The new physiology of vision—Chapter XVII. Location of visual pigments in the retina

SIR C V RAMAN

We proceed to consider the significance of the results of our studies on the chromatic responses of the retina and to view them in the light of the conclusions regarding the identity and spectroscopic behaviour of the visual pigments arrived at in earlier chapters. For this purpose, it is necessary to summarise the results of those studies. As has already been explained, what the observer notices when he views a brightly illuminated screen through a colour filter and then suddenly removes the filter depends very much on the spectral region in which the absorption by the filter is manifested and hence differs from filter to filter.

On the basis of the observed phenomena the part of the visible spectrum in which the absorption by the filter is effective may be placed in any one of the following four divisions, viz., I: from 4,000 to 5,000 A.U.; II: from 5,000 to 5,600 A.U.; III: 5,600 to 6,000 A.U. and IV: from 6,000 to 7,000 A.U. These regions will, in what follows, be referred to as the blue, green, yellow and red sectors of the spectrum, these being the colours which are dominant respectively in these four regions. The picture of the retina as perceived by the observer following the removal of the filter may likewise be divided into three regions. A: the fovea; B: a circular area surrounding the fovea and having a well-defined margin and a diameter about four times that of the fovea; C: the surrounding field. The luminosity and colour exhibited by these regions are related to the spectral region of absorption by the filter in the clearly definable fashion. We may indeed say that the part or parts of the spectrum in which the absorption by the colour filter appears determines the picture seen of the retina in all its details.

By far the most spectacular effects are those observed with the colour filters of which the absorption completely covers the yellow sector of the spectrum. Indeed, the phenomena observed with such filters are altogether different from those observed with the filters which exhibit absorption exclusively in the blue, green or red sectors. The striking feature exhibited by them is the manifestation of the fovea as a luminous disk conspicuous by reason of its brightness which much exceeds that of the surrounding areas. Surrounding the foveal disk and of a lesser brightness, but nevertheless clearly differentiated from the outer parts of the field is a circular area having a diameter about four times greater than that of the fovea.

These features are not observed when the filters employed have an absorption lying exclusively in the blue, green or red sectors.

Thus, the observations with the colour filters demonstrate that the yellow sector of the spectrum stands in a class by itself and that it plays a highly significant role in the phenomena of vision. The same conclusion has already been arrived at and stated in earlier chapters on the basis of other considerations. But the new result which now emerges is that the visual pigment which enables us to perceive light appearing in the yellow sector of the spectrum is concentrated in the foveal region of the retina and in the areas immediately surrounding it. Only on that basis is it possible to understand the facts of observation.

The distributions in the retina of the visual pigments which enable us to perceive the blue, green and red sectors of the spectrum are clearly of a different nature. This is made evident by the picture of the retina which is seen when the filter made use of has its absorption in one or another of these three sectors. The glow exhibited by the area of the retina under observation (blue, green, red in colour as the case may be) in the areas surrounding the fovea is of uniform brightness. The fovea itself presents a different appearance in the three cases. With the filters which have a cut-off in the blue, the fovea does not exhibit the blue glow but is seen as a disk with a sharply defined edge and of a pale yellow colour. Likewise, with the filters having a cut-off in the green sector of the spectrum, the fovea does not exhibit the glow seen outside of it, but is seen dimly with a bluish tinge. In the case of the filters having a cut-off in the red, the glow seen elsewhere covers the fovea as well.

Thus, a systematic survey of the retina with the aid of colour filters exhibiting absorption in a relatively narrow range of the spectrum but which between them cover the entire visible spectrum from end to end enables us to establish the result that there are four visual pigments which function in the perception of light in ordinary or daylight vision. It also enables us to indicate the regions of the spectrum on which they respectively function and the manner in which they are distributed over the retina.

In earlier chapters, the visual pigments functioning in the yellow and green sectors of the spectrum were identified respectively as the fully oxygenated form and as the reduced form of heme. The former identification was based on some very significant facts of observation, viz., that the yellow of the spectrum appears precisely at the same position as the sharply defined peak of light-absorption at 579 mμ exhibited by oxygenated heme, that a remarkably high power of colour discrimination is manifested in the vicinity of that wavelength and that the spectrum also exhibits a high luminous efficiency in that region. The observations made with the colour filters fit in perfectly with this situation. It is found, as is to be expected in these circumstances, that the retinal pictures alter in a remarkable fashion as the region of absorption by the filter moves from the red into the yellow sector of the spectrum. The foveal disk appears quite suddenly and exhibits at first a yellow hue. It then gains in luminosity and takes on a greenish yellow colour

and finally appears a brilliant green when the absorption by the filter covers the wavelength region between 600 and 560 mμ and extends further into the green. But filters exhibiting absorption in the green sector alone and not extending into the yellow sector do not produce any such effects.

