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On the sensations of colour and the nature of the visual mechanism*

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1. Introduction

Light and colour play a fundamental role in human life and activity. We are therefore naturally led to ask various questions concerning them and the sensations which they evoke. How do our eyes perceive light? Why is it possible for our eyes to discriminate between different kinds of light, thereby enabling us to label them with distinctive names? It is proposed in this address to consider these and related questions and endeavour to answer them.

We may usefully remind ourselves at the outset that the physical phenomena exhibited by light may be divided into two classes. The first class includes various optical effects, such as reflection, refraction, interference and diffraction. In all these effects, we are concerned with the propagation of light considered as wave-motion in space. In the other class of phenomena which includes the emission and absorption of light, fluorescence and the photoelectric effect, we are concerned with energy transfers and energy transformations. Such phenomena find a satisfactory explanation only when we consider light to consist of discrete units or quanta of energy. Accordingly, they fall within the scope of the quantum theory of radiation.

The dual role played by radiation is also evident in the functioning of our visual organs. The formation of well-defined images on the retina of our eyes is clearly a phenomenon falling within the range of wave-optics. But it is clear that the visual mechanism by which we perceive light and colour lies outside the scope of wave-optics and should be considered and investigated from the standpoint of the quantum theory. This is the point of view adopted and developed in the present address.

We shall begin with a brief survey of the facts of the subject.

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2. The perception of light and colour

The sensations excited by light are of two distinct kinds, luminosity and hue or colour. Though they are essentially subjective in nature, they can be brought within the scope of physical definition and measurement by inter-comparison and equalisation of the luminosity or colour of two adjacent illuminated areas. This is indeed the procedure on which visual photometry and colorimetry depend. The human eye can function over an enormous range of intensities. But at the lowest levels of illumination, e.g., in night-vision, the eye can perceive only differences of luminosity but is unable to appreciate colour. At such levels also, it is insensitive to the light which is normally perceived as red in hue. For the proper appreciation of colour, it is necessary to work at levels of illumination which are fairly high and which have to be employed so that, in other respects as well, our eyes can function efficiently. Colour and colour differences are also best observed and studied in direct vision, in other words when the eyes are turned to view the objects under observation and their images are formed at or near the fovea centralis on the retina. Colour can be perceived also in averted vision up to fairly large angles, but it does not then lend itself to any precise comparison and measurement.

Two kinds of light are of special importance. One of them is white light, in other words light exhibiting no perceptible colour. The other kind of light is that which appears at various points in a well-resolved spectrum. The colours ordinarily met with may be described as a mixture of white light with some particular spectral colour, the result of such mixture exhibiting the same hue as the pure spectral colour but in an unsaturated or diluted form. This way of describing and classifying colours may be made completely comprehensive, if besides the pure spectral colours, we also consider the colours which are not observed in the spectrum but which may be obtained by superposing light from the two ends of the visible spectrum, viz., red and violet, in various proportions. Taking the pure purples arising in this fashion together with the pure colours of the spectrum, we may say that all colours that come within the scope of colorimetry may be described as mixtures arising from the addition therewith of appropriate quantities of white light. It follows from what has been stated that our chief concern is with the subject of monochromatic colour vision. The results of colour mixture are a matter of secondary importance.

Conventionally, the colours of the spectrum are described as six in number. Actually, the normal human eye can discern in the spectrum not less than 150 distinct patches of colour which cannot be made to match one another in colour merely by adjusting their intensities. Except at the two extreme ends of the visible spectrum, a change of 50 Å in wavelength is more than sufficient to result in an observable differences in colour. Indeed, a much smaller difference suffices over a large part of the visible spectrum. The change in wavelength needed for an observable change of colour has been determined over the whole range of the visible spectrum by several investigators and the hue-discrimination curve thus drawn shows some remarkable features. At four points in the spectrum, at the wavelengths (in Å units) 4400, 4900, 5900 and 6300, it dips down and the change in wavelength required for a perceptible change of colour reaches low values. The wavelengths 4900 and 5900 are specially conspicuous in this respect, a change of 10 Å in wavelength sufficing to produce an observable change of colour, while at intermediate wavelengths it is larger, rising to 20 Å at 5400 Å. The dips in the curve at 4400 and 6300 are less conspicuous, the minimum change of wavelength needed in their neighbourhood being about 20 Å, while at the intermediate wavelengths 4600 and 6200, it rises to 30 or 40 Å.

3. The physical basis of colour

The facts of observation set forth above lead us to ask ourselves the question, what is the physical basis of colour? In other words, what is it that enables the eye to distinguish between various kinds of monochromatic light? The answer to this question has clearly to be sought for in the known physical properties of light itself. The physical characters which distinguish one beam of monochromatic light from another are firstly, the quantity of energy traversing unit cross-section of the beam per unit of time and secondly, the magnitude of the individual energy-quanta. The subjective characters, which enable one such beam to be distinguished from another, are the luminosity of a white surface on which the beam falls and the colour which the surface then exhibits. It is a natural inference that the physical and subjective attributes of the light are related to each other in a fundamental way, viz., total energy flow with luminosity, and the magnitude of the individual quanta, with colour. Indeed, if it were not so, photometry and colorimetry would be meaningless exercises of human ingenuity.

We are thus led to conclude that our power to distinguish between different monochromatic radiations by the colour sensations which they excite is a consequence of the fact that light consists of distinct units or quanta of energy and that these units are of different magnitude, increasing continuously from one end of the spectrum to the other. It follows from this again that the nature of the visual mechanism is such that it enables these differences to be perceived. We may also infer that the variation in the power of the eye to detect changes of colour in various regions of the spectrum is a consequence of the special features of the visual mechanism.

4. The nature of the visual process

A difference of 10 Å in the wavelength of monochromatic light represents a change of only two parts per thousand in the magnitude of the individual light-quanta of which it is composed. We may well ask ourselves, what is the nature of the visual process or mechanism which makes it possible for our eyes to appreciate or detect such a very small change?

The anatomy of the retina makes it clear that its function is to receive the incident light energy and to transform it into impulses (presumably of an electrical nature) which travel along the optic nerve to the cerebral centres. If the distinguishing character of the light, viz., the magnitude of the energy quanta of which it consists, is to reach the cerebral centres, it is clearly necessary that the energy of the quantum incident on the retina is in the first instance completely absorbed and is then transferred completely and immediately to the nervous system. Any additions to or subtractions from the energy would result in an alteration in the characters of the excitation and therefore also of the resulting sensation. The latter, in such circumstances, may indeed be the perception of light but it would lack the specificity indicated as necessary by the facts of colour perception. For the reasons stated, we may exclude from consideration visual mechanisms which assume photochemical changes to occur involving absorption of energy by the retina, and confine ourselves to the simplest possible process, viz., the quanta of light energy falling on the retina are absorbed and the energy absorbed is immediately transferred to the nervous system, the absorbing centres then returning to their original state. The fact that the normal human eye can perceive colour throughout the visible spectrum without a gap indicates that it is adequately covered by the absorption spectra of pigments present in the retina, the molecules of which can function in the manner indicated.

The level of illumination at which the colour sense is at its best is fairly high, in other words there is plenty of light which could enable the process contemplated to operate. Hence, even if only a fraction of the number of energy-quanta incident on the retina are absorbed and then passed on to the nervous system, the resulting effect would be of adequate magnitude. Moreover, as we have seen, the pigments which act as absorbers of light return immediately to their normal states and can therefore function repeatedly. In other words, they are not expendable. It is evident that in these circumstances, small quantities of the absorbers would suffice, so small that their presence in the retina need not be very conspicuous. For their functioning, it is clearly necessary that the absorbing substances are diffused through the material of the retina. Hence, they should be either themselves proteins or else substances of biological origin which can co-exist with the proteins and other substances present in the retina.

5. The retinal pigments

Amongst the products of biological activity that exhibit absorption spectra in the visible region of the spectrum, the carotenoids and the blood pigments are of special importance. The carotenoids are so named, as they are derivatives of the hydrocarbon carotene, the chemical formula of which is $C_{40}H_{56}$ and which has several isomers, the most important being α-carotene and β-carotene. The carotenoid pigment with which we are specially concerned here is dihydroxy-α-carotene whose chemical formula is $C_{40}H_{56}O_2$. Together with the isomeric dihydroxy-β-carotene (zeaxanthin), it forms the principal constituent of the yellow pigment present in the yolk of the domestic hen's egg. It has also been identified as being responsible for the yellow colour of the region in the retina long known as the macula lutea and has been appropriately named as lutein, though the alternative name of xanthophyll is also to be found used in chemical literature.

It is of interest to note that the presence in the foveal region of the retina of a pigment which strongly absorbs blue light can be demonstrated in a simple manner. A cloudless sky is viewed for a few minutes through a filter of deep blue glass which transmits only the wavelengths of the spectrum smaller than 5000 Å. If the filter is then suddenly removed and the sky viewed directly, an image of the fovea which can be recognized as such by its angular dimensions is seen clearly projected against the sky. The image, however, soon fades away.

Viewed in the ophthalmoscope, the retina appears of a rich red hue, which masks the colouration of the macula lutea. The latter can only be distinguished by using red-free light when it appears as an elliptic spot with the major axis horizontal. The red colour of the retina has itself been attributed to the selective diffusion by the choroid of the light which has penetrated the epithelial pigment of the retina, in other words of the light which has passed twice through the latter before it can re-emerge and be observed. Quite apart from the question of the sufficiency or correctness of this explanation, it has to be remarked that the retina is richly supplied by blood vessels which enter into the nervous layer and pass forwards through it, and from their branches give off a minute capillary plexus. The macula receives two small branches and also small twigs directly from the central artery. Though these latter do not reach the fovea centralis and the latter has therefore no blood vessels, the anatomical drawings indicate that the entire blood-supply system of the retina has been so contrived that its central region where vision is most perfect is completely surrounded by blood-rich material from which it could receive the blood-pigments necessary for its functioning. That the blood-pigments are powerful absorbers of light is indicated by the fact that blood is opaque to light and that oxyhaemoglobin can be spectroscopically detected in aqueous solutions as dilute as one part in a hundred thousand. As has already been remarked, no great quantity of a light-absorbing material is needed to enable it to function in the visual mechanism. In these circumstances, we are entirely justified in assuming that blood-pigments are present in the retina in sufficient quantity to function in the manner already explained and that they play a highly important role in the visual process.

6. The absorption spectra of the retinal pigments

Lutein: The absorption spectrum of lutein (xanthophyll) can be readily studied with the material obtained from the yolk of an egg. The pigment is completely transparent to all wavelengths in the red, orange, yellow and green regions of the spectrum. Its absorption is limited to the blue region in which three bands can be seen, of which the maxima are located at 4800, 4475 and 4200 Å, the first two being much more conspicuous than the third. The drop from complete transparency at 5200 to almost complete opacity at 4800 is rather abrupt; the steepest part of the spectrophotometer curve exhibiting this transition appears in the wavelength region around 4900 Å. The absorption by lutein diminishes notably as we approach the violet end of the spectrum.

Oxyhaemoglobin: The scarlet or oxygenated form of blood-pigment exhibits two clearly marked absorption bands, one in the yellow region of the spectrum centred at 5775 and the other in the green at 5385, the first of them being much sharper than the second. A graph exhibiting the transmission of light through an aqueous solution of oxyhaemoglobin shows a deep trough lying in the region of wavelengths between 5000 and 6000 Å, the two absorption bands mentioned above appearing at the bottom of the trough. The percentage of light transmitted rises very steeply on the side of longer wavelengths, the steepest part of the rise appearing in the region of wavelengths around 5900. At wavelengths greater than 6000 Å, the absorption is small, though remaining perceptible up to about 6800 Å. On the other hand, the transmission which is a maximum around 5000 Å diminishes again at still smaller wavelengths and indeed there is very little transmission below 4400 Å. However, by using very dilute solutions or very small absorption depths, the study of the transmission of light at the violet end of the spectrum reveals the presence of a powerful absorption maximum centred at 4145 Å, known as the Soret band.

Ferrohaemoglobin: The two absorption bands of oxyhaemoglobin at 5775 and 5385 are replaced in the case of its reduced form by a single diffuse band centred at 5575 which covers the entire region between them and also extends beyond them, though not very distinctly. In other respects, the spectroscopic behaviour of the two substances is nearly the same. The Soret band of haemoglobin has its maximum at 4250.

Ferrihaemoglobin: This pigment exhibits a marked absorption of light over the whole of the visible spectrum including the red end, in this respect differing markedly from the two other blood-pigments. At wavelengths greater than 6300, however, the absorption diminishes rapidly and becomes weak at the extreme red of the spectrum. Absorption maxima may be recognized which are centred at 6300, 5765, 5365 and 4995, the last-mentioned being very broad and diffuse. The maximum of its Soret band is located at 4060.

We may summarise the foregoing as follows:

A. Lutein is an efficient absorber of light in the region between 4900 and

4400 Å. It is wholly ineffective at wavelengths greater than 5000 but can absorb (though only feebly) wavelengths at and near the violet end of the spectrum.

B. Ferrohaemoglobin and its oxygenated form exercise a powerful absorption of light in the wavelength range between 5000 and 6000, with a resultant maximum centred at 5580 Å.

C. Ferrihaemoglobin has an absorption extending over the entire visible spectrum and differs from the other two blood-pigments in possessing a well-defined absorption band at 6300 Å.

No reference has been made above to the retinal pigment known as visual purple, since we are concerned here with the colour sensations experienced at normal illumination levels, in which, as is well-known, visual purple plays no role.

7. The luminous efficiency curve

A remarkable feature of the perception of monochromatic light by the eye is the manner in which its luminous efficiency varies with wavelength over the range of the visible spectrum. A highly pronounced maximum appears at a certain wavelength in the green region of the spectrum and on either side of it, the luminous efficiency falls off steeply. The wavelength of maximum efficiency observed with different individuals is found to vary from 5490 to 5700 Å, the average being 5576.

The most reasonable explanation of the fact stated above is that it is a consequence of the variation with wavelength of the strength of absorption of light by a pigment present in the retina which receives the energy of the light quantum and passes it on to the nervous system. In the preceding section, it has been remarked that ferrohaemoglobin has an absorption band of which the centre is located at 5575 Å. This agrees with the observed average for the wavelength of maximum luminous efficiency of the normal human eye. If its oxygenated form were the operative pigment, it would show two maxima at 5775 and 5385 respectively with a dip midway between them. But since the reduced form would also be present and its aborption band covers the region between the two bands of oxyhaemoglobin, the resultant would be a maximum at nearly the same position, viz., 5580. The agreement which thus emerges between the location of the absorption maximum of the blood-pigments and of the maximum luminous efficiency in the spectrum is scarcely a matter for surprise in view of the immensely important role that blood and its constituents play in the maintenance of life.

The observed form of the luminous efficiency curve indicates that two other pigments should be present in the retina which are effective absorbers respectively for wