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The perception of light and colour and the physiology of vision—Part VII. General summary

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1. Observations of the retina

A simple but extremely powerful technique has been devised which enables an observer without any instrumental aid to see his own retina and study its functioning in varied circumstances. The observations made by this method have enabled important conclusions to be arrived at regarding the constitution of the retina and the mechanism by which light and colour are perceived. The observer sits facing a brightly lit white screen and views it through an appropriate colour filter held in front of his eye. After a sufficient interval of time, he fixes his vision on some particular point on the screen and then removes the filter. An enormously magnified picture of the retina then appears on the screen, the nature of which depends very much on the particular colour filter used. The explanation of the phenomenon is that the rays of the spectrum which is the first instance are absorbed by the filter, suddenly impinge on the retina when the filter is removed, and excite localised sensations over its different areas. These sensations project themselves on the observing screen as an enlarged image of the retina.

By correlating the absorption spectra of the filters used with the pictures of the retina perceived by the observer, it has been ascertained that the retina contains three visual pigments whose absorption spectra lie in different regions of the spectrum: Pigment A has an absorption lying in the spectral range 4000 to 5000 Å. Pigment B exerts an extremely powerful absorption in the wavelength range between 5000 and 6000 Å, while pigment C exerts a moderately powerful absorption in the region from 6000 to 7000 Å, but its absorption also extends into and partly overlaps the region covered by pigment B.

2. The role of the visual pigments

The nature and properties of light when correlated with the observed facts concerning the perception of light and colour enable us to determine the role played by the visual pigments in the retina. Each different monochromatic light in the spectrum represents radiation characterised by a different energy-quantum; the magnitude of the quantum increases progressively from the red to the violet end of the spectrum. It is a fact also that the colours observed in the spectrum change progressively and continuously from one end of it to the other. Some 250 different colours can be perceived over the whole range. A change of only one half of 1% in the magnitude of the light-quantum incident on and absorbed by the retinal pigments is usually sufficient to make an observable change of perceived colour, while in some parts of the spectrum a much smaller difference is thus detectable.

Monochromatic radiation is the fundamental entity with which the physicist is concerned in optics and spectroscopy. It follows from what has been stated that the fundamental visual sensations are also those excited by monochromatic radiation. The observed precision of colour perception would be inexplicable except on the hypothesis that the function of the visual pigments in the retina is to receive, absorb and then to pass on the absorbed energy-quanta to the central parts of the visual mechanism without any addition or subtraction, themselves returning to their original energy-states.

3. Identification of the visual pigments

The identification of the visual pigments presents no particular difficulties. In day-light vision, there is a highly pronounced maximum of luminosity in the spectrum at about 5600 Å, on either side of which the brightness falls off rapidly. It follows that pigment B of which the absorption lies in the green plays the major role in human vision, a role somewhat analogous to that which the absorption in the red by chlorophyll plays in the photosynthesis by green leaves. We can, therefore, unhesitatingly identify our pigment B with ferroheme which exhibits a powerful absorption of light in the green sector located at the same position as the maximum of visual luminosity in the spectrum.

Oxidation-reduction mechanisms play a fundamental role in the chemistry of the living structures of aerobic organisms. The recognition of ferroheme as the principal visual pigment thus automatically involves the identification of pigment C which appears in the retina in close association with pigment B as ferriheme. It is known that the absorption of light by ferriheme is weaker than that of ferroheme, but extends much further towards longer wavelengths and is indeed sensible up to the extreme red and of the spectrum. These are the properties needed for the visual pigment which functions in that region.

The pigment A which absorbs light between 4000 and 5000 Å and is the mediator of vision in the blue and violet sectors of the spectrum can be none other than the carotenoid pigment xanthophyll which gives the characteristic golden yellow colour to the yoke of the common hen's egg. Xanthophyll finds its way into the human body through the consumption of food products containing it, and its presence in the retina is therefore not a matter for surprise. Indeed, it is the same yellow pigment which led to the anatomical name of *macula lutea* being given to the physiologically most important area in the retina.

4. Colour and luminosity in the spectrum

The known features of the absorption spectra of the visual pigments enable a satisfactory explanation to be given of the distinctive features noticeable in the different sectors of the spectrum. The very steep rise in the absorption by xanthophyll which appears in the wavelength range around 4900 Å is responsible for the rapid change in the colour of the spectrum from green to blue and the very low value of the limen of wavelength alteration needed for observable change of colour appearing in that region. The similar but less striking fall of the limen in the region around 4400 Å where the colour of the spectrum changes from blue to violet is likewise attributable to the rapid fall of the absorption by xanthophyll with diminishing wavelength appearing in that region.

The overlap in the absorption spectra of ferroheme and ferriheme between 625 and 566 mμ gives rise to the appearance of yellow and orange in the spectrum as an interpolation between the green and red sectors, the yellow where the absorptions of the two pigments are of comparable strength, and the orange where the absorption by ferriheme is stronger than by ferroheme. The steep fall in the absorption by ferroheme in the same region is responsible for the limen of wavelength change needed for an observable difference of colour reaching very low values in the region around 590 mμ.

The progressive fall in the luminosity of the spectrum and the increasing limen of wavelength change for a perceptible colour difference manifested near the extreme violet and red ends of the spectrum appear as consequences respectively of the diminishing absorption and the diminishing slope of the absorption curves of xanthophyll and of ferriheme in those two regions.

Some remarkable effects are observed when a colour filter which transmits only the blue-violet part of the spectrum is held in front of the eye and a polaroid is placed and alternately taken out and put in before the filter. These effects cease to be observable when the illumination of the field under observation is diminished so as to fall below the photopic level. They afford a conclusive demonstration that xanthophyll is the visual pigment which enables us to perceive the blue and violet colours of the spectrum.

5. Non-homogeneous light

The visual sensations produced by heterogeneous light result from the synthesis by the centre of the sensations excited by the monochromatic radiations of which it is composed. The results of the synthesis may be either a chromatic or an achromatic sensation. Chromatic sensations arise when only two of the three visual pigments function, as for example when the radiations from the extreme red and violet ends of the spectrum are superposed, giving rise to the purples, or when the superposed radiations lie in the spectral range where xanthophyll has no absorption, viz., in the red and green sectors; the resultant sensation is then a pure spectral colour.

The achromatic sensation arises when all the three visual pigments function in appropriate strengths. This enables a satisfactory explanation to be given of the fact that in a whole series of cases, the superposition of only two monochromatic radiations of appropriately chosen wavelengths results in the complete abolition of colour. In general, the sensations excited by heterogeneous light are a mixture of the chromatic and achromatic sensations which may be regarded as independent effects. The fact that all observable colours may be regarded as a superposition in appropriate proportions of white light and a pure spectral colour (including the pure purples) thus receives a satisfactory explanation.

The results obtained in experiments in which a pure spectral colour is sought to be reproduced by the superposition of other spectral colours may be interpreted in the same manner. The so-called spectral chromaticity coefficients determined in such experiments, when they have positive values, exhibit a parallelism with the absorption strength of the visual pigments which function in the respective spectral regions. *Per contra*, the appearance of negative values of the coefficients indicates that achromatic sensations are produced.

6. Defective colour vision

The existence of both ferroheme and ferriheme as visual pigments in the retina presupposes that there is a biochemical mechanism which determines the proportions in which they are normally present. Any deviations of the mechanism from normality would result in ferriheme being either totally absent or else being present much in excess. There would also be intermediate cases. The existence of four types of inheritable defect in colour vision would thus be explicable in terms of the biochemical mechanism which determines the ferroheme-ferriheme ratio in the retina. These are respectively the protanopic, protanomalous, deuteranomalous and deuteranopic types of colour vision. The features of these different types of defects are readily predictable and the results thus deduced are in agreement with the observed facts. Tritanopia is likewise explicable as due to the complete absence of xanthophyll from the retina.

7. References

The literature on colour vision and related topics is very voluminous. The under-mentioned books were found very useful by the writer. Besides containing extensive bibliographies, they gave clear accounts of the present state of knowledge in their respective fields and factual information of value:

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The following is a selected list of papers containing factual information of importance in relation to the subject-matter of the present memoir.

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