SYSTEM OF OPHTHALMOLOGY

EDITED BY

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VOL. I

THE EYE IN EVOLUTION

BY

SIR STEWART DUKE-ELDER

WITH 902 ILLUSTRATIONS, 15 COLOURED PLATES AND 350 MARGINAL ILLUSTRATIONS

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PREFACE

THE reception accorded to my Textbook of Ophthalmology has persuaded me that there is a need for its continuation in a second edition. The seven volumes of the Textbook took almost a quarter of a century to write, a period unfortunately longer than it might have been owing to the exigencies of war. The first four volumes have long been out of print—and intentionally so because they have long been out of date. It is to be remembered that the second volume was written before the sulphonamides were introduced ; the third before the antibiotics revolutionized the therapeutics of infective diseases ; both of them before the role of viruses in ocular disease was adequately appreciated ; the physiology of the eye of yesterday is unrecognizable when compared with that of today ; even the anatomy has been transformed by more elaborate optical and chemical methods of investigation and the advent of the electron microscope. The re-writing of the whole work if its comprehensive nature were to be retained would be an immense task occupying more time than I could reasonably expect to have at my disposal. Moreover, tomorrow will be different from today, and if a work such as this is to be of any lasting value it would seem to me desirable that a new edition be published at least every fifteen or twenty years ; fortunately, ophthalmology is no static science.

It therefore seemed to me wise to share the task of re-writing the original Textbook with my colleagues at the Institute of Ophthalmology in London. I am grateful that they have accepted this burden. For this reason I have changed the name of the book to a "System of Ophthalmology" since it will necessarily be less personal.

This first volume in the new series is an extension of the first twenty pages of Volume I of the old Textbook ; this I have written myself, largely because it is a subject in which I am particularly interested—and I wished to write it. The subject-matter has never been gathered together in a single book before and it is my hope that it will interest ophthalmologists in so far as it forms the basis of the science of vision ; and it may be that it will be of value also to those whose interest is biological rather than clinical.

The numerous marginal sketches are not usual in a book of this type. To the student of natural history they may seem superfluous, but to the ophthalmologist some of the animals may be unfamiliar and the drawings may perchance add meaning to the zoological nomenclature and thus give the text more life and interest. It is to be noted, however, that they are drawn not to scale, but approximately to a standard size to fit into a 1-inch margin.

STEWART DUKE-ELDER.

INSTITUTE OF OPHTHALMOLOGY,
LONDON,
1957.

ACKNOWLEDGEMENTS

IN the preparation of this book I have incurred a considerable amount of indebtedness which is a pleasure to record.

Many of the illustrations are borrowed, and in each the source is acknowledged. There are, however, five sources from which I have liberally drawn, and these merit special thanks : Dr. Gordon Walls, for a number of his original drawings ; Masson et Cie of Paris, who have allowed me to use some illustrations from Rochon-Duvigneaud's classical work, *Les Yeux et la Vision des Vertébrés* ; Dr. Maurice Burton and his publishers, the Elsevier Publishing Co. of Holland, for some illustrations from *The Story of Animal Life* ; the Royal Society for permission to use a large number of Lindsay Johnson's illustrations published in their *Proceedings* ; and Macmillan & Co. for giving free permission to copy a large number of the illustrations of animals in the *Cambridge Natural History* in the form of marginal sketches.

In preparing the illustrations I have had the willing co-operation of Dr. Peter Hansell and the Department of Medical Illustration of the Institute of Ophthalmology, the assistance of which, particularly that of Mr. T. R. Tarrant, the Medical Artist, has been invaluable. The Zoological Society of London has lent me a number of photographs, as also has the Natural History Museum of London, together with specimens of various invertebrates. Professor Ida Mann has allowed me to use a large number of her illustrations of the eyes of animals, and Dr. Kevin O'Day of Melbourne has allowed me to use photographs and slides of the eyes of Monotremes and Marsupials which are unobtainable outside Australia ; while in this Institute Professor Norman Ashton and Dr. Katharine Tansley have provided me with sections and photographs of the eyes of a number of animals.

