

## The new physiology of vision—Chapter XXXVI. The postulated duality of the retina

SIR C V RAMAN

Received February 16; 1966

The facts of observation set out in the preceding chapter lead us to make a critical examination of the belief, firmly held by physiologists at the present time, that the human retina exhibits a duality in its structure as well as in its functioning. This belief finds concrete expression in the distinction drawn between two types of vision which are termed respectively as "Photopic Vision" and as "Scotopic Vision" and which are assumed to exist and to be distinguishable from each other. While "Photopic Vision" is effective at the higher levels of illumination, "Scotopic Vision", as its name indicates, functions at the lowest levels. "Photopic Vision" alone exhibits differences of colour, while "Scotopic Vision" is achromatic. The acuity of vision is high in "photopic vision" and is almost non-existent in "scotopic vision". To give plausibility to these beliefs, it is suggested that "photopic vision" may be identified with "cone-vision" and "scotopic vision" with "rod-vision". So strongly are these beliefs entrenched in the literature of the subject that it may come as a surprise to the reader to be informed that the purpose of the present chapter is to demonstrate that the supposed duality of the human retina is a myth and that the ideas regarding human vision which rest on the assumption of such duality are altogether erroneous.

*The falsity of the postulate:* We may begin by pointing out that the differences in the characteristics of human vision at high and at low levels of illumination which have been sought to be interpreted as a consequence of the rod-cone duality of the structure of the retina have, in reality, an altogether different origin. It will suffice to point out that in all critical observations we naturally make use of the foveal region of our retinae, and these regions, as is well-known, contain only cones and no rods. Nevertheless, the fading away of colour and the loss of visual acuity which are associated with low levels of illumination are conspicuously evident in such observations. If, for example, the Great Nebula in Orion is viewed through a pair of binoculars, it appears as a luminous cloud without a trace of colour. On the other hand, seen through the great telescopes of the world, it appears as a vast area exhibiting resplendent colours.

Elsewhere than in the fovea, the rods and cones appear interspersed in the

retinal structure. It may therefore be taken for granted that the characteristics of human vision are determined by the rods and cones functioning jointly and not independently. Indeed, the assumption that rod-vision and cone-vision function independently of each other is ruled out by various facts of experience. We may here, for instance, recall the studies of the half-tone process of colour reproduction set out in an earlier chapter. It emerged from those studies that the retina integrates the different colours incident on it in adjacent areas and perceives them as a single resultant colour.

From the known fact of observation that fainter objects appear distinctly brighter when seen by averted vision than when viewed directly, we infer that the rods are more sensitive as detectors of radiation than the cones. This indeed becomes evident when a very faintly illuminated screen of plastic material which diffuses the light incident on it is viewed in a dark room. The marginal regions of the screen appear distinctly brighter than the central area. But the latter area continues to be perceived even at the lowest levels of illumination, thereby showing clearly that the fovea does not cease to function even in the dimmest light.

That the retina functions as a single unit and not as two retinae with different characteristics becomes even clearer when the observations set forth in the preceding chapter are recalled. An elongated slit backed by an extended source of light is viewed by the observer through a replica diffraction grating. Diffraction spectra having the same length as the illuminated slit are then seen in the field of view of the observer going right across the retina of the observing eye. When the luminosity of the source behind the slit is varied, the character of the spectra also alters. This is a demonstration that the so-called "luminous-efficiency" of radiation is itself dependent on the intensity of the light under observation. It alters progressively as we proceed from high to low levels of illumination. What is particularly significant is that these changes are not observably different for the different parts of the retina on which the spectra fall with the arrangement described.

Very significant also are the changes noticed and described in the preceding chapter in the character of the spectrum of white light as we proceed towards low levels of illumination. In succession, the red sector, the yellow sector and the blue sector of the spectrum pass out of sight, till, finally, only the green sector in the wavelength range between 560 and 500  $m\mu$  survives. It is this part of the spectrum which enables us to perceive light at the very lowest levels of brightness. It is evident that these faintest observable spectra bear no resemblance to the "scotopic spectrum" which has been described as covering the entire range of wavelengths from 400 to 700  $m\mu$  and as exhibiting the "maximum luminous efficiency" at the wavelength of 500  $m\mu$  or thereabouts. The inference is that the "scotopic spectrum" is an artificial concept which has no real significance in relation to the facts of human vision. We are also justified in inferring that the "visual purple" which has an absorption spectrum extending over the entire

wavelength range from 400 to 650  $m\mu$  does not function as the visual pigment which enables us to perceive light at low levels of brightness.

We proceed now to describe the results of some further experimental studies designed to carry the investigation of the visual perception of light in the various parts of the spectrum down to the lowest levels of illumination.

*Techniques of study:* We shall begin with the description of an experimental arrangement which enables an observer directly to view a spectrum at levels of brightness which can be progressively altered from high values down to the lowest levels till we reach the threshold of human vision at which light ceases to be visible. The apparatus is essentially a prismatic spectrograph of substantial dimensions but with a rather small dispersive power. Special devices enable the brightness of the spectrum as perceived by an observer to be varied over a great range. The collimator is a telescope with a 3-inch objective which has a focal length of 4 feet; the eye-piece is removed and replaced by a spectrometer slit. The light from the collimator passes through a  $30^\circ$  prism of dense flint glass with a square face 3 inches in height and in breadth. The light dispersed by this prism enters the observing telescope which has an objective of 6 inches diameter and a focal length of 13 feet. Between the prism and this objective is placed an iris-diaphragm, the diameter of which can be progressively reduced from a maximum of 4 inches down to a minimum of  $\frac{1}{8}$ th of an inch, thereby reducing the area of the opening to 1/1000th part of its maximum value.

The maximum brightness of the spectrum is obtained when the source of light is held close to the slit. By increasing the distance of the source from the slit, this brightness can be diminished. To obtain a further large step-down in intensity, the light from the source is first allowed to fall on a diffusing screen of milk-white plastic material, instead of falling directly on the slit. The light diffused by the screen then enters the slit of the spectrograph. Likewise, instead of the observer viewing the spectrum directly, a milk-white plastic screen is placed at the focus of the 13-foot objective. The light reaches the screen and is focused on it. The spectrum appearing on the screen is visible to the observer by reason of the light diffused backwards by the surface. Thereby results a large reduction of its observed luminosity.

The entire apparatus and the observer himself are located in a large room which could be completely darkened. The source of light and the diffusing screen which illuminates the slit are both placed in a covered passage which leads up to the observing room. But no light is permitted to enter that room except that passing through the slit and spectrograph. The complete spectrum when formed on the viewing screen is about 10 cm long and about 2.5 cm broad. The observer remains in complete darkness for at least one hour before commencing his observations. He can view the spectrum either directly, or by averted vision if he so desires.

*Observations with a mercury lamp:* It is useful in the first instance to make use of a source of light exhibiting the discrete lines of the mercury arc on the background of a continuous spectrum. Such a lamp being available, when it is placed directly against the slit, the mercury arc lines  $\lambda$  5790–5770, 5461, 4916, 4358 and 4046 can all be seen and recognised on the continuous background, provided the iris-diaphragm between the prism and the objective is fully open. When the iris is progressively closed down, the luminosity of the entire spectrum falls off, but to quite different extents in its different parts. In particular, the continuous spectrum seen in the red sector becomes weaker and finally disappears, the yellow doublet  $\lambda$  5790–5770 becomes much fainter than the green line  $\lambda$  5461, the continuous spectrum in the region of wavelengths less than  $\lambda$  5000 ceases to be noticeable,  $\lambda$  4358 becomes very weak and barely observable while the  $\lambda$  4046 line completely disappears from sight.

If, instead of allowing the light from the lamp to fall directly on the slit, we use the diffusing screen as explained above, the brightness of the observed spectrum is greatly reduced. Even when the iris is fully open, all that can be seen of in the spectrum is the yellow doublet  $\lambda$  5790–5770 and the green line  $\lambda$  5461 of the mercury and a faint continuum covering the green sector of the spectrum upto about  $\lambda$  5000. The yellow doublet is seen to be feebler than the green line. When the iris is closed down, the continuum disappears and both the yellow and green lines become very faint, the former much more so than the latter. Further reductions in the level of brightness may be effected by moving the lamp away from the diffusing screen. By increasing their separation from 15 to 150 cm, we lower the brightness by a factor of 100. In the spectrum as then observed, only the  $\lambda$  5461 line is seen even when the iris is fully open. When the iris is progressively closed down, this line falls off in brightness and finally disappears from sight.

*Observations with a source of white light:* If instead of a lamp containing mercury vapour, we use a coiled-coil tungsten filament emitting light at a high temperature, its continuous spectrum is that of white light extending over the wavelength range from 700 to 400  $m\mu$ . The alterations in the appearance of this spectrum as seen by the observer at various levels of brightness can be followed step by step in the same manner as described above in the case of the mercury vapour lamp. The red sector of the spectrum, the yellow sector and the blue sector each becomes progressively weaker and finally disappears from sight. All that is left of the spectrum is then the green sector in the range of wavelengths between 560 and 500  $m\mu$  with very feeble extensions on either side. These extensions also disappear until we are left only with a patch of light covering the green sector of the spectrum. The weakening and final disappearance from sight of this green sector is most conveniently produced by a progressive closing down of the iris-diaphragm separating the prism and the objective of 13-foot telescope. It is of

interest to note that the patch of spectrum when actually visible appears noticeably brighter when seen by averted vision than when directly viewed.

*The spectra of the moonlit and starlit skies:* A very convenient arrangement which enables an observer to view the spectrum of the faint light reaching the earth from various parts of the sky at night is for him to locate himself beneath the covered dome of an observatory of moderate size, e.g., one of 16-foot diameter. Seated on the floor of the observatory in total darkness, and holding a replica diffraction grating before his eye, he views the sky through the narrow opening, about an inch wide, left between the almost completely closed shutters which cover up the sky when the observatory is not in use. The diffraction spectra of the light entering the dome of the observatory through this narrow opening are seen projected against the inner surface of the dome as curved arcs of light on either side of the slit. They run parallel to each other and to the slit from end to end. The spectra of the first order are usually the brightest; one of them may be brighter than the other. It is noteworthy that the spectrum exhibits the same features over the entire length of it traversing the field of view of the observer, irrespective of the particular point on which the latter fixes his vision.

The brightness of the spectra as seen by the observer naturally depends on the circumstances of the case. If the sky is clear and is lit up by the light of the full-moon, the spectra are particularly conspicuous. But their features differ greatly from what would be seen in similar circumstances when the sunlit sky is observed. The width of the spectrum is much reduced and it can be readily ascertained with the aid of a comparison spectrum that the only part of it actually visible is confined to the wavelength range between 560 and 500  $m\mu$ , in other words, the green sector. The red, yellow and blue sectors of the spectra are absent. Except that the spectra are less brilliant, precisely the same features are exhibited when the sky is clear and the moon is not full and hence the illumination of the sky by scattered moonlight is feebler. Indeed, the observations show that even when the moon is absent and the spectrum under observation is that due to starlight alone, the spectrum exhibits the same features though, of course, it is much less bright.