Edited by Hugh Davson

the EYE

Volume 2

THE EYE

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VOLUME 2

The Visual Process

1962

ACADEMIC PRESS, *New York and London*

ACADEMIC PRESS INC.
111 FIFTH AVENUE
NEW YORK 3, N.Y.

United Kingdom Edition
Published by
ACADEMIC PRESS INC. (LONDON) LTD.
BERKELEY SQUARE HOUSE, BERKELEY SQUARE,
LONDON W.1.

Library of Congress Catalog Card Number 61-10694

PRINTED IN GREAT BRITAIN

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Foreword

THE study of the physiology of the eye employs a wide variety of scientific disciplines; for example, its vegetative physiology and biochemistry bring us into the realms of electron-microscopy of such structures as the ciliary epithelium, vitreous body and cornea; the active transport mechanisms concerned with the function of the aqueous humour; the special problem of a vascular circulation in a semi-rigid cavity; the metabolism of avascular tissues, and so on. Similarly with other aspects, so that the compilation of an authoritative treatise on the eye is best carried out by a group of research workers who are experts in particular aspects. In the present work the Editor has attempted to provide a well-integrated and authoritative account of the physiology of the eye, and to this end the fractionation of the subject, necessary in a multi-author work, has been minimized as far as practicable, so that it is hoped that the book will be read more as an advanced text than consulted as a "Handbook". The emphasis has been on function so that the Editor has been content with an elementary introductory outline of the anatomy and embryology of the eye, detailed descriptions of the anatomy of any part being postponed until they could be given in their immediate physiological context.

Whilst the emphasis has been on readability rather than exhaustiveness, the various accounts are sufficiently well documented to make the treatise valuable not only to teachers in physiology, psychology and ophthalmology, but also to research workers in all branches of ocular physiology.

HUGH DAVSON

Acknowledgments

PART I

The preparation of Chapters 1 to 16 has been assisted by grant No. B-1810 from the National Institute of Neurological Diseases and Blindness, United States Public Health Service. We are also greatly indebted to Dr. W. S. Stiles and Dr. B. H. Crawford for discussions and unpublished information.

M. H. PIRENNE
F. H. C. MARRIOTT

PART II

Without the encouragement and exhortations of my wife this contribution would not have been completed in the short time available.

I am grateful also to Sir Stewart Duke-Elder, Dr. Katharine Tansley and Dr. C. D. B. Bridges for reading all or part of the text, and to my assistant Mrs. Margaret Bright for drawing many of the original figures.

H. J. A. DARTNALL

PART III

The publishers acknowledge with thanks permission granted to reproduce the illustrations on the following pages: p. 542, Presses Universitaires de France; pp. 545, 546, 699, 704, University of Chicago Press; p. 589, Fig. 6, M. Pierre Danis; p. 627, National Physical Laboratory; p. 646, Oxford University Press; pp. 746, 748, Methuen & Co.

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CHAPTER 21

Introduction

In view of the amount of space allotted to this part of the book—ample in itself but modest considering the enormous literature on the anatomy and physiology of the visual pathway—some indication of what can be aimed at is needed. A major sacrifice is the omission of historical background. The anatomical aspects will be found detailed in Polyak's (1957) comprehensive historical summary. The history of the neurophysiology of the retina, reasonably complete up to 1945, has been described in the author's (1947) "Sensory Mechanisms of the Retina." In terms of neurophysiological experimentation the rest of the visual pathway has a fairly brief history. The first steps were summarized by Bartley in 1941, later developments by Albe-Fessard in 1957. Recently Müller-Limmroth (1959) has published a book on the retina and the visual pathways aiming at completeness with regard to references from the electrophysiological field; to this work the reader is referred for the literature on a large number of special questions such as, for instance, effects of cold, pressure, and drugs on the electroretinogram. Below it has been found necessary to introduce descriptive material of this kind in a manner wholly determined by the relevance of such facts to knowledge of a more coherent type. Albeit deficient, there exists at the moment neurophysiological knowledge with some structure to it and the author's aim is to explain, for beginners, the aims of the experimenters, what has been achieved and also to mention some major deficiencies in our knowledge. Some examples should make clear why this attitude has been adopted.

