# PHYSIOLOGY of the EYE

By HUGH DAVSON, D.Sc.

Assistant Director, Ophthalmological Research Unit, Medical Research Council; Honorary Research Associate, University College, London

With a Foreword by
SIR STEWART DUKE-ELDER
K.C.V.O., M.A., D.Sc., Ph.D., M.D., F.R.C.S.

Several years of teaching physiology and physiological optics to medical men taking the Diploma in Ophthalmology have convinced the author that these subjects are full of difficulties for people with only a medical training. This book is therefore designed for those students who, realising that a fundamental knowledge of physiology is an important clinical weapon, are prepared to face these difficulties. It will also be of value to the medical student and progressive optician.

J. & A. CHURCHILL LTD.
104 GLOUCESTER PLACE, LONDON, W.1.

# THE PHYSIOLOGY OF THE EYE

By

# **HUGH DAVSON**

D.Sc. (Lond.)

Assistant Director, Ophthalmological Research Unit, Medical Research Council, London. Honorary Research Associate, University College, London. Lecturer in Physiology, School of Orthoptics, Moorfields, Westminster and Central Eye Hospital.

> With a Foreword by SIR STEWART DUKE-ELDER, K.C.V.O., M.A., D.Sc., Ph.D., M.D., F.R.C.S.

> > WITH 301 ILLUSTRATIONS



LONDON

J. & A. CHURCHILL LTD.

104 GLOUCESTER PLACE, W.1

Reprinted 1950

## To W.S. and P.M.

$First\ edition$				1949
Reprinted	•	•	•	1950

#### ALL RIGHTS RESERVED

This book may not be reproduced by any means, in whole or in part, without permission. Application with regard to copyright should be addressed to the Publishers.

#### **FOREWORD**

In the average physiological text-book the physiology of the eye necessarily takes a subordinate place and tends to be lost in the exposition of the main principles of the subject. It is true that those principles are applicable to the eye, but it is equally true that, as seen in this organ, they are frequently specialised and individualistic. Moreover, the average text-book of ophthal-mology assumes acquaintance with physiology so that the student often has difficulty in finding a comprehensive and handy source of information. This book, therefore, fills a want both for the student whose ultimate aim is clinical ophthalmology and for those whose interests in the special senses are more academic.

Dr. Davson's name is already well known in the literature of this subject, and his original researches on the fundamental problems of ocular physiology are evidence that the following pages are written not only by a post-graduate teacher of long experience, but also by one who has done not a little to create the body of knowledge with which they deal.

STEWART DUKE-ELDER.

LONDON.

#### **PREFACE**

THE research worker and advanced student in the physiology of the eye have been overwhelmed with monographs and textbooks. First and foremost, they have Duke-Elder's monumental "Volume One"; whilst individual aspects have been covered by the recent excellent monographs of Bartley, Bellows, Detwiler, Granit, Krause, Polyak, Walls, Whitnall, Willmer, Wolff, and Wright. In the field of physiological optics and the psychology of visual perception they have Helmholtz's "Physiological Optics" (translated into English by Southall), a book getting on to its centenary but no more out of date than many monographs of ten years ago.

The medical student, optician, and prospective diplomatist in ophthalmology have, in comparison, been less well treated, and the present book has been written with these in mind. I trust, however, that it is not a simple re-hash of the more specialised Several years of teaching physiology and physiological optics to medical men taking the Diploma in Ophthalmology have convinced me that these subjects are full of difficulties for people with only a medical training, and the book is designed for those students who, realising that a fundamental knowledge of physiology is an important clinical weapon, are prepared to

face up to these difficulties.

The section on optics may require some apology, in view of the number of books already published treating with this subject. From the point of view of the diploma course in ophthalmology, no one of these books is satisfactory. The ophthalmologist is not concerned with formulæ, still less with their mathematical derivation; he must, in my view, understand sufficient of the general principles to enable him to speak intelligibly on the This understanding is best achieved subject to the optician. by the simplest possible exposition; formulæ must be cut to a minimum and the diagrams illustrating ray-tracing must be clear; it is easy enough to devise complex diagrams that will demonstrate a number of points at once, but it is quite another matter to decipher them. If, in addition to simplifying the presentation, I have avoided introducing new errors, the space devoted to this subject will be justified.

Detailed acknowledgments follow below; here I must express my thanks to Prof. C. Lovatt Evans for extending to me the hospitality of his laboratory while my own is being built and thus providing me with the facilities for continuing my researches on the eye, interrupted by the war, and for writing this book.

HUGH DAVSON.

University College, London, W.C.1.

#### **ACKNOWLEDGMENTS**

It is too much to hope that this book is free from those tiresome errors which perplex the student and irritate the expert; if it approximates at all to this immaculate condition it will be due in large measure to the inquisitorial zeal of my colleagues Mr. D. M. Maurice, Mr. E. J. Ross, Mr. M. Langham and Mr. D. P. Choyce, who very kindly corrected the proofs. Dr. Ernst Bárány was good enough to read Section IV on "Visual Perception" in manuscript and to suggest many alterations, all of which were incorporated in the final draft.

In the preparation of the original illustrations I owe a great debt to Mr. C. A. R. Tayler, of the Physics Department, University College, London, who painstakingly executed all of the diagrams in Section V: those in Section IV were chiefly carried out by Mr. L. J. Shaw, of the Physiology Department, University College. In the reproduction of illustrations from the literature, I and my publishers were greatly helped by the expert photographical assistance of Mr. C. A. Evans of the Physiology Department, University College. To the authors and publishers who gave permission for these depredations I tender my sincere thanks; it is perhaps invidious to make special mention of any of the authors, but rather than appear unappreciative I must thank Sir Stewart Duke-Elder for giving me carte blanche with all his published illustrations, in addition to kindly reading and commenting upon my manuscript, and Mr. Eugene Wolff, Mr. Edgar F. Fincham and Dr. K. W. Ascher for so generously placing original photographs or drawings at my disposal.

The publishers who gave permission to reproduce figures are as follows:—

American Journal of Ophthalmology, Figs. 15, 16, 17; American Journal of Physiology, 52; Biological Reviews, 129; British Journal of Ophthalmology, 14, 86, 87, 90, 91; Cranbrook Institute of Science, 132; H.M. Stationery Office, 74, 92, 93; Illuminating Engineering Society, 80, 82, 83, 85; Journal of Cellular and Comparative Physiology, 54; H. Kimpton, 10, 22, 27, 29, 31, 32, 89, 97, 98, 99, 276, 278; Hatton Press, 273, 279; H. K.

Lewis, 1, 2, 4, 5, 20, 141, 142; Long Island Biological Association, 69, 72, 73; Longmans Green, 290, 291; Macmillan, 64; E. V. Mosby, 24, 26, 124; Nature, 61, 95, 96; Optical Society of America, 49, 50, 51, 57, 68; Oxford University Press and Pennsylvania University Press, 45, 121, 133, 143, 144; Physical Society, 23, 136, 138; Physiological Society, 46, 47, 48, 54, 58, 65, 66, 67; Rockefeller Institute for Medical Research, 56, 62, 76, 79; The Royal Society, London, 55, 81, 88, 258; W. B. Saunders, 123; University of Chicago Press, 28, 30, 33, 75.

It is a pleasure to record my gratitude to the Medical Sciences Librarian of University College, Mr. C. F. A. Marmoy, and his assistants, who rendered me such courteous and willing help, and to my publishers who, through their representative, Mr. A. Knightley, lightened, by their kindness and tolerance of alterations, the work of preparing this volume for the press.

H.D.

