end of the book.

Bad Nauheim, October 1982 Eberhart Zrenner

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Contents

1 Introduction

The ultimate purpose of the visual system is the detection of objects and their spatial relationship. These objects appear in a continuously changing environment concerning their brightness, their position, and distance to the observer. In this respect, the primate visual system performs with great precision a number of outstanding tasks, which to a large degree even conflict with each other. Visual perception of brightness contrasts has an enormous dynamic range from a bright sunny beach (about 10^4 cd/m^{-2}) to a moonless night (about 10^{-7} cd/m^{-2}) without considerably losing its time resolution, as happens with photographical material at low light levels. Moreover, small spatial details, down to a few seconds of arc, can be resolved, *without* sacrificing the large visual field of more than $120°$.

Color vision plays an important role in carrying out these functions. Since the borders of objects often have the same luminance as their background, only the capability of discerning illuminated areas by the wavelengths of the light quanta reflected enables the visual system to detect these objects (see Cavonius and Schumacher 1966). Moreover, differences in the spectral reflection properties of objects and the background on which they are presented are often small, so that the ability to discriminate adjacent colors must be outstanding in order to permit orientation in a spectrally more or less homogeneous environment. For instance, primates living in trees, surrounded by myriads of green leaves with very similar spectral reflectance and brightness, would easily become disoriented if they had to rely on a visual system which signalled only some twenty shades of grey. Color vision expands the range of discernable light stimuli to about seven to ten million (Judd 1952) taking into consideration different degrees of brightness and saturation of the about 200 hues which we can differentiate in the sun's spectrum. To this end, nature has to make compromises; for instance, the visual system obviously does not need to analyze the entire spectrum of frequencies in a stimulus (as the auditory system can to a certain extent), but it only needs to differentiate between groups of frequencies.

How was knowledge about color vision gained in the past few centuries?