

The role of the retina in vision

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1. Introduction

Our sense-organs are the gateways through which a knowledge of the external world reaches us. The relationships which exist between our sensory impressions and the nature of the stimuli which excite those impressions are thus matters of great importance. For, they furnish us with indications regarding the processes by which the stimuli received by the sense-organs are transformed into sense-impressions. Studies on the perception of stimuli of the simplest character are particularly important, since their results are most readily analysed and understood.

Light which appears as a sharply-defined line in the spectrum is the simplest type of radiation. It is appropriate therefore that we recognise the sensations excited by monochromatic lights of various colours as the primary or fundamental visual sensations. Likewise, when a continuous spectrum of radiation is dispersed by a prism into a band of colour, each strip which the eye can distinguish as being different in hue from the strips on either side can be regarded as a primary or fundamental visual sensation. Hence the primary visual sensations are as numerous as the hues which can be distinguished from each other in the spectrum by the eye under the most favourable conditions of observation.

We may here usefully recall various facts of observation. It is known that as many as 250 different hues in the spectrum can be distinguished under appropriate conditions. The spectral shift which results in an observable change of hue is less than 20 \AA over the greater part of the spectrum and as little as 10 \AA in some parts. It is also known that the addition of white light in any desired proportion to a pure spectral colour does not change the observed hue. Quantitative studies have further established that the power of the eye to discriminate between the hues of adjacent regions in the spectrum is not sensibly diminished even when the colours are diluted by considerable additions of white light to the fields under comparison.

The facts of experience stated above are just what we would expect to find if the colours of homogeneous light are the primary or fundamental colour sensations. That such a relationship exists is not in the least surprising. For, our organs of vision would be of little use to us, if the external stimuli and the sensations which

they excite are not very simply related to each other. We are, therefore, entirely justified in concluding that the basic or primary sensations with which physiological optics has to concern itself are those produced by the radiations which are recognised by the physicist as simple and homogeneous. These sensations stand in a category by themselves and they are clearly distinguishable from the sensations excited by compound or heterogeneous radiation.

The basic problem in physiological optics is thus to find an answer to the question, how does the apparatus of human vision function and enable us to distinguish the colours of monochromatic lights from each other with the degree of precision actually observed?

2. The nature of the visual process

Geometrical optics and the wave-theory of light form an appropriate basis for a consideration of the propagation of light in refractive media. Thus, they enter into the realm of physiological optics when we consider the functioning of the cornea and the crystalline lens and the formation of images of external objects on the retina. But when we reach the retina, wave-optics ceases to be relevant, and Einstein's concept of light as consisting of discrete energy-quanta or photons necessarily takes its place. For, the wave-theory is incapable of giving any acceptable explanation of such phenomena as the emission or absorption of light and the transformations of light-energy. Hence, we must lay aside the ideas and language of the wave-theory and think of light as a stream of photons, if we are to make any progress towards an understanding of the facts of human vision.

Homogeneous light may be described as a stream of radiant energy consisting of units or quanta which are all identical. The quanta increase progressively in magnitude as we move up the spectrum from the red towards the violet end. The colour of the perceived light also changes progressively in the same circumstances. We are, therefore, justified in associating the sensation of colour experienced in homogeneous light with the energy carried by the individual photons or light-quanta. The other sensation excited by light, viz., its luminosity, is determined by the number of photons traversing any given area per unit of time. Thus, the two physiologically experienced sensations of colour and luminosity excited by homogeneous light are connected respectively with the two specifiable properties of the radiation in the language of the quantum theory.

A fuller insight into the nature of the visual process is furnished by quantitative data of two different sorts which are available regarding the sensations excited by homogeneous light. These data are represented in the form of the curves known respectively as "the luminous-efficiency curve" and "the hue-discrimination curve" of the visible spectrum. The luminous-efficiency curve exhibits the results of a comparison of the visual luminosity of the different parts of the visible spectrum for a constant energy-flux. The hue-discrimination curve represents

determinations of the smallest difference of spectral position necessary to give an observable difference in colour between two fields of illumination, the luminosities of which are equal.

The data of observation represented in the hue-discrimination curve are particularly significant. In the entire range of the visible spectrum, a change in the energy of the photon of 1% is sufficient to give a perceptible change of colour. Indeed, this statement underestimates the power of the visual mechanism to perceive differences of colour. Except near the ends of the spectrum where the luminosity is low, a change of one-half of 1% in the energy of the photon is everywhere detectable. In the blue-green region, a change of one-fifth of 1% and in the orange-yellow, of one-sixth of 1% reveals itself by an alteration of the observed colour.

The facts of experience stated above are most readily understood if vision is assumed to result from the acceptance of the energy of the photon by the retina and its immediate transference without addition or subtraction to the centres of perception. We do not have to assume that all the photons incident on the retina are thus dealt with. A considerable proportion, especially in daylight vision, may be expected merely to pass through the retina and suffer absorption by the pigmented choroid coat behind it. The energy of the other photons may be expected to be used up in producing thermal effects or photochemical changes in the substance of the retina. The photons thus disposed of cannot be effective in vision. The observed precision of the colour sense over the entire visible spectrum precludes any such possibility.

The distribution of visible luminosity in the continuous spectrum of radiation emitted by a hot body differs greatly from the distribution of energy in it. This difference is a characteristic property of human vision and arises from the enormous differences between the luminous efficiencies of homogeneous radiation in the different parts of the spectrum. The efficiency exhibits a pronounced maximum in the green and falls off rapidly as we proceed away from it either towards the red or towards the violet end of the spectrum, but more rapidly so in the latter case. Indeed, the luminosity of the violet end of the spectrum is very low. These differences in the ability of photons of different energies to excite the sensation of luminosity are ascribable to the differences in the probability of their energies being taken over by the retina and transmitted to the centres of perception as indicated above. On this basis, we should expect to find noticeable relationships between the variations of luminosity and of colour in the different parts of the spectrum, and this is actually the case. We shall return to these topics later.

3. The spectral sensitivity of the retina

A technique of observation has been devised and used by the author which is both simple and effective and which enables an observer to see a greatly enlarged

picture of his own retina in the act of functioning. The technique enables highly important information regarding the structure of the retina and its sensitivity to light in different areas and in different parts of the spectrum to be obtained.

We may first briefly explain the technique and how it works. By screening the eye from an external illumination for a short period which need not exceed a few minutes, it is possible greatly to increase the sensitivity of the retina to light. This improvement may be made spectrally selective, in other words, restricted to any desired part of the spectrum by using an appropriately chosen colour filter and holding it before the eye for a suitable interval of time. Accordingly, when the filter is removed and a brightly lit white surface is viewed by the observer, he sees on it a picture of his own retina which exhibits the selective responses of its different areas to the parts of the spectrum which had been screened off by the filter before its removal. This picture, of course, is fugitive. But it may be recalled as often as desired by putting back the filter and then removing it from before the eye.

A series of ten drawings of the retina showing the effects observed with different colour-filters in the manner explained above are reproduced in the accompanying colour plates. The colour-filters were prepared by dyeing gelatine films on glass with different water-soluble dyes to an appropriate depth of colour and then washing and drying the film. The commercial names of the colouring matters used are entered against each figure. We shall proceed to comment briefly on the effects noticed with the different filters.

It is significant that a rhodamine filter, which cuts off the green sector of the spectrum without weakening other regions, gives no observable effect following its removal. This indicates that the sensitivity of the retina to the green which is the most luminous part of the spectrum is not sensibly enhanced by its being screened off from the eye for a brief period.

Very striking and beautiful effects are observed using a filter dyed with methyl-violet. The density of the filter and the accompanying changes in the strength of the absorption and the extent of cut-off in the spectrum greatly influence the observed results. In all cases, the foveal area and the foveolar depression are conspicuous features, the colour which they exhibit varying with the density of the filter. A lightly-dyed filter cuts off the yellow and orange sectors and weakens the green of the spectrum. With such a filter, the foveal region appears green, while yellow and orange are the dominant colours elsewhere in the field. A halo of orange-red hue appears encircling the foveal disc (figure 1 in the colour plate).

Using filters whose absorption is at the violet end of the spectrum and which accordingly appear yellow or orange by transmitted light, the retina exhibits a blue glow following the removal of the filter (figure 9 in the colour plate). With filters which cut off the red of the spectrum and allow the rest to pass through freely, a rose-red glow appears covering the entire field following the removal of the filter (figure 3 in the colour plate). The fovea is either not seen at all or is only very dimly visible in the retinal picture in these cases. Filters which appear green

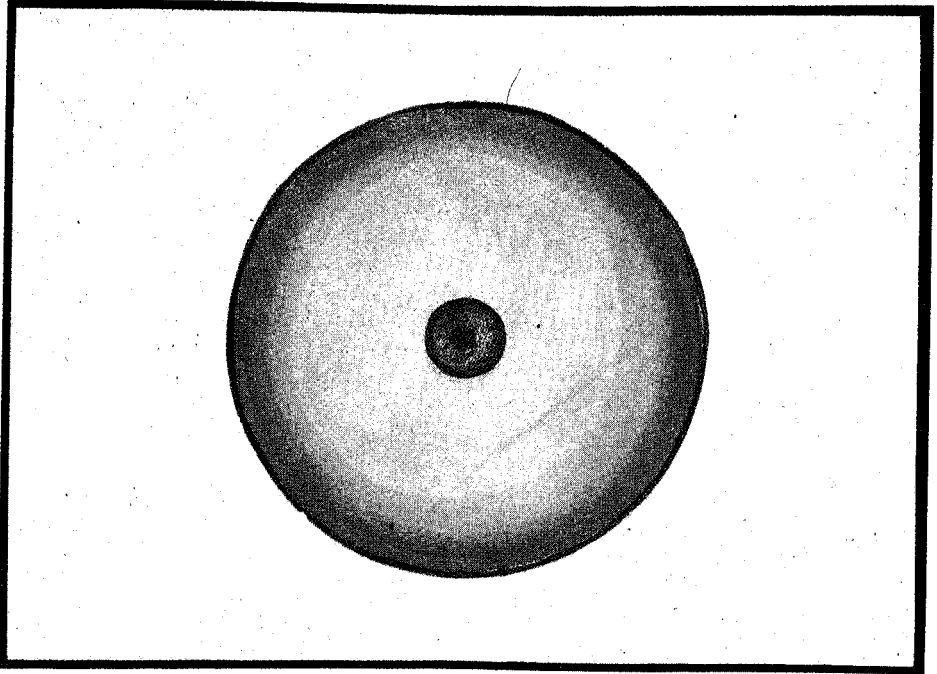


Figure 1. Picture of retina seen by methyl violet filter.