### CONTENTS

TMTDODICTION		PAGE
INTRODUCTION		
STRUCTURE OF THE EYE	•	1
SECTION I		
INTRA-OCULAR DYNAMICS AND THE TRANSP TISSUES	ARE	ENT
AQUEOUS HUMOUR AND THE INTRA-OCULAR PRESSURE		8
THE TRANSPARENT STRUCTURES		40
SECTION II		
THE MECHANISM OF VISION		
STRUCTURE OF THE RETINA		62
MEASUREMENT OF THE STIMULUS	•	68
GENERAL ASPECTS OF VISION	•	75
ELECTRICAL EFFECTS OF STIMULATION		92
PHOTOCHEMICAL ASPECTS		102
FLICKER		121
VISUAL ACUITY		131
Adaptation		140
THEORY OF COLOUR VISION		<b>15</b> 9.
SECTION III		
THE MUSCULAR MECHANISMS		
Extra-Ocular Muscles and their Actions		- :177
Torsion and Listing's Law		191
BINOCULAR MOVEMENTS		198
:		

CI	7	V''	$^{1}E$	N	T	Q

xii	$C\epsilon$	ONTI	ENTS	!			
Nervous Mechanisms	IN	THE	Con	FROL	OF	THE	EYE
		•				•	•
THE PUPIL						•	
ACCOMMODATION .							
THE PROTECTIVE MECH	ANIS	SM	•	•	•	•	•
	SE	СТІО	N IV	7			
VISU	JAL	PE	RCEF	TIOI	N		
THE VISUAL PATHWAY			•				•
HIGHER INTEGRATIVE A	CTI	VITY					
PROJECTION OF THE RE	MIT	Α.					
MONOCULAR PERCEPTION	N O	f Dei	PTH				
CYCLOPEAN PROJECTION	1			•			
STEREOSCOPIC DEPTH P	ERC	EPTIO	N .	•			
RETINAL RIVALRY AND	Oc	ULAR	Dom	INANC	E .		
BINOCULAR ASPECTS OF			•				
Senses							
THE PERCEPTION OF M	OTIO	ON .	•		•	•	•
	OT	TOWNT (	\ <b>\</b> \	+			
	21	ECTIO OPT:		,			
<b>.</b>							
REFLECTION							•
REFRACTION AT PLANE							•
REFRACTION AT A SING REFRACTION BY SPHER						•	
REFRACTION BY SPHER REFRACTION BY THE E							
AMETROPIA AND ACCOM							
Non-Spherical Lenses							
NEUTRALISATION AND I				4.1.19M	•	•	•
CONTACT LENSES .	PBU.	en iki	NG	•	•	•	•
OPHTHALMOSCOPY .	•	•	•	•	•	•	•
RETINOSCOPY .	•	•	•	•	•	•	•
OPTICAL CONSTANTS OF	י בדיתייק	ne Ev	· Te:	•	•	•	•
DEFECTS IN THE IMAG		الند سد.		•	•		
INTERFERENCE, ETC.		•	•	•	•		
TAIL TOTAL TOTAL TOTAL TOTAL	•	•	-	•	•		

#### INTRODUCTION

#### STRUCTURE OF THE EYE

The globe of the eye consists essentially of three coats enclosing the transparent refractive media. The outermost, protective tunic is made up of the sclera and cornea—the latter transparent; the middle coat is mainly vascular, consisting of the choroid, ciliary body, and iris. The innermost layer is the retina, containing the essential nervous elements responsible for vision—

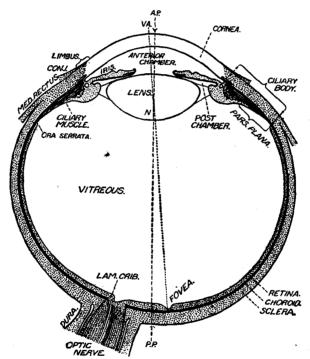


Fig. 1. Horizontal section of the eye. P.P. = Posterior pole; A.P. == Anterior pole; V.A. = Visual axis. (Wolff, "Anatomy of the Eye and Orbit.")

the rods and cones; it is continued forward over the ciliary body as the ciliary epithelium.

The dioptric apparatus (Fig. 1) is made up of the transparent structures—the cornea, occupying the anterior sixth of the surface of the globe, and the *lens*, supported by the *zonule* which is itself

attached to the ciliary body. The spaces within the eye are filled by a clear fluid, the aqueous humour, and a jelly, the vitreous body. The aqueous humour is contained in the anterior and posterior chambers, and the vitreous body in the large space behind the lens and ciliary body. The posterior chamber is the name given to the small space between the lens and iris.

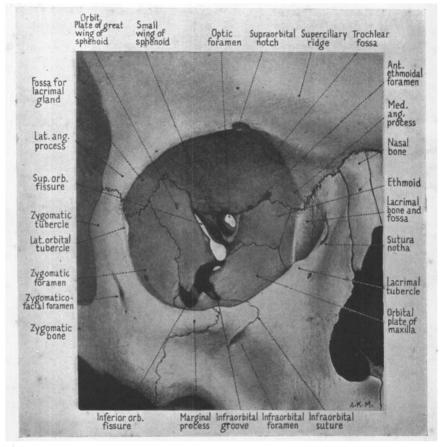


Fig. 2. The orbit from in front. (Wolff, "Anatomy of the Eye and Orbit.")

The iris behaves as a diaphragm, modifying the amount of light entering the eye, whilst the ciliary body contains muscle fibres which, on contraction, increase the refractive power of the lens (accommodation). An image of external objects is formed, by means of the dioptric apparatus, on the retina, the more highly specialised portion of which is called the *fovea*. The

retina is largely made up of nervous tissue—it is an outgrowth of the central nervous system—and fibres carrying the responses to visual stimuli lead away in the optic nerve through a canal in the bony orbit, the optic foramen (Fig. 2); the visual impulses are conveyed through the optic nerve and tract to the lateral

geniculate body and thence to the cerebral cortex; on their way, the fibres carrying messages from the medial or nasal. half of the retina cross over in the optic chiasma, so that the lateral geniculate body of the left side, for example, fibres from receives temporal half of the left retina and the nasal half of the right. The nerve trunks, proximal to the chiasma, are called the optic tracts. This decussation may be regarded as a development associated with binocular vision: it will be noted that the responses stimulus from any one part of the visual field are carried in the same optic tract (Fig. 3), and the necessary motor response, whereby both eves are directed to the same point in the field, is probably simplified by this arrangement. It will be

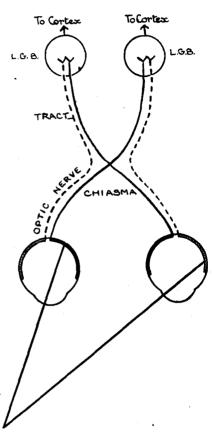


Fig. 3. The decussation of the optic pathway.

noted also that a right-sided event, i.e., a visual stimulus arising from a point in the right half of the field, is associated with impulses passing to the left cerebral hemisphere, an arrangement common to all peripheral stimuli.

The outermost layer of the retina is the pigment epithelium, which lies in contact with the choroid.

The nutrition of the eye is taken care of largely by the capillaries of the vascular coat; let us examine this structure more

closely. The choroid is essentially a layer of vascular tissue next to the retina; it is separated from this nervous tissue by two membranes—the structureless membrane of Bruch and the pigment epithelium. The retina comes to an end at the ciliary body, forming the ora serrata (Fig. 4), but the vascular coat continues into the ciliary body as one of its layers, the vessel layer, which is separated from the eye contents by membranes—the two layers of ciliary epithelium which, as we have indicated,

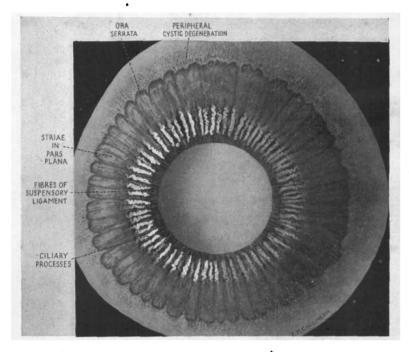


Fig. 4. Posterior view of the ciliary body showing ora serrata and corona ciliaris. (Wolff, "Anatomy of the Eye and Orbit.")

is the forward continuation of the retina, and the lamina vitrea which is the continuation forward of Bruch's membrane.