To the beginner too many loosely connected facts merely would be confusing. Actually they fall into two categories: on the one hand we have facts at the moment really confusing, or facts insignificant, striking, stimulating, as the case may be, on the other hand we have facts that have been assembled in order to illuminate a piece of structural knowledge. This structure may not always be easily discernible. Thus, for instance, the beginner, who is bewildered by the large number of purely descriptive papers dealing with the electroretinogram (ERG) of different animals including man, may not realize that much of this material has served to test the generalization (Granit, 1935) that there are two main types of ERG, those of rod and cone systems respectively—originally called E- and I-retinograms—and that in mixed eyes both types co-exist and can be separated by measures such as light-adaptation, flicker-frequency, and choice of wavelength. This is the kind of organized knowledge that can be built up only by extensive team work on a variety of animals. Today one is entitled to state that we know the main features of rod and cone electroretinograms and can predict fairly well what will happen in mixed eyes when experimental conditions are varied in certain directions so as to replace scotopic with photopic vision. This means that the results of a very large number of papers now can be briefly summarized in support of a single, broad generalization. Many neurophysiological problems run through such a phase of "accumulation" of facts.

On the other hand there are neurophysiological questions which from the very beginning can be stated with considerable precision and which require a few decisive experiments to exclude some alternatives in favour of others. Thus Himstedt and Nagel in 1902 raised the question of whether the region of maximum spectral sensitivity of the frog's eye—as in man—shifted towards the short wavelengths in dark-adaptation (an effect that in honour of its discoverer we call the Purkinje shift (Purkinje, 1823)) and the reply was "yes", even though, at the time, it was not qualified by precise energy calibrations of the spectrum used. A related problem (Granit *et al.*, 1938, 1939) was whether the amplitude of the ERG in rod vision simply reflected the available amount of visual purple or rhodopsin—the photochemical pigment of the rods—and the answer was "no," as was established by parallel measurements of the two.

Two major aims have animated physiological research on the visual system. In one group stand the biochemical or biophysical questions which to some extent are independent even of the kind of organ that happens to be their subject, and which generally in the last instance lead to the cellular or molecular stage. The aim of the other line of research is to understand the organization of the sensory message in order to elucidate principles of information and control. This is often called integrative physiology. There is no hard and fast boundary between the two modes of approach. But "organization" and "information" touch upon a host of interesting epistemological problems. Constant interchange between the organism and its environment has created biological structures which from this point of view are manifestations of certain aims. Thus the eyes of night animals and day animals are very different and in biology it is just as legitimate to describe the "meaningful" adaptations for these two extreme conditions as to determine, say, the quantum efficiency of rhodopsin. Another example is the mechanism of colour reception. If colour had not been perceived by man, the problem might never have occurred to us and, when studying electrophysiologically the effects of variations of wavelength on the eye, our own world of colour and light remains in the background as a secret frame of reference, guiding or misguiding—as the case may be—by preconceived notions our research, and again secretly introducing questions of purpose and meaning, the general problem of how something is organized to perform certain tasks.

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ADDENDUM

This review was completed in January 1960. Since then the following major summaries have appeared:

Brindley, G. S. (1960). "Physiology of the Retina and Visual Pathway". Edward Arnold, London.

Galifret Y. (Ed.) (1960). "Mechanisms of Colour Discrimination". Pergamon Press, London.

Jacobson, J. H. (1961). "Clinical Electroretinography". Charles C. Thomas, Springfield.

Jung, R., and Kornhuber, H., (Eds.) (1961). "The Visual System: Neurophysiology and Psychophysics". Springer Verlag, Berlin, Göttingen, Heidelberg.

