THE NEW PHYSIOLOGY OF VISION

Chapter IX. The Structure of the Fovea

BY SIR C. V. RAMAN

Received December 18, 1964

THE preceding chapter commenced with an account of the author's studies of the phenomenon known as Haidinger's brushes seen when the polarised light of the sky is viewed by an observer. Investigations of the same phenomenon under controlled conditions and especially the studies in which monochromatic light was made use of showed clearly that these brushes have a physiological origin and represent a visual perception of the polarisation of light which takes its place along with the perception of form and the perception of colour as one of the special faculties associated with human vision. In the present chapter we shall concern ourself with the nature of the physiological mechanism which makes the perception of polarisation possible.

It is a remarkable circumstance that though the Haidinger phenomenon has been known for over a century, its importance in relation to the physiology of vision remained unrecognised. Largely, this was due to the general acceptance of an explanation of the phenomenon suggested long ago by Helmholtz, *viz.*, that it is an effect arising from the dichroism of material contained in the macular region of the retina. This explanation, if correct, would make the brushes a physical curiosity having no physiological significance. It is therefore appropriate here to point out that the explanation given by Helmholtz is wholly untenable. This becomes evident when we examine the assumptions on which that explanation is based and also when we compare its consequences with the actual facts of the case.

As already stressed in the preceding chapter, special techniques are necessary for the visual perception of polarised light to manifest itself in an impressive fashion. One of the essentials is the use of a colour filter which cuts out all light having a wavelength greater than 500 mμ and transmits freely the region of the spectrum having shorter wavelengths. The luminosity of the field as seen through such a filter combined with a polaroid should also be adequate. When these requirements are satisfied, the field exhibits a bright brush running parallel to the direction of vibration of the light and a dark brush transverse to the direction of vibration. Employing the proper technique, we observe that the brush running transverse to the direction of vibration is completely dark.

If the facts of observation indicated above are to be explained on the assumption that the material of the retina in its foveal region has a radially symmetric structure which exhibits dichroism, it would be necessary for the absorption of light by the material to be effective and indeed total for optical vibrations along directions transverse to the radii of the structure and over the entire wavelength range between 400 mμ and 500 mμ. Further, there should be no absorption at all for directions parallel to the radii of the structure. These assumptions are inadmissible for the following reasons. In the first place, the retina being a thin membrane and especially thin in the region of the fovea, the presence in it of sufficient absorbing material completely to block out the entire spectrum between 400 mμ and 500 mμ is scarcely possible. Indeed, our eyes would then be unable to perceive the blue light of the spectrum. Another cogent objection is the known behaviour of fibrous materials dyed with organic dye-stuffs. In numerous cases where the dye-stuffs have elongated molecules, the dyed fibres do indeed display marked dichroism. But in all such cases, the strong absorption is manifested for directions of vibration *parallel* to the length of the fibres and not for directions *transverse* to them.

That an explanation of the brushes as a phenomenon of a purely physical origin is inadmissible becomes even clearer when we recall the observed features which indicate its physiological origin. The diminishing visibility of the brushes when the illumination of the field falls off and their disappearance at low levels of brightness puts the phenomenon in the same category as other aspects of our visual faculties. Striking evidence for their physiological nature is also forthcoming from the fact that an earlier exposure of the eye to polarised light has a great effect on their visibility. Indeed, such exposure can even result in the brushes being seen reversed when the polaroid is removed and the light incident on the eye is unpolarised. To exhibit this effect, the observer should hold the colour filter and polaroid before his eye and view a field which is adequately luminous for a sufficient interval of time to allow the brushes seen at first completely to fade away. He should then suddenly remove the polaroid, but allow the colour filter to remain in place. *He will then see the brushes once again but turned through a right angle.* In other words, the fovea then perceives with enhanced brightness that part of the incident unpolarised light which was cut off by the polaroid when it was in place before the observer's eye.

The Carotenoid Pigments.—That the power to recognise polarised light and to locate its plane of polarisation is exhibited by the foveal region of the retina and that it is limited to the blue-violet sector of the spectrum indicates that the brushes arise as a consequence of some special features in the distribution within the fovea of the material which enables us to perceive light in that part of the spectrum. We have, therefore, firstly, to identify the nature of that material and secondly, to find how it is distributed within the fovea.

