

THE PHYSIOLOGY OF VISION

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CHAPTER I

Introduction

The nature and properties of light and its interactions with material bodies obviously play a fundamental role in the functioning of our visual organs. A clear understanding of the physical constitution of light and of the phenomena resulting from its incidence on the visual organs is therefore essential for any valid interpretation of our visual sensations. It is precisely in these respects that the excursions into the field of visual physiology made in the nineteenth century were at fault. As is well known, light was regarded in the nineteenth century as a form of energy which propagates itself as wave-motion, and is distributed through space in a continuous manner. Its interactions with material bodies were also interpreted on the same basis. Present-day ideas regarding these matters are, of course, altogether different. There is therefore no reason to believe that the ideas regarding the nature of vision and of visual processes inherited from the nineteenth century would be sustainable at the present time, either on theoretical grounds or even as purely empirical descriptions or interpretations of the observed phenomena.

Two beliefs or hypotheses handed down from the nineteenth century figure prominently in the literature of the physiology of vision. The first is the trichromatic hypothesis usually associated with names of Thomas Young and Hermann von Helmholtz. The other is the duplicity theory of vision which postulates that there are two distinct kinds of vision, known as photopic vision and as scotopic vision which function respectively at the higher and at the lower levels of luminosity, photopic vision enabling us to perceive both light and colour, and scotopic vision only light but no colour. Of more recent origin is the so-called photo-chemical theory of vision which has received a measure of acceptance from several authors but has not escaped criticism by others.

The purpose of the present volume is to set out in a systematic manner the methods and results of the experimental investigations on diverse aspects of vision carried out by the author during recent years. The aim of the studies was to obtain an insight into the subject by independent study without being influenced by ideas and beliefs inherited from the past. It has emerged from the author's studies that none of the notions referred to in the preceding paragraph is reconcilable with the actual facts of the case. The studies have led to a new picture of the nature of vision and new interpretations of our visual experiences. These have been described in detail and discussed in the chapters which follow.

CHAPTER II

Waves and corpuscles

The phenomena which light presents to us for study fall into two groups. The first class of phenomena comprises those which can be described or explained on the assumption that light is a species of wave-motion in space which possesses a great velocity and other characteristics related to its propagation. In the second class of phenomena, we are concerned with light as a form of energy which is emitted or absorbed or scattered by material substances and which changes its form as the result of its incidence on such substances. In all cases of this kind, it becomes necessary to recognise the corpuscular nature of light, in other words to assume that it consists of discrete units of energy of which the magnitude is related to the frequency of wave-motion as recognised in the first class of phenomena by the simple relation $\varepsilon = h\nu$. Here ε is the energy of the corpuscle, ν is the frequency and h is Planck's constant of action. These two descriptions of the nature of light are mutually complementary. In other words, they refer to two distinct and non-overlapping sets of cases. But both descriptions have to be accepted to enable us to obtain a complete picture of the nature and behaviour of light.

Wave-optics includes within itself the entire body of theory and practice known as geometrical optics. This concerns itself with the functioning of optical instruments, treated on the basic assumptions of the rectilinear propagation of light and that the media traversed by light possess known refractive indices and dispersive powers. But the wave-like characters of light are most clearly manifested in the class of phenomena designated as interference and diffraction. In these phenomena, the periodic nature of wave-motion and its relation to the wavelength come directly within the reach of observation. The length λ of the waves as thus determined is connected with their frequency ν and their velocity c in the medium by the simple relation $\lambda = c/\nu$. The cases in which λ has a definite value and hence the frequency ν and the energy $h\nu$ of the light corpuscle are precisely known are of special importance. The light which can thus be specified appears as a single sharp line in the spectrum of the radiation as exhibited by a prismatic spectrograph or by a diffraction grating. It is then referred to as monochromatic light and it is composed of corpuscles all having the same energy. If, on the other hand, the spectrum as exhibited by such instruments is a continuous band of light, the wavelength λ and hence the frequency ν and the corpuscular energy $h\nu$ show corresponding ranges of variation.

From what has been said above, it follows that the formation of optical images

by the dioptric media of our eyes on their retinae falls within the scope of wave-optics. But, on the other hand, the actual perception of such light following its incidence on the retinae lies entirely outside its scope. For, the perception of light involves the absorption of the incident light as well as the transformation of its energy to a form that can be transmitted through the optic nerves to the centres of perception in the brain.

The role played by the corpuscular nature of light in its visual perception will occupy us in later chapters. It will be useful, however, to devote the rest of the present chapter to the consideration of the wave-optical properties of light. For, as we shall see later, the phenomena encountered in this field are helpful to us in the study and interpretation of our visual perceptions.

The simplest technique for exhibiting the interference of light is to lay one clean glass plate on another such plate and to view the air-film enclosed between the two plates by reflected light, making use of an extended source of light. The two streams of light reflected respectively at the two surfaces bounding the air-film reach the eyes practically in the same direction and with intensities which are nearly identical. But the optical paths traversed by them differ by twice the thickness of the air-film, if we assume that it is viewed in the direction of the normal to the surfaces. Interference then results either in the extinction of the reflected light or in a four-fold increase of its brightness according as the two streams of light are in opposite phases, or in agreement of phase. The varying thickness of the air-film then manifests itself as an alternation of dark and bright bands over its area, provided that the light employed has a definite wavelength, as is the case if, for example, the light of a sodium-vapour lamp is used for the observations. The two nearly coincident yellow lines in the spectrum of the lamp then give us the needed "monochromatic" light.

Photographs of two interference patterns of this kind recorded with the yellow light of a sodium lamp are reproduced as figure 1(A) and (B) in plate I. In figure 1(A), the interferences appear as concentric circular rings around a central dark region where the two plates were in actual contact, the thickness of the air-film increasing rapidly as we proceed outwards from this centre. In figure 1(B), the fringes appear as a series of approximately parallel bands, commencing from the region where the plates (which were both optical flats) had been forced into contact and the air-film between the plates is thus a wedge of small angle. As already stated, the fringes were in each case observed and photographed with monochromatic light, and the interferences are therefore seen at their best. In a later chapter, we shall describe and discuss the phenomena observed in such cases, when instead of the light of a sodium-vapour lamp, white light is employed for viewing the interferences.

A tungsten filament heated to a high temperature by the passage of an electric current emits a brilliant white light. Examined through a prismatic spectroscope, the emitted light appears as a continuous spectrum exhibiting the usual sequence of colours. The wavelength of the light in such a spectrum increases progressively

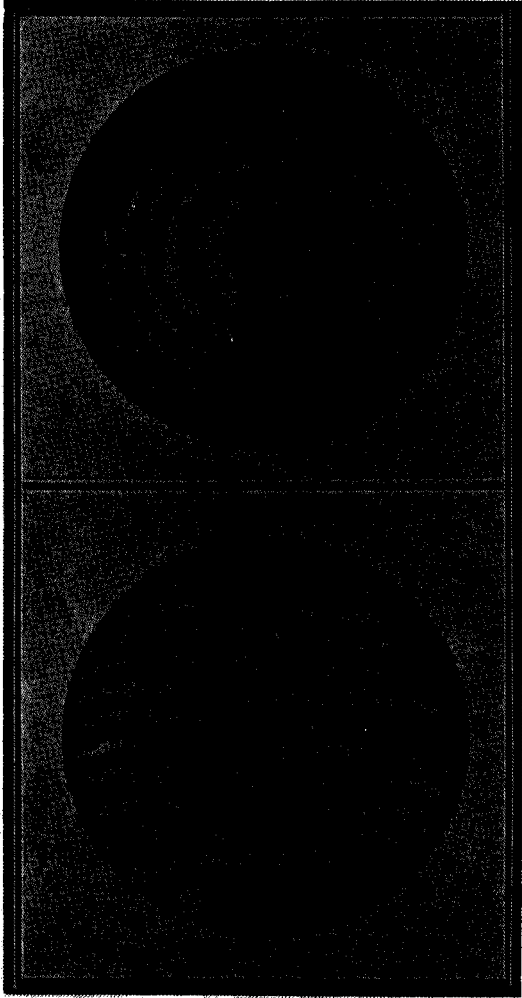


Figure 1. Interference patterns in sodium light.