CHAPTER 22

Retina and Optic Nerve

I. Features of Retinal Organization

The amount of organizational detail that the histologists have detected in the retina is far in excess of what physiologists have been able to make use of. Ramón y Cajal's (1894, 1933) and Polyak's (1941) use of the Golgi silver stain is responsible for this state of affairs as it revealed so much of the synaptic organization of this "true nervous centre" (Ramón y Cajal's words). Ontogenetically the retina is well known to be derived from the brain. Thus, in the eye a nervous centre closely co-operates with the lining of receptors directly behind it (or inwards since the vertebrate eye has been inverted in the course of ontogenetic development). This centre is a veritable microcosm of its own. Some simplification in its complex anatomy can be introduced by emphasizing fundamental features with probable physiological correlates at the expense of features which at the moment only make the subject difficult to understand.

A. Receptors

The receptors fall into two categories, rods and cones, which through an internuncial neurone, the bipolar cell, are connected to the ganglion cell whose axon runs upwards as a fibre in the optic nerve. The retinal centripetal path is therefore disynaptic. (It might be noted that Polyak (1941) in his monumental work on the retina uses "monosynaptic" and "polysynaptic" in a sense which is altogether different from what is customary in neurophysiology.) Definitions of rods and cones have been discussed, for example, by Walls (1942), Detwiler (1943) and Granit (1947). Recent extensive

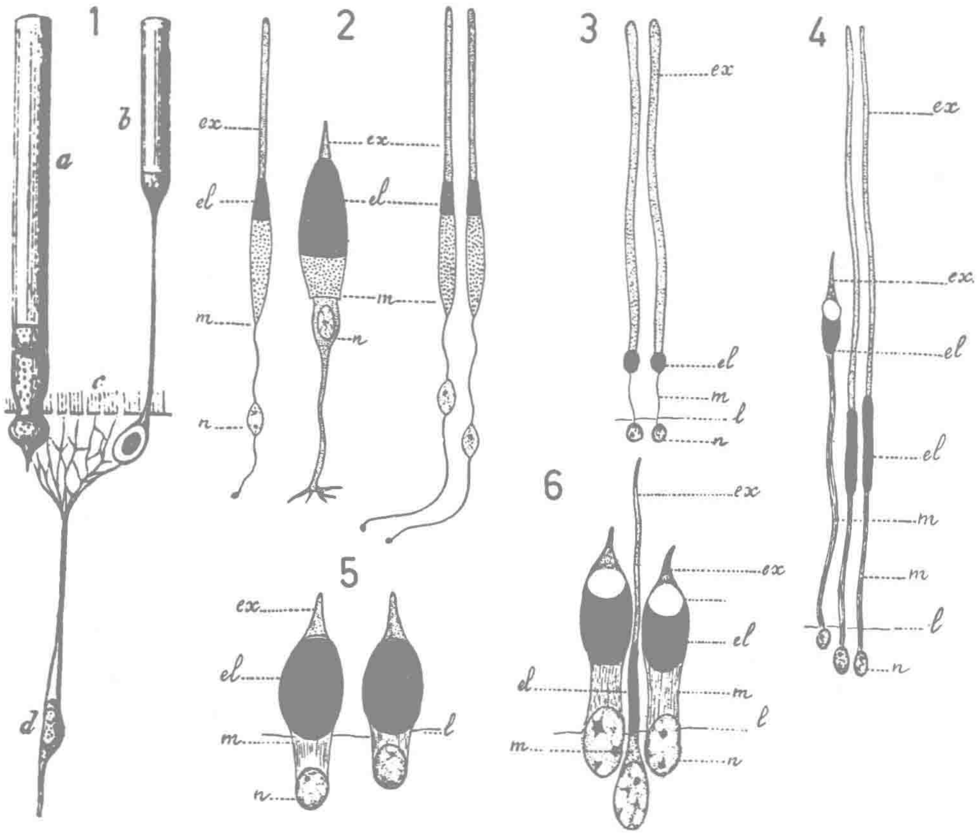

FIG. 1. Samples of rods and cones from different retinae.

1. (*a*) common or rhodopsin rod; (*b*) "green rod" (Schwalbe, 1874); (*c*) membrana limitans externa.
2. on the left, rod and cone from the periphery; on the right, cones from fovea of human retina.
3. Rods of the conger eel (*Conger vulgaris*).
4. Rods and cones of a bird (*Tyto alba*).
5. Cones of a snake (*Tropidonotus piscator*).
6. Rods and cones of pig (*Sus scrofa*). *ex*, external segment; *el*, ellipsoid; *m*, myoid; *l*, membrana limitans externa; *n*, nucleus.