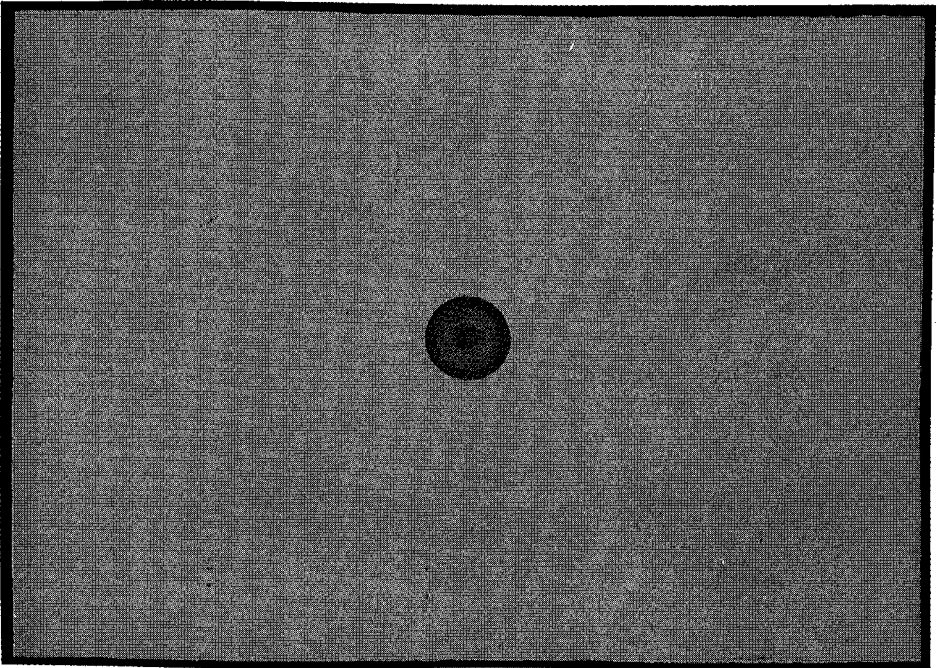


Figure 2. Picture of retina seen by coomassie brilliant blue filter.

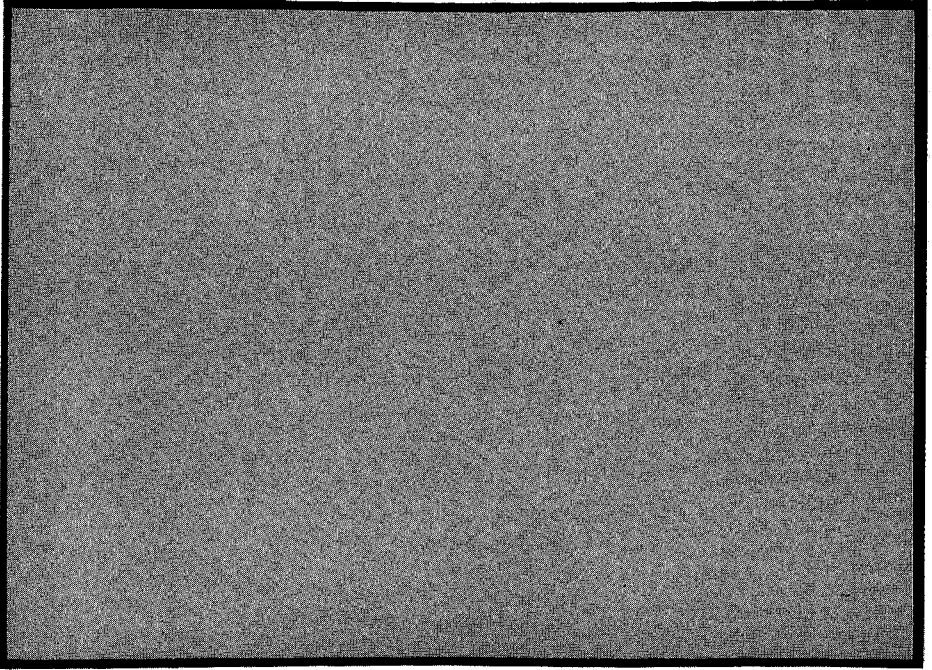


Figure 3. Picture of retina seen by light lissamine green filter.