In several instances my knowledge of zoology has been brought up to date by the great kindness of Dr. Mary Whitear of the Zoology Department of University College, London, who has read the proofs of those sections dealing with zoological classification ; while Dr. Katharine Tansley and Dr. Robert Weale of this Institute have given me most helpful criticism in some aspects of the visual problems discussed. Miss M. H. T. Yuille, Mr. A. J. B. Goldsmith and my wife have shared with me the onerous task of proof-reading.

It is difficult for me to express my indebtedness to my secretary, Miss Rosamund Soley, who has borne much of the burden of the technical aspects of the production of this Volume. She has typed and prepared the manuscript, corrected the proofs, and undertaken the immense and somewhat thankless task of verifying the bibliographies, prepared the Zoological Glossary and the Index, and drawn the 350 marginal sketches.

Finally, my indebtedness to my publishers, Henry Kimpton, continues to be immense. They have assisted me in every possible way. Why Mr. G. E. Deed continues to put up with my moods and vagaries after thirty years is to me quite incomprehensible.

STEWART DUKE-ELDER.

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PART I

THE EFFECT OF LIGHT ON LIVING ORGANISMS

INTRODUCTION

THE EFFECT OF LIGHT ON METABOLISM

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THE EMERGENCE OF VISION

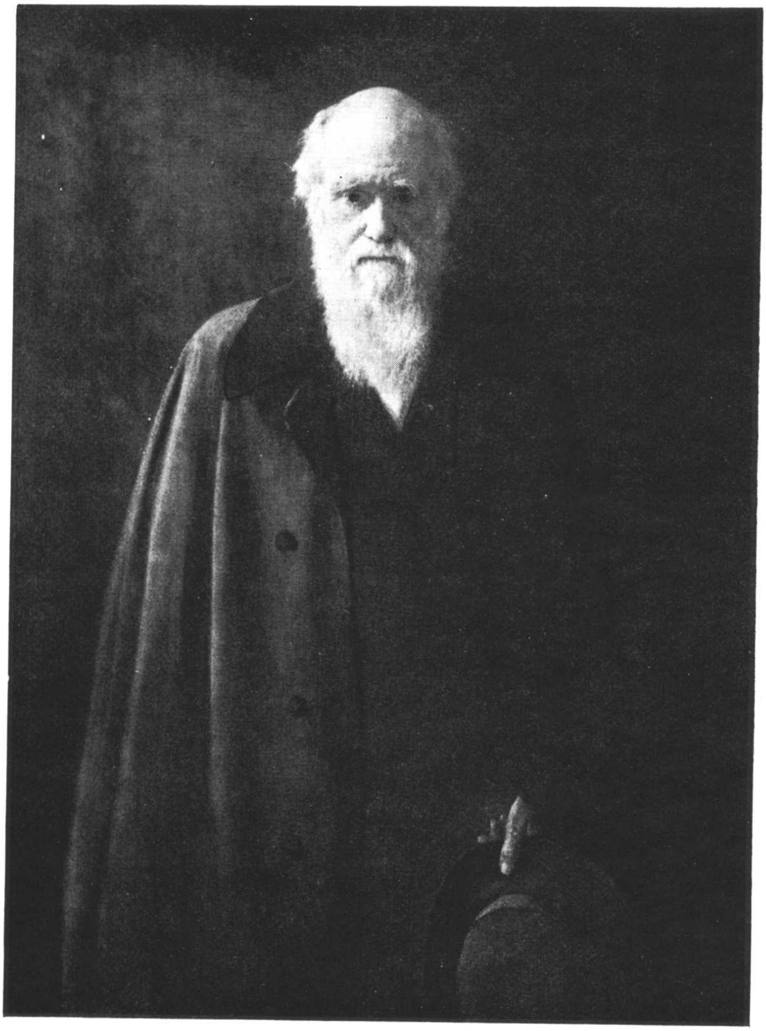

FIG. 1.—CHARLES DARWIN (1809–1882).