One of the very striking features of the visible spectrum is the rapidity of the transition from the blue into the green region. The transition takes place within a range of some 20 mμ and is centred around the wavelength 500 mμ. We may infer from this that the material which activates the perception of light in the blue-violet sector of the spectrum has an absorption which falls steeply from a large value to nearly zero at 500 mμ. The absorptive power should also be large in the spectral region between 400 mμ and 500 mμ and should drop down to low values for wavelengths less than 400 mμ. Two pigments which are known to exhibit these features in absorption are β-carotene and dihydroxy-α-carotene. They are plant pigments almost universally present in the green leaves of plants. They find their way into the human body as the result of the consumption of various food products and are present as colouring matters in the serum of human blood. β-carotene and dihydroxy-α-carotene differ distinguishably in their spectroscopic behaviour. The former is optically inactive, being symmetric in its structure. The latter substance which we shall hereafter refer to as xanthophyll exhibits optical activity as its structure is asymmetric. The two substances also differ by reason of β-carotene being a precursor of vitamin A, whereas xanthophyll is not.

Both β-carotene and xanthophyll have been reported as having been found in the human retina. We shall not here pause to discuss which of the two should be identified as the pigment present in the retina enabling us to perceive bright light in the blue-violet range of the spectrum. It is not necessary to discuss that issue here, since they both have elongated molecules and possess the optical behaviour which could provide an explanation for the perception of polarised light.

The Distribution of the Pigments in the Fovea.—The fovea is a circular depression in the retinal membrane having a diameter of about one millimetre. Its structure exhibits some very special anatomical features. It is densely packed with a mosaic of the visual receptors known as cones. In this region these cones are much elongated and have a much smaller cross-section than elsewhere. The smaller thickness of the retina in the foveal region is the result of several nervous layers present in other parts of the retina being either absent or greatly reduced in thickness in the foveal depression. In this region, also, the nerve fibres connected with the cones are pushed to one side and run an oblique course, except at the very centre of the foveal depression where they form a criss-cross pattern. Thus, if we exclude this central region, the fovea exhibits a radially symmetric structure by reason of the disposition of the nerve-fibres leading away from the mosaic of cones which fills the pit in the retina.

The carotenoid pigments have highly elongated molecules. β-carotene and xanthophyll have respectively the chemical formulae $C_{40}H_{56}$ and $C_{40}H_{56}O_2$. Apart from the two end groups which are different in the two cases, each molecule in these compounds consists of a long chain of carbon atoms held together by an alternation of double and single bonds of which there are nine pairs. It is this structure that enables the molecule to exhibit an absorption stretching far into the visible region of the spectrum from its violet end up to and inclusive of the blue sector. The geometry of the structure would necessarily lead to this absorption having selective directional properties, being confined to directions of vibration parallel to the long chain and absent for vibrations in directions transverse to that chain.

Highly elongated molecules such as those of β-carotene and xanthophyll finding themselves in an environment of nerve-fibres disposed with radial symmetry in the regions of the foveal depression around its centre may be expected to align themselves parallel to the nerve-fibres and hence also to exhibit a radial symmetry in their disposition. Jointly as a result of such disposition and the optical characters indicated above, it would follow that the absorption of the light by the molecules would be effective for directions parallel to the radii and would be absent for vibration directions transverse to the radii. If the energy of the light corpuscles thus taken up is passed on to the cones nearest to them, the result would be the perception of light for vibration directions parallel to the radii and the absence of such perception for vibration directions transverse to the radii. In other words, in the field of view corresponding to the foveal region of the retina, we would observe a bright brush running parallel to the direction of vibration in the polarised light and a dark brush running transverse to the direction of vibration. This is actually what is observed.

We may remark that the explanation set forth above would cover the details of the picture actually perceived by the observer. It may be mentioned that a colour filter well suited for such observations is a solution of cuprammonium of which the strength is so adjusted that it cuts off the green, yellow and red of the spectrum completely without any sensible absorption in the blue and the violet. A glass tube three centimetres in diameter and one centimetre long fitted with flat end plates and filled with the solution makes a very efficient filter. With the cell and a polaroid held up against the bright sky the configuration of the brushes can be very conveniently studied. It is readily verified that the dumbell-shaped brushes are confined to a region in the field of view corresponding to the part of the fovea where the nerve-fibres as shown in the anatomical drawings run obliquely. The region corresponding to the very centre of the fovea where the dark and bright brushes cross, is, of course, never quite dark. Its appearance alters with the orientation of the observing polaroid to a certain extent. This indicates that the molecules of the pigment in this region have preferred orientations.