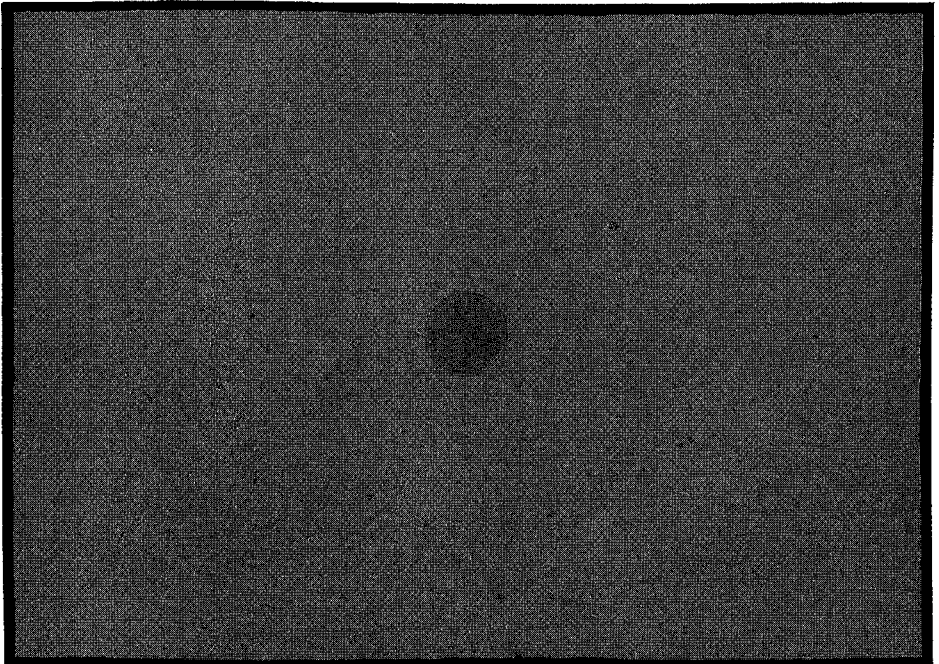


Figure 4. Nickel chloride.

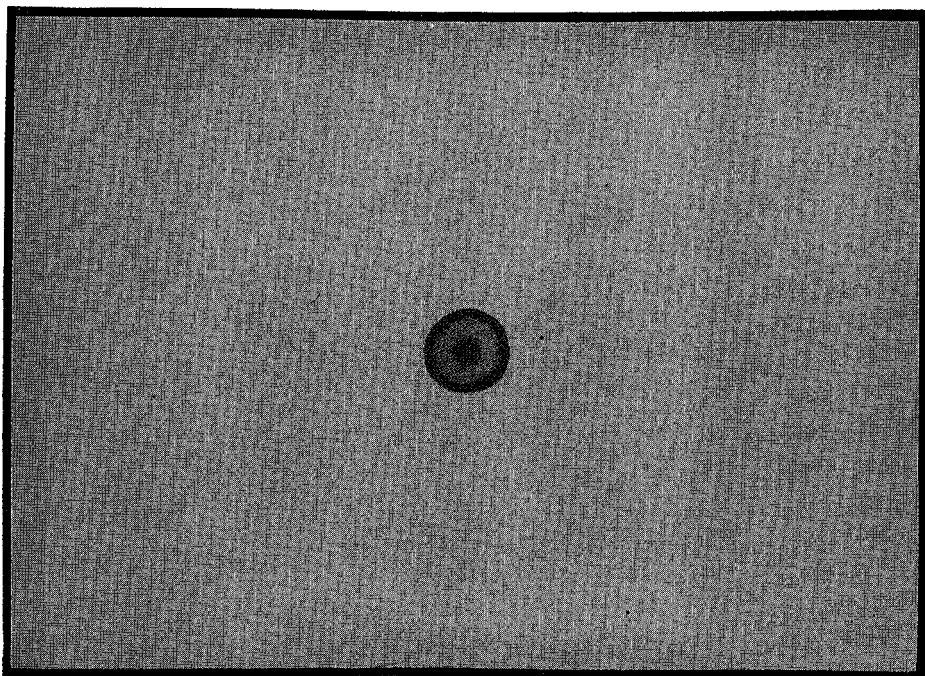


Figure 5. Picture of retina seen by coomassie navy blue filter.

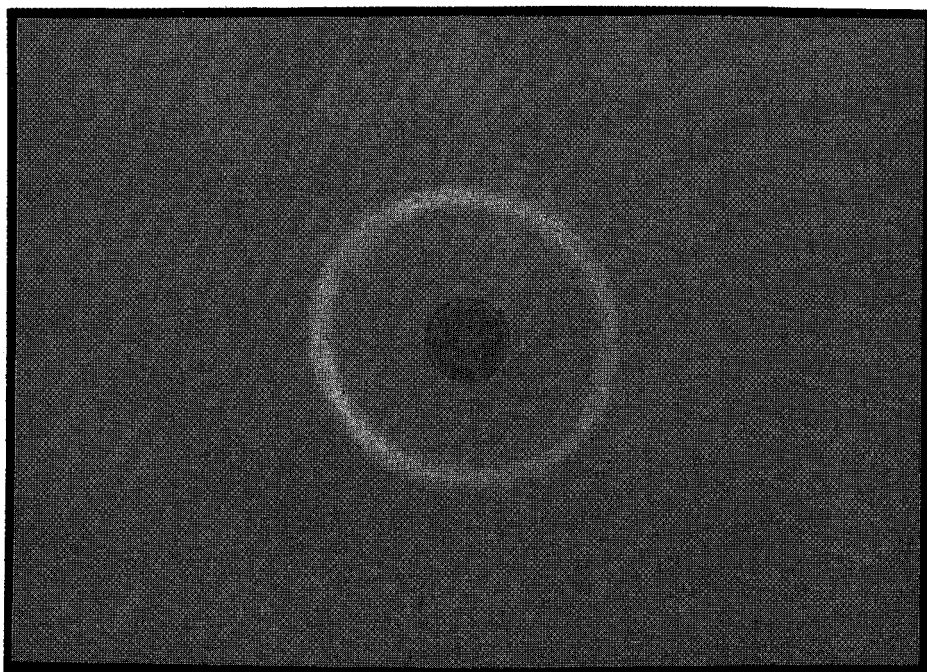


Figure 6. Picture of retina seen by deep lissamine green filter.

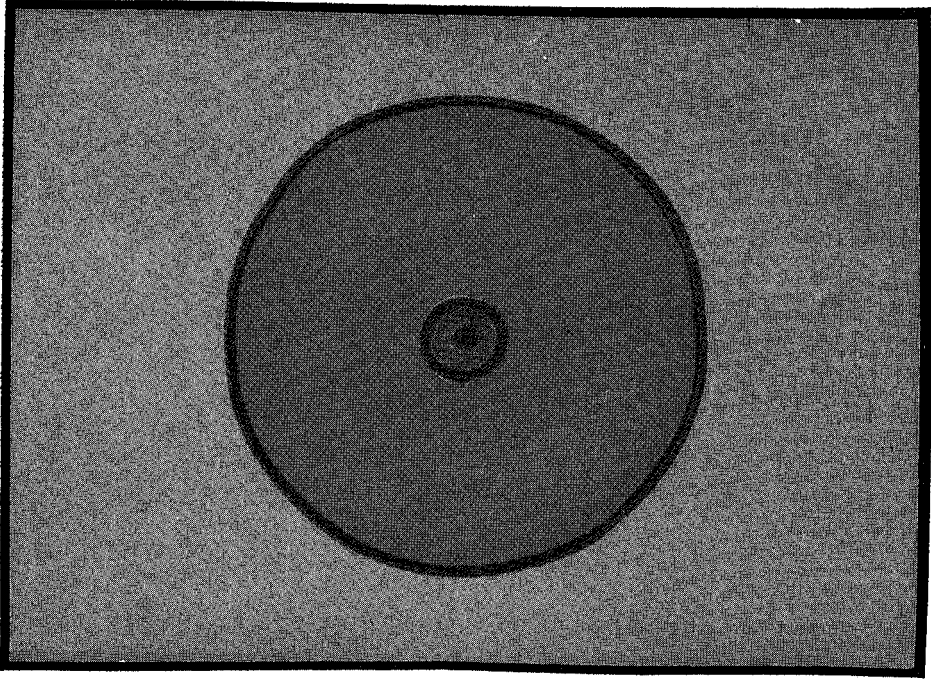


Figure 7. Picture of retina seen by deep blue filter.

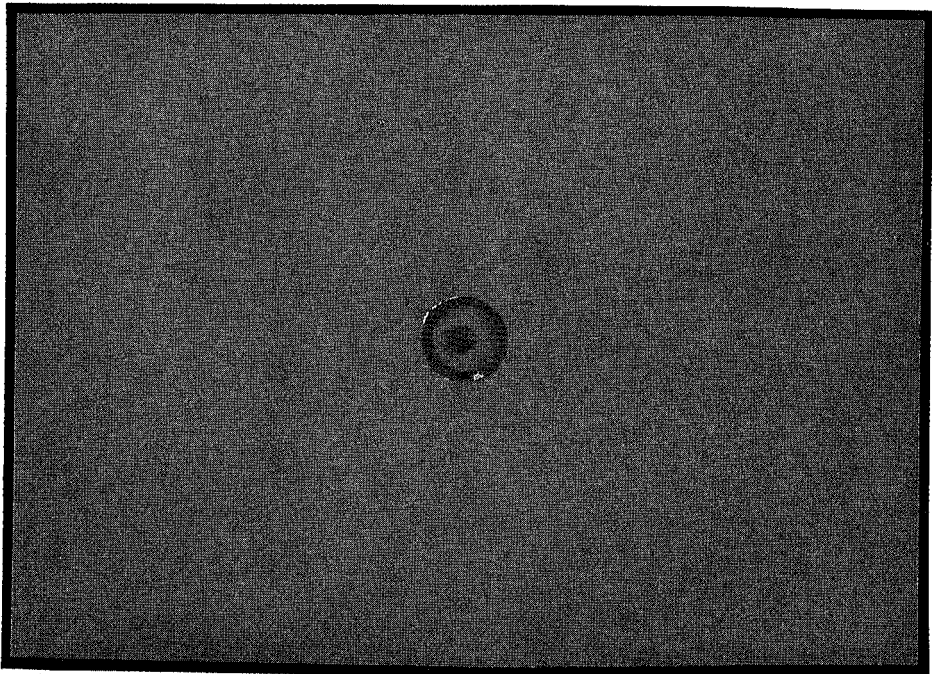


Figure 8. Picture of retina seen by greenish blue filter.