Plate I

from one end to the other, from say 4000 Å units at the violet end to say 7000 Å units at the red end. The principle of interference may be utilized to exhibit this progression of wavelength to the observer's eye, the continuous spectrum being transformed into a succession of sharply-defined bands of progressively increasing wavelength. The technique needed to achieve this result is fairly simple. Two circular plates of optical glass are made use of. Their faces are ground flat and polished to a high degree of perfection. One face of each plate is half-silvered, and the two plates are held within a tubular support in such manner that the silvered faces are adjacent and parallel, their separation being a mm or less. The gap between them should be capable of being varied from zero upto the desired value, while their parallelism remains perfect. The use of suitable guides and a fine screw permits of this being achieved. The plates thus mounted are held normally before the slit of a spectroscope. White light from a small but brilliant source, e.g., a glowing tungsten-filament, passes normally through the plates and enters the slit of the spectroscope. The spectrum as seen through the eye-piece then exhibits a succession of bright lines on a dark field. The spacing of these lines can be varied by moving the two plates closer together or further apart as desired.

In a later chapter, we shall see that the technique here described can be used to study the progression of colour in the spectrum of white light and to estimate by simple inspection, the capacity of human vision to detect colour differences. An interesting feature of the technique is that the bands in the spectrum produced by it are equally spaced in respect of wave-number differences, in other words, the successive lines represent equal increments of the corpuscular energy of the light. This follows from the fact that the successive bands correspond to successive integral values of the number $2d/\lambda$, where d is the separation of the plates and λ is the wavelength of the light. Figure 2(A), (B), (C) in plate II reproduce the banded spectrum of the light of a tungsten lamp photographed in the manner described with three different separations of the plates in the interference apparatus. The number of bands into which the spectrum is channelled is 120, 60 and 30 while the wave-number separation between each band and the next is 72, 144 and 288 respectively in the three figures.

CHAPTER III

The structure and functioning of the retina

A role of outstanding importance in the functioning of the organs of vision is played by the retina, which is the sensitive screen at the back of the eye on which the picture of the world outside formed by its dioptric media falls. Indeed, it may be said that what the retina is capable of accomplishing determines what we can see and recognise in the objects under view. We shall concern ourselves in the present chapter with the methods of observation which enable us to view the living retina and thereby to gain some understanding of its structure and functioning.

The instrument referred to as the ophthalmoscope enables the interior of the eye to be illumined and to be viewed by another observer. What is known as the fundus of the eye then comes into view. The position of the details seen on it naturally depends on the direction in which the eye which is observed is orientated with respect to the illuminating beam. Pictures in colour of the appearance of the fundus are to be found reproduced in numerous treatises. Particularly striking are those which appear in Polyak's monumental treatise entitled *The Vertebrate Visual System* published by the Chicago University Press in the year 1957. We may here refer to figures 148, 165 and 363 which appear facing respectively pages 258, 280 and 606 of that work. These three pictures between them serve to give us a fairly complete idea of the structure of the retina, so far as the ophthalmoscope can reveal it.

It is a remarkable fact that the central part of the retina, in other words, the area which is made use of when we turn our eyes towards the objects which particularly interest us appears comparatively featureless as viewed through the ophthalmoscope. It is possible, however, to recognise a circular patch at its centre which appears different in colour or in brightness from its surroundings. At a considerable distance from this central region, and indeed almost on the periphery of the fundus, if the former appears at the middle of the picture, is seen the most conspicuous feature of the retina, viz., the region known as the optic papilla. This appears as a round disc. Surrounding it and emerging at various points inside the area, blood vessels are seen, both arteries and veins, traversing the retina. A feature particularly worthy of remark is that these larger blood-vessels curve round so as to avoid the central region of the retina. Blood-vessels of smaller diameters which take off from the larger vessels however traverse the retina and proceed towards the central area. But even these do not actually extend to or reach the central area.

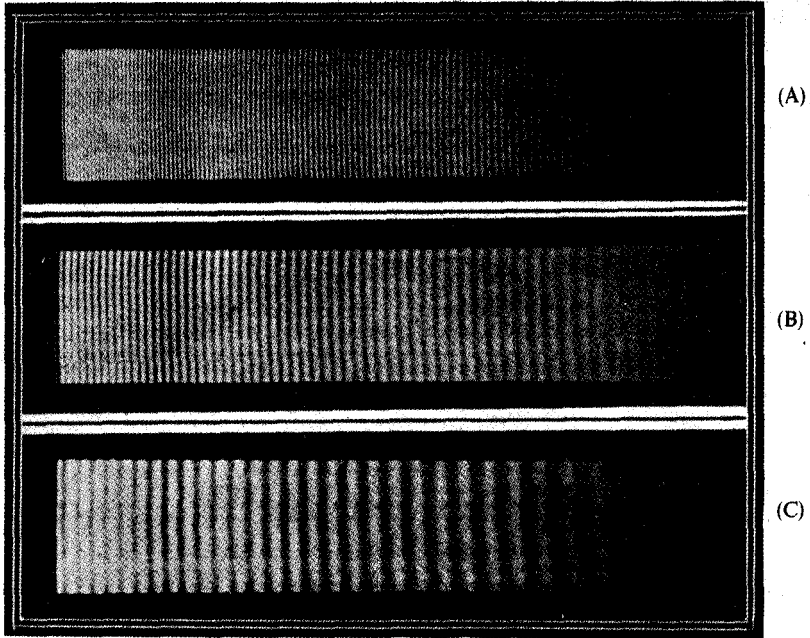


Figure 2. Channelled spectra of white light.

Plate II

The optic papilla is also the region towards which the nerve-fibres converge from various parts of the retina. Here they are bunched together and finally emerge as the optic nerve from the eye-ball towards the brain. This feature is well shown in figure 148 of Polyak's book and even better shown in figure 165 which is a picture of the fundus of a Nubian youth aged 17. Translucent bundles of optic nerve-fibres can be traced for a great distance beyond the disc of the optic papilla. Another noteworthy feature is that the nerve-fibres from other parts of the retina do not proceed across its central region but arch round it, both above and below, to avoid traversing it.

The avoidance of the central area of the retina by the larger blood-vessels, as also by the nerve-fibres streaming towards the optic papilla from other parts of the retina, is a feature which evidently favours the clear perception of the images of external objects falling on the central region. Apart from giving this indication, the ophthalmoscopic view does not really tell us very much about how the retina actually functions. Much less does it reveal the great differences in the activity of the retina over its different areas. These aspects of the structure and functioning of the retina are, however, exhibited in a most striking fashion when it is studied making use of a technique devised and perfected by the author which will presently be described.

The technique employed is the use of a colour filter which freely transmits light over the entire range of the visible spectrum except over a limited and well-defined region which it completely absorbs. It is possible by the use of suitable dye-stuffs in appropriate concentrations to prepare colour filters of gelatine films on glass exhibiting the spectroscopic behaviour described. Holding such a colour filter before his eye, the observer views a brilliantly illuminated screen for a brief interval of time and then suddenly removes the filter while continuing to view the screen with his attention fixed at a particular point on it. He then observes on the screen a picture in colours which is the chromatic response of the retina to the light of the colour previously absorbed by the filter and which impinges on it when the filter is removed. Actually, as will become clearer presently, what the observer sees is a highly enlarged view of his own retina projected on the screen and displaying the response of the retina in its different areas produced by the incidence of the light of the selected wavelengths. By using a whole series of colour filters whose characteristic absorptions range from one end of the visible spectrum to the other, we are enabled to explore the behaviour of the retina over an extensive region under excitation by light of different wavelengths which in the aggregate cover the entire visible spectrum.

Why the phenomenon described above manifests itself is not difficult to understand. A colour filter completely absorbing a selected part of the spectrum when placed before the eye of the observer protects the retina from the incidence of light from that part of the spectrum, and if such protection continues for a sufficient period of time, it has the result of sensitising the retina for the reception of light of those wavelengths when the filter is removed. *Per contra*, light of wavelengths not absorbed by the filter being incident on the retina both when the filter is in position and after its removal, the visual sensation which it excites becomes enfeebled by the continued exposure. Accordingly, when the filter is removed, the visual response of the retina to light of the wavelengths for which its sensitivity has been enhanced is far stronger than the continuing response to the other wavelengths and manifests itself vividly to perception. The nature of the picture seen is determined by the part of the spectrum which is absorbed by the colour filter and differs enormously for the different filters employed in the study. The usefulness of the technique for the study of the functioning of the retina over its different areas is thereby greatly enhanced. Here, we should mention the essentially fugitive nature of the phenomenon. But this is no obstacle to the study of the effects. For, the image of the retina seen by the observer on removing the colour filter and which fades away is restored and can be examined again and again merely by putting back the filter in front of the eye for a little while and then removing it.

For an observer to study the results of using the colour filters in the manner explained above, a screen of the kind used for projection work containing a great many small glass spheres embedded in plastic is found to be particularly suitable. Placed facing the windows in a well-lighted room, such a screen is quite brilliant