The ciliary body in antero-posterior section is triangular in shape (Fig. 5) and has a number of processes (seventy) to which the zonule is attached; viewed from behind, these processes appear as radial ridges to which the name corona ciliaris has been given (Fig. 4).

The relationship of the iris to the ciliary body is seen in Fig. 5;

the blood vessels supplying it belong to the same system as that supplying the ciliary body. The vessels are distributed through the stroma which is separated from the aqueous humour in the anterior chamber by the anterior epithelium (or iris endothelium), a single layer of cells continuous with the innermost layer of the cornea. Posteriorly, the stroma is separated from the aqueous

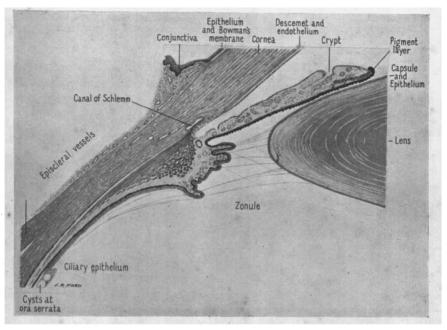


Fig. 5. Anterior-posterior section through the anterior portion of the eye. (Wolff, "Anatomy of the Eye and Orbit.")

humour by the posterior epithelium, a double, heavily pigmented layer.

The vessels of the vascular coat nourish the internal structures of the eye; so far as the lens is concerned, this process must take place by diffusion of dissolved material from the capillaries through the aqueous humour and vitreous body. The inner (nearest the vitreous) nervous elements of the retina, however, are provided for by a functionally separate vascular system derived from the central artery of the retina; this artery, a branch of the ophthalmic, enters the globe with the optic nerve and it is its ramifications, together with the retinal veins, that give the fundus of the eye its characteristic appearance. The choroid, ciliary body, and iris are supplied by a separate system of arteries.

also derived from the ophthalmic—the ciliary system of arteries.

The anterior portion of the sclera is covered by a mucous membrane, the *conjunctiva*, which is continued forward on to the inner surfaces of the lids, thus creating the *conjunctival sac*. The remainder of the sclera is enveloped by *Tenon's capsule*.

Movements of the eye are executed by the contractions of the six extra-ocular muscles; the space between the globe and orbit being filled with the orbital fat, the movements of the eye are essentially rotations about a fixed point in space.

The essentials of the nerve supply to the eyeball are indicated in Fig. 6; sensory impulses (excluding, of course, the visual ones) are conveyed through the long and short ciliary nerves.

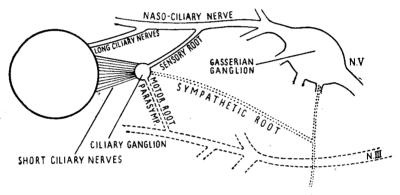


Fig. 6. Nervous supply to the eye-ball.

The long ciliary nerves are composed mainly of the axons of nerve cells in the Gasserian ganglion—the ganglion of the trigeminal (N. V); they convey impulses from the iris, ciliary body, and cornea. The short ciliary nerves also contain axons of the trigeminal; they pass through a ganglion in the orbit, the ciliary ganglion, into the naso-ciliary nerve; the fibres carry impulses from all parts of the eyeball, but chiefly from the cornea.

Motor impulses to the ciliary muscle and the constrictor of the pupil are carried by way of the lower division of N. III as the motor root of the ciliary ganglion; post-ganglionic fibres to the muscles are contained in the short ciliary nerves which enter the globe. The extra-ocular muscles are supplied by N. III, IV and VI.

Sympathetic fibres from the superior cervical ganglion enter the orbit as the sympathetic root of the ciliary ganglion and run in the short ciliary nerves to supply the vessels of the globe and the dilator fibres of the pupil. Other sympathetic fibres avoid the ciliary ganglion, passing through the Gasserian ganglion and entering the globe in the long ciliary nerves.