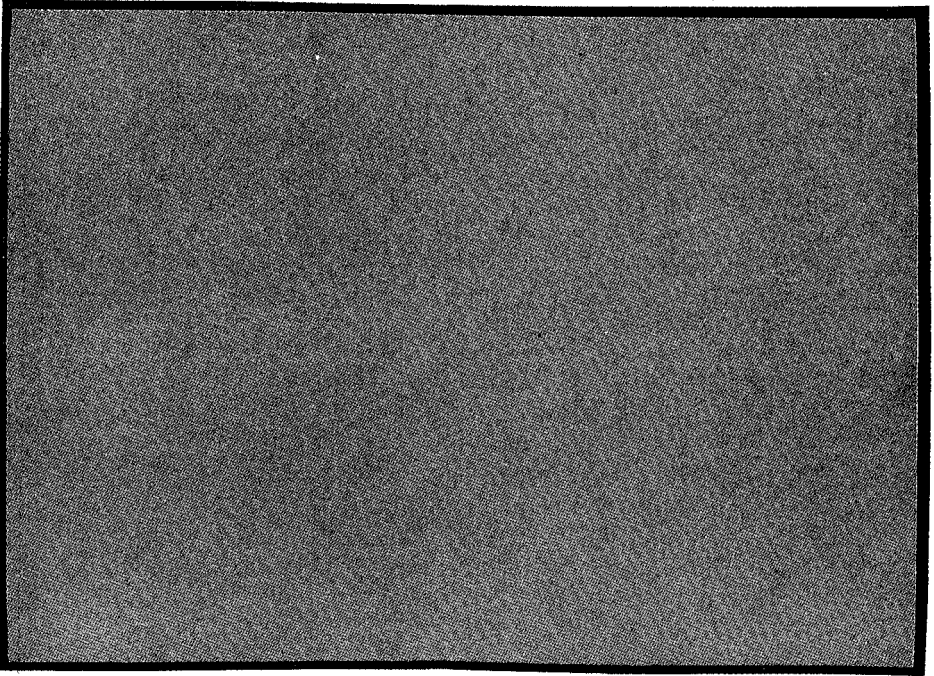


Figure 9. Picture of retina seen by deep orange filter.

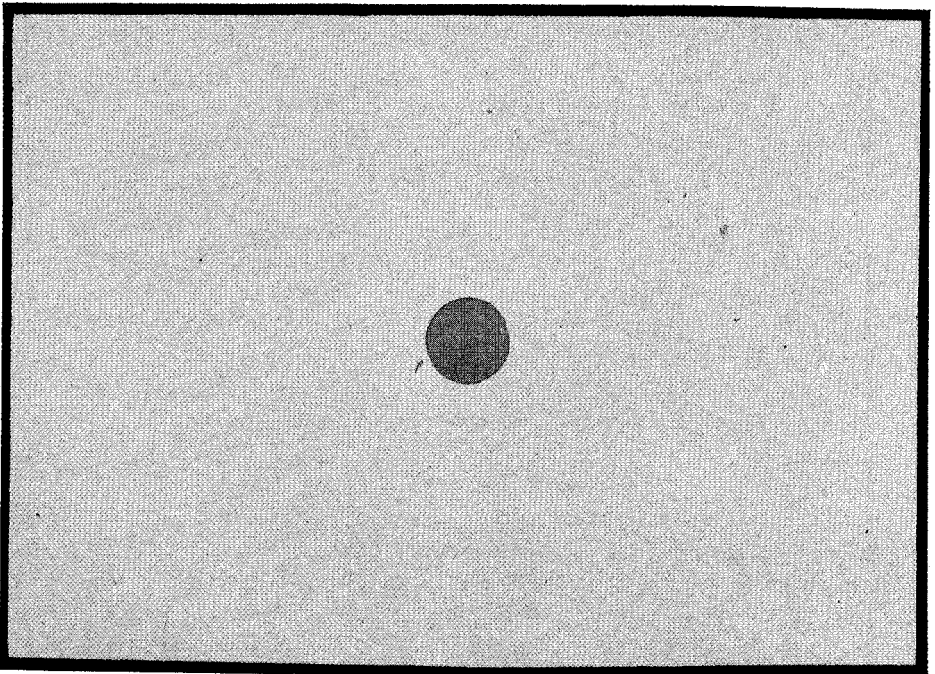


Figure 10. Picture of retina seen by light green filter.

or greenish-blue by transmitted light usually exhibit a cut-off at both ends of the visible spectrum. If the cut-off covers the yellow and orange regions of the spectrum, the retinal picture shows the fovea very clearly as a yellow ring with a bright yellow spot at the foveola (figures 4, 8 and 10). With the more deeply coloured filters, the foveal region appears also encircled by a halo or haloes (figure 6).

A variety of blue filters may be prepared by dyeing gelatine films on glass. All such filters cut off the yellow and orange regions of the spectrum, and hence when they are used, the fovea is invariably seen in the picture, the colour which it exhibits and the colour of the surrounding field varying with the nature of the spectral cut off by the filters. Very similar effects may also be observed using commercially available blue glasses. If such a filter cuts out the green, yellow and red sectors completely, its transmission is a clear deep blue of low intensity. When a filter of this kind is held against the eye against a bright background and then suddenly removed, a multi-coloured picture flashes into view in which the fovea with the foveola at its centre appears as a bright disc surrounded by a less luminous field and further encircled by a halo. This picture slowly fades away.

4. Observations with polarised light

The use of a polaroid in combination with a colour filter in observations of the kind described above reveals some highly significant facts. It may be stated at once that the special effects observed with polarised light are restricted to the foveal area on the retina. They are seen with filters transmitting the violet and blue sectors of the spectrum and are unobservable with filters which do not transmit those parts of the spectrum. The use of filters which transmit other parts of the spectrum besides the blue and the violet serves only to dilute the observed effects and make them less readily observable.

We shall now proceed to state what is actually observed. Placing a blue filter in front of the eye, a bright field of illumination is viewed; after a few minutes, a polaroid is placed in front of the filter. A dark brush shaped like a dumbbell crossed by a bright brush of similar shape then springs into view in the foveal area of vision. This picture slowly fades away. The polaroid is then suddenly removed, the blue filter remaining in place. *The brushes then reappear, but turned through a right angle, in other words, the bright brush takes the place of the dark brush and vice-versa.* This again duly fades away. The observations may be repeated as often as desired.

Observations of the same nature may also be made with the polaroid alone but without any colour-filter. Putting the polaroid in front of the eye, we observe the well-known phenomenon of Haidinger's brushes, a feeble yellow brush crossed by a blue brush appearing in the foveal area of vision. When this has faded away, the polaroid is suddenly removed. The brushes then reappear but with the yellow brush and the blue brush interchanged in their positions.

Another significant result emerges when the brightness of the field against which these brushes are viewed is varied. The polaroid and the blue filter should be used together so that the brushes are seen with the maximum clarity. Their fading-away is obviated by the simple device of oscillating the polaroid in its own plane through a right angle, so that the brushes remain continually visible, though constantly shifting their position. When the brightness of the field viewed by the observer through the polaroid-filter combination is progressively diminished. It is found that the visibility of the brushes vanishes when the level of illumination is reduced to the point at which the blue colour of the light becomes inconspicuous. In other words, the phenomena exhibited in polarised light are confined to the photopic levels of illumination and disappear when we pass into the scotopic range.

5. The visual pigments: Xanthophyll

We shall now proceed to make use of the facts and results set forth in the preceding pages to establish the chemical identity of the colouring matters present in the retina which enable it to function as a receptor of vision in the photopic range of illumination. The functioning of the retina in the lowest or scotopic levels of illumination will not be dealt with here.

Xanthophyll is a plant pigment of very wide occurrence. Its chemical name is dihydroxy- α -carotene and its chemical formula is $C_{40}H_{58}O_2$; it is dextro-rotatory and has no vitamin-A activity. The spectral properties of xanthophyll are similar to those of α -carotene. Xanthophyll is sensibly transparent for all wavelengths greater than $520\text{ m}\mu$; the absorption-strength becomes sensible at $500\text{ m}\mu$ and rises very steeply beyond $490\text{ m}\mu$; it reaches a pronounced maximum at $477\text{ m}\mu$ and this is followed by a second and even more pronounced maximum at $448\text{ m}\mu$. It falls off at shorter wavelengths and after exhibiting a third and minor maximum at $420\text{ m}\mu$ goes down steeply to small values beyond $400\text{ m}\mu$.

Like all the carotenoid pigments, xanthophyll exhibits in its structure a long chain of conjugated carbon-carbon double bonds, to which it owes its power to absorb light in the visible region of the spectrum. It may be remarked that this absorption appears only in the violet and blue sectors of the spectrum. The presence of xanthophyll in the retina is unquestionable. Indeed, the yellow colour of the *macula lutea* has long been known and that it is due to xanthophyll was established by extraction and the study of its absorption spectrum, notably by Wald. What we are now concerned with is to demonstrate that xanthophyll is the visual pigment which enables the eye to perceive light and colour in the violet and blue sectors of the spectrum. Several items of proof are forthcoming which will be set out in proper order.

The absorptive properties of xanthophyll account satisfactorily for the observed features of colour and luminosity in the spectrum. The region between 490 and $440\text{ m}\mu$ usually marked out as the blue sector in the spectrum is also the

region where the absorption of xanthophyll rises steeply from very small values to maximum strength. The region beyond $440\text{ m}\mu$ designated as the violet sector of the spectrum is also the region where the absorption of xanthophyll having passed its zenith drops down to small values.

The wavelengths at which the absorption-curve of xanthophyll exhibits its steepest gradients are also the wavelengths at which the hue-discrimination curve in the spectrum exhibits the most pronounced dips, in other words, the wavelengths at which the spectral shifts necessary to produce an observable change of colour reach their minimum values. The very steep rise in absorption at $490\text{ m}\mu$ corresponds exactly with the conspicuous dip of the hue-discrimination curve at $490\text{ m}\mu$. The second and much less conspicuous dip of the hue-discrimination curve at $440\text{ m}\mu$ also coincides in its position with the steep fall of the absorption of xanthophyll after it has reached its maximum value.

The effects observed with polarised light and described in the preceding section are a conclusive demonstration that xanthophyll is the visual pigment for the blue and violet sectors of the spectrum. They are explained as follows: Xanthophyll has long-chain molecules containing an alternation of single and double bonds; they can absorb light and function as a visual pigment only if the light is polarised with the electric vibrations parallel to the chain-structure of the molecules. On the slopes of the foveal area, the nerve fibres have a radial setting. In that region, therefore, the xanthophyll molecules lie parallel to the nerve fibres and also have a radial setting. Hence, in the foveal area, a bright brush is seen in the same plane as the electric vector of the incident light and a dark brush in the transverse direction. That the brushes are visible only in the blue and violet sectors of the spectrum and not elsewhere is readily intelligible. For, the absorption of light by xanthophyll appears only in the former regions and not elsewhere.

That the brushes reappear turned through a right angle following the removal of the polaroid has already been mentioned. This is a further proof that we are here concerned with a physiological phenomenon and not with an effect of physical origin. When the polaroid is kept before the eye long enough, the sensitivity of the foveal region to light is enhanced in the region of the dark brush and diminished in the region of the bright brush. Hence, when the polaroid is taken out, the brushes are seen again but with the dark and bright brushes exchanged in their positions.

Xanthophyll functions as a visual pigment only under photopic conditions. It is therefore to be expected that the brushes observed in polarised light over the area of foveal vision disappear when the illumination is reduced from the photopic to the scotopic level.

6. The visual pigments: Heme-proteins

The observations with colour filters described earlier make it evident that the pigments which enable the retina to function in the red and green sectors of the

spectrum are different. However, it is also clear from those observations that there is an overlap of the regions of the spectrum in which the two pigments function and that they co-operate in the perception of light and colour in the regions of such overlap. It is in these regions that the spectral colours of yellow and orange are perceived.

That the pigments which enable us to perceive the green and the red of the spectrum are heme-proteins of the ferrous and ferric types respectively is indicated by various considerations. In the first place, the absorption of light by these pigments appears in just those regions of the spectrum where they are needed to account for the observed facts of vision. Ferroheme exhibits a pronounced maximum of absorption around $550\text{ m}\mu$. Likewise, the luminous efficiency in the spectrum exhibits a highly pronounced maximum around $550\text{ m}\mu$. Accordingly, we are justified in recognising ferroheme as the visual pigment which functions in the green sector of the spectrum. Ferriheme behaves differently. Its absorptive power is much weaker than that of ferroheme in the green but is much stronger in the red. Hence, we are led to assign to ferriheme the role of the visual pigment which functions at the red end of the spectrum.

As is well-known, defects and anomalies in the perception of red and green in the spectrum are fairly common. It is very significant that these defects and anomalies are congenital and that they are transmitted from generation to generation according to the laws of heredity. Further, whereas the condition of night-blindness arising from dietary deficiency can be rapidly cured by an adequate addition of vitamin A to the food consumed, the defects of photopic colour-vision cannot thus be dealt with. These facts very clearly indicate that the visual pigments which enable us to perceive the green and the red of the spectrum are products of biological activity in the human body itself and that they are not plant products which have entered the retina by way of the articles of food consumed.

Having thus set aside the possibility of the carotenoids being the visual pigments for the green and the red, we naturally turn to the other great class of pigments of biological origin, viz., those in which the chromophore is a tetrapyrrolic group with a metallic atom located at its centre. Thus, by a simple process of exclusion, we are led to the identification of our visual pigments as heme-proteins, as already indicated. Heme is ubiquitous and we need therefore have no hesitation in assuming its presence in the retinal structures. The analogy with the activity of chlorophyll in the green leaves of plants indicates that heme which is a powerful absorber of light is also capable of transferring the energy absorbed to the retinal structures and thus enabling it to be perceived. Heme is also fairly stable chemically. Though a substantial fraction of the incident photons may be used up in effecting photochemical changes, enough would be left over to make vision in daylight both possible and efficient.

7. Defects and anomalies of colour vision

The characteristics of the rare condition known as tritanopia may be explained as arising from the absence of the pigment xanthophyll from the retina. The defects and anomalies of colour vision more commonly met with appear in the part of the spectrum between the termination of the blue and the extreme red end. The recognition that the heme pigments in the ferrous and ferric states are the mediators of vision in these regions makes these defects and anomalies explicable. Indeed, it is also possible to elucidate in detail the results of quantitative studies of those defects and anomalies. The subject has been fully discussed in an earlier memoir by the author¹. It will therefore suffice here to indicate broadly the approach developed in that publication.

As has already been explained, ferroheme is the visual pigment functioning in the green and ferriheme in the red; in the region of overlap of the absorption spectra of the two pigments, homogeneous light exhibits the various intermediate colours. The precise sequence of the luminosity and colour observed would evidently depend on the proportions of ferroheme and ferriheme functioning in the retina. The proportion in which iron is present in the ferrous and ferric states would presumably be determined by some regulating biochemical mechanism. Any malfunctioning of that mechanism would result in an alteration of the proportion in one direction or the other. This is the clue to the explanation of the observed deviations from the normal in the perception of light and colour.

If ferriheme be totally absent in the retinal pigment, the observer would fail to perceive the red end of the spectrum and the latter would therefore appear distinctly shortened. This is the state referred to as protanopic vision in the literature of the subject. If, on the other hand, the ferriheme is present in excess of the normal proportion, the region in which the two pigments function jointly would extend further towards the green. In consequence, the regular sequence of colour normally seen between the green and the red would tend to disappear. Ultimately, green and red would merge and be indistinguishable. This is the condition known as deuteranopia. Both in protanopia and in deuteranopia, the rapid change of hue appearing at 490 $m\mu$ would be observable. In both cases also, the colour progression from the green to the red would be unobservable, but for wholly different reasons.

Protoanomalous and deuteranomalous vision may be considered as intermediate states between the normal condition and the conditions of protanopia and deuteranopia respectively. The luminosity and hue discrimination curves determined by observation for these anomalous types of vision are in satisfactory accord with the results to be expected on that basis.

¹"The Perception of Light and Colour and the Physiology of Vision," Memoir No. 125 of the Raman Research Institute, *Proc. Indian Acad. Sci.*, A52, 255, 1960.