These experiences are readily understood when we take note of the form of the light-absorption curves of the oxygenated and of the reduced forms of heme in the wavelength range between 600 and 500 mμ. Both forms of heme exhibit a powerful absorption in this range. But the oxygenated form has a sharply defined and intense absorption at 579 mμ, falling off steeply towards greater wavelengths and much less steeply towards shorter wavelengths. It also has a second weak and diffuse maximum of absorption around 542 mμ. The reduced form of heme has only a single wide-band maximum of absorption around 555 mμ and since this form of the heme pigment is not present in quantity in the region of the fovea, filters of which the absorption appears only in the region between 500 and 560 mμ do not exhibit any such effects as those described above.

We may here appropriately mention the remarkable changes in the relative intensity of the yellow and green sectors of the spectrum as visually observed which accompany a progressive fall in the absolute intensity of both sectors. These effects may be conveniently observed in the following fashion. The light emerging from a bulb containing luminous mercury vapour is examined through a pocket spectroscope with the slit opened rather wide. The green and yellow lines of the mercury arc spectrum then appear as patches of light side by side exhibiting these colours. A progressive reduction of their absolute luminosities may be readily obtained by interposing a sheet of opal glass between the lamp and the spectroscope and by the observer moving away from the lamp together with the opal glass sheet and the spectroscope. When he is close to the lamp, the green and yellow patches appear of comparable brightness. But when he is at the other end of the room, both the green and yellow patches exhibit their respective colours, but the yellow appears much less bright than the green. When a further reduction of intensity is produced by the introduction of additional diffusing screens, e.g., sheets of white paper, the yellow becomes progressively feebler and in the limit extremely weak relatively to the green, while the latter continues to be readily observable.

The phenomenon described above is obviously complimentary to the enormously enhanced brightness of the yellow region in the spectrum observed at high levels of luminosity and described in detail in an earlier chapter. In other words, the observed fall in luminosity of the yellow relatively to the green at low levels of brightness is a part of the same sequence of changes in the visual luminosity of the yellow sector as that produced by increases in its absolute level of brightness. That this is actually the case may be demonstrated using the same techniques as those employed earlier for observations of the yellow sensation at high levels of luminosity. The spectrum of a straight tungsten filament heated by an electric current is viewed by the observer from an appropriate distance holding

a replica grating before his eye. As the heating current is progressively diminished, it will be noted that the brightness of the yellow sector in the spectrum relatively to the green and the red sectors on its two sides falls off, until it becomes barely recognisable .

The presence of the oxidised form of the heme pigment in notable quantities in the region of the fovea and in a circular area surrounding that region finds a ready explanation if it be assumed that the pigment enters the retina as an exudate from the highly vascular choroid coat immediately behind it. After entering the foveal pit which is the thinnest part of the retina, it would spread symmetrically outwards from it into the surrounding region. If, further, it be assumed that the quantity of the pigment thus made available for vision varies with the demand for it, in other words, with the level of luminosity at which the retina is functioning, the preponderance of the yellow sensation of high levels of luminosity, and its relative weakness or even total absence at low levels of brightness would find a ready explanation. Since the luminous efficiency of the spectrum in the wavelength range from 600 to 500 mμ is determined jointly by the oxidised and reduced forms of heme, the relative proportion in which these are present would influence the spectral distribution of luminosity in this range of wavelengths. If the oxidised form is present in prepondering measure, the yellow sector would be much more luminous than the green. If it is absent, or deficient, the green sector would be far more luminous than the yellow.

The presence of the heme pigment in its fully oxidised form in the retina may be expected to involve as a natural consequence its being accompanied by the same pigment in its ordinary or reduced form. The latter pigment exhibits a wide-band absorption maximum located at 555 mμ which is the same wavelength as that at which the luminous efficiency in the spectrum at normal levels of illumination as reported by various observers is a maximum. Thus, the identification of the reduced form of heme as one of the major visual pigments is, apart from all other considerations, fully justified by the actual facts of vision.

The presence in or behind the retina of a biochemical mechanism by which the oxygenated heme pigment in the ferrous state is transformed by auto-oxidation to the ferric form of the pigment would provide the visual pigment needed for the red sector of the spectrum. The identification of the ferric form of heme as that functioning in the spectral range between 600 and 700 mμ is confirmed by the fact that it exhibits a peak of absorption at 630 mμ beyond which the absorption falls off rapidly. This is just what is needed to explain the rapid change of colour from orange to red which appears at 630 mμ, beyond which the change of colour becomes extremely slow. Further, the spectroscopic behaviour of the ferric form of heme is precisely that needed to account for the observed features of the Purkinje phenomenon which have been fully described and discussed in an earlier chapter.