(Verrier, 1935)

histological studies will be found in works by Rochon-Duvigneaud (1943), Verrier, (1935), Walls (1942) and Verriest *et al.* (1959).

Visual receptors (for structural details, see Part II) are known to vary a great deal in form (Fig. 1), especially in lower vertebrates. This seems to apply to cones more than to rods when any one single species is considered. Yet in frogs there are two kinds of rods, the ordinary, or *rhodopsin*, rods and the *green* rods discovered by Schwalbe (1874). Sjöstrand's work (1953b) has led to a separation of two kinds of rods, α- and β-rods, in a mammal such as the guinea-pig, but for this electron-microscopy has been needed. Twin cones or various types of double cones are known in several lower vertebrates, including the frog (from a large number of histological papers; Walls, 1942). The frog is of particular interest because there is a considerable amount of neurophysiological and photochemical work done on its eye and it has been concluded by Donner (1958), on the basis of experiments by himself and Rushton, that its spectral sensitivity is strongly reminiscent of that of man. Our own eye has very slender elongated cones in the fovea where they look like rods whilst the peripheral cones really look like cones (see Fig. 1).

1. FOVEA

The fovea defined physiologically as the rod-free area has a diameter of the order of 1°. Anatomically this is the middle of the well-known central depression whose diameter approaches 5° (Polyak, 1941, p. 198). Lower mammals lack a rod-free area of physiological fovea. It is best developed in primates and in birds, many of which have two foveae. Most mixed eyes possess, however, an area centralis retinae with a relatively greater number of cones; described for some domestic animals including the cat by Chiewitz (1889) and Zürn (1902). There are also some exceptional foveae based entirely on rods. A most interesting case is a fish (*Bathylagus*), studied by Vilter (1954a), which has a temporal fovea for binocular vision with 800,000 rods/mm.^{2}, arranged in several layers, as many as six in the middle of the fovea (cf. man with 200,000 cones/mm.^{2} in the fovea, Vilter, 1954b).

The dimensions of the rod-free area in the human fovea are a much discussed theme. The reason for this is that the work of early psychophysical research workers, which led to the conclusion that rods are twilight or scotopic organs and cones daylight or photopic receptors, was based on comparisons between foveal and peripheral vision (von Kries, 1929; Dieter, 1931; later summarized by Hecht, 1937).

2. DUPLICITY THEORY

Max Schultze (1866, 1867, 1871) laid the anatomical foundations for this important generalization, the so-called duplicity theory. This he did by extensive histological studies of the retinae of animals that were nocturnal, diurnal or ambivalent. Subsequent work has confirmed his conclusions which have survived, the only modification being that, in certain reptiles like the gecko, some rods may be transmuted cones. Walls (1942) in formulating the latter theory, drew his evidence from structural similarities between undeniably diurnal reptiles and nocturnal ones. Some support for this theory is found in recent histological work by Underwood (1951) and Tansley (1959). Today we possess a number of physiological criteria for differentiating rod- and cone-eyes which will be discussed below. Suffice it here to mention that in some species of nocturnal geckos Dodt and his collaborators (Dodt and Heck, 1954; Dodt and Walther, 1959) using the electroretinographic method have obtained cone-like responses, but not in others. More recent evidence for and against the transmutation theory will be found summarized in the papers by Dodt and by Tansley. (See also discussion by Verriest *et al.*, 1959; for photochemical aspects, see Crescitelli, 1958.)

3. SPECTRAL SENSITIVITY

In much work on the retina it has been found most convenient to distinguish rods from cones by their spectral response curves and adaptive properties (see Chapter 23 and Part II). The rods of man, cat and frog, for instance, all have their maximum average sensitivity in the blue-green around 500 mμ, the cones around 560 mμ (yellowish green). The rods adapt to maximum sensitivity in the dark more slowly than the cones. Parallel with this runs the change of average spectral sensitivity, first observed by Purkinje (1823) and above defined as the Purkinje shift. In terms of everyday experience it means that blue flowers, for instance, lighten in the evening while red ones look darker.

4. TRANSDUCER

From the neurophysiological point of view the receptor is merely the initial link of a complex retinal organization which rearranges or interprets the information received. This is done according to principles which we, in our turn, try to elucidate by combining anatomy with physiology into a common framework of reasonable hypotheses. The receptor serves as a transducer of energy into a form suitable for stimulating the next station, which in vertebrates is the bipolar cell. On this general problem (Granit, 1947) an instructive paper has recently been written by Lipetz (1959) who bases his arguments on Hartline's well-known invertebrate preparation, the lateral eye of the horseshoe crab *Limulus*. Still more primitive transducers are various pigmented neurones such as giant cells in the mollusc *Aplysia* which discharge impulses upon illumination. These have been studied by Arvanitaki-Chalazonitis (summarized in 1959).

B. Synaptic Relationships

In the schematic picture of Fig. 2 we can see that the synaptic contact between receptors and bipolars is different for rods and cones, the former

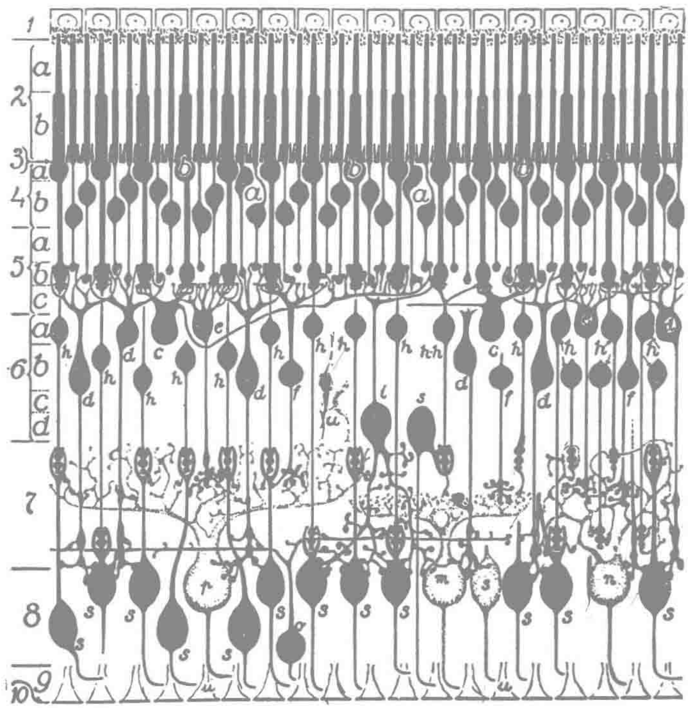

Fig. 2A. Scheme of the structures of the primate retina as revealed by the method of Golgi. The layers and the zones are designated as follows: (1) pigment layer; (2–*a*) outer zone and (2–*b*) inner zone of the rod and cone layer; (3) outer limiting membrane; (4–*a*) outer zone and (4–*b*) inner zone of the outer nuclear layer; (5–*a*) outer zone, (5–*b*) middle zone and (5–*c*) inner zone of the outer plexiform layer; (6) inner nuclear layer with its four zones; (7) inner plexiform layer; (8) layer of the ganglion cells; (9) layer of the optic nerve fibres; and (10) inner limiting membrane. The nerve cells are designated as follows: (*a*) rods, (*b*) cones, (*c*) horizontal cells, (*d*, *e*, *f*, *h*) bipolar cells, (*i*, *l*) so-called "amacrine cells," (*m*, *n*, *o*, *p*, *s*) ganglion cells and (*u*) "radial fibres" of Müller. In this scheme the nervous elements are reduced to their essentials, with, however, the characteristic features of each variety preserved—the location of the cell bodies, the size, the shape, and the spreading of the dendrites and of the axis cylinders—and with the synaptic contacts presented accurately. (Polyak, 1941)

ending in knobs, the latter in small dendritic pedicles. This is the most useful criterion for differentiating rods from cones but its precise meaning is not understood. Fundamentally all nerve cells forward their message either by