(From a portrait by John Collier in the Linnean Society.)

CHAPTER I

INTRODUCTION

We begin with a drop of viscid protoplasm the reactions of which we do not understand, and we end lost in the delicacy of the structure of the eye and the intricacies of the ten thousand million cells of the human brain. We begin with photosynthesis in a unicellular plant, or with a change in the viscosity produced by light in the outer layers of the amœba, and we end with the mystery of human perception. We begin some one or two thousand million years ago in the warm waters of the Archeozoic era and we end with the speculations of tomorrow. And as we travel together tracing the responses of living things to light from the energy liberated by a simple photochemical reaction to the faculty of appreciating and interpreting complex perceptual patterns, neither in fact nor in fiction does a story more fascinating unfold. It is a story which traces a development from a vague sentiency to apperception, from vegetative existence to the acquisition of the power to mould the environment, from passive reactivity to the ability to create history. Nor is there a story more important. Even at the physiological level some 38% of our sensory input is derived from the retinæ,[1] impulses from which, even in the complete absence of visual stimuli, are largely responsible for maintaining a tonic influence upon the level of spontaneous activity in the brain.[2] From the psychological point of view the importance of vision is still greater. If, indeed, the proper study of mankind is Man, and if (as we must agree) his behaviour and his contact with the outside world are mediated through his senses, what can be more fundamental than the study of the sense which, more than any other, determines his intelligence and regulates his conduct, of the faculty which eventually played the preponderant role in assuring his dominance and determining his physical dexterity and intellectual supremacy? We are indeed highly visual creatures.

It would seem appropriate to introduce a book devoted to the evolution of vision with a portrait of CHARLES DARWIN (1809–1882) (Fig. 1), the great English naturalist who, like Newton in the world of physics, was one of the very few men who revolutionized world thought in the subject on which he worked—and beyond. But Darwin has a special claim to introduce this chapter, for at a time when the conduct of animals was generally ascribed to the existence of vital forces or psychic activities, and when the orientation of plants was thought to be due to the direct influence of physical stimuli such as light and heat upon the

[1] According to the calculations of Bruesch and Arey (*J. comp. Neurol.*, **77**, 631, 1942).

[2] See Claes (*Arch. intern. Physiol.*, **48**, 181, 1939) and many others, admirably summarized in Granit (*Receptors and Sensory Perception*, New Haven, 1955).

plant as a whole, he transformed biology to a more factual plane based on observation and experiment, and was the first to show that in the higher plants receptor tissues existed separately from motor tissues, and that the orientation of plants to light was due to the transference over some distance of stimuli appreciated by the former to be made effective by the latter. These observations which appeared in the last of the classical books derived from his pen [1] form a typical example of the revolutionary nature of Darwin's philosophy—the result of a unique combination of experimental genius with penetrative powers of interpretation which have rarely been equalled—and from these observations have directly followed our understanding of the development of the sensory organs and their effect on the evolution of the higher species in the animal scale.

The son of a doctor in the English country town of Shrewsbury, he went to the University of Edinburgh to study medicine ; this, however, he forsook and went to Cambridge with the intention of entering the Church ; but here Sedgwick and Henslow, the professors of geology and botany, inspired him again with a love of natural history which eventually was to become a passion. Darwin's assessment of the qualities responsible for his own success is worth remembering : " the love of science, unbounded patience in long reflecting over any subject, industry in observing and collecting facts and a fair share of invention as well as of common sense ". And again : " I have steadily endeavoured to keep my mind free so as to give up any hypothesis, however much beloved (and I cannot resist forming one on every subject), as soon as facts are shown to be opposed to it ".[2]

THE RESPONSES OF ORGANISMS TO LIGHT

LIGHT—the visible radiant energy derived from the sun—is responsible for the whole existence of living things on the earth, and without question PHOTOSYNTHESIS IN PLANTS—the reaction whereby the carbon dioxide and water which permeate the atmosphere and the earth's crust are converted into the organic substances which constitute the basis of all living things—is the most fundamental and important chemical process on our planet. Not only was photosynthesis responsible for the origin of life but it maintains the perpetual cycle of the activities of living things. By oxidation, living structures are continuously broken down to their initial constituents (carbon dioxide and water), the process being accompanied by the liberation of the energy required by organisms to perform their varied activities ; by photosynthesis the carbon dioxide and water produced by the oxidation of living matter are perpetually reunited by an opposite process of reduction with the return of oxygen to the atmosphere, the high energy requirements necessary being supplied by the capacity of the chlorophyll group of pigments in green plants to absorb sunlight. This reaction whereby the chlorophyll system stores and then liberates light-energy is thus not only the source of the activities of all living things but supplies much of the energy at the disposal of the civilized world in the stores of coal and petroleum formed throughout the ages.

[1] *Power of Movements in Plants*, London, 1880.
[2] *Life and Letters of Darwin*, by Francis Darwin, 1887.

It would be out of place to enter fully into the mechanism of photosynthesis by chlorophyll here ; for a recent summary the reader is referred to the monograph by Hill and Whittingham.[1] The chlorophyll group of pigments are tetrapyrrolic compounds in which magnesium is present in non-ionic form ; they are related to hæmin which, however, contains a central iron atom. The completed process whereby carbohydrates are synthesized has long been known and may be represented by the equation :

$$xCO_2 + xH_2O + \text{radiant energy} \rightarrow C_xH_{2x}O_x + xO_2 + \text{stored energy}.$$

The intimate mechanism, however, has only recently begun to be analysed, an advance largely due to the use of radio-active carbon (^{14}C) as a " tracer ". Although many of the details are still obscure, particularly the way in which chlorophyll absorbs radiant energy and directs it into chemical processes, the basic reactions are known and can indeed be carried out in the test-tube. The essential process is the photolysis of water. Chlorophyll induces the energy derived from light to break the hydrogen-oxygen bonds in the molecule of water ; the hydrogen therefrom is used to convert the single carbon atoms of CO_2 into long-chained carbohydrates through the medium of phosphoglyceric acid and the oxygen is liberated as a free gas ; meantime a store of chemical energy is provided by the photosynthesis of energy-rich compounds such as adenosine triphosphate, the break-down of which by simple hydrolysis releases large amounts of energy to drive the process. It is probable that these and the many other compounds found in plants are formed by enzyme-reactions from one or more of the constituents of the photosynthetic cycle at either the C_3 or C_6 level.[2]

Apart from this basic activity which characterizes the vegetable world, light produces photochemical reactions of great variety in living organisms. The energy thus liberated produces in the most primitive creatures the only response available—a change of general activity, frequently of motion, just as do other stimuli, mechanical, gravitational, thermal, chemical or electrical ; in the higher forms a multitude of activities may be initiated or influenced.

These responses we will review under four main headings. In the first place, the response may take the form of *a change in general metabolic activity*, usually, but not invariably, an increase of activity under the influence of light. As a natural extension of this, the diurnal cycle of light and darkness has in the course of evolution so impressed itself upon a number of the fundamental activities of many organisms (including man) that these show a corresponding rhythm which has eventually become innate and endogenous (photoperiodism). In the second place, the response may be expressed as *a variation in movement*. In its simplest form this is also merely a change in general activity wherein movements are random in nature and undirected (photokinesis) ; as an evolutionary extension of this the movements initiated by light come under the directional control of the stimulus so that the organism is orientated by light in a definite way ; such movements

[1] *Photosynthesis*, London, 1955. See also *Proc. roy. Soc. B*, **157**, 291 (1963).

[2] For reviews, see Arnon (*Ann. Rev. plant Physiol.*, **7**, 325, 1956, *Nature* (Lond.), **184**, 10, 1959), Rosenberg (*Ibid.*, **8**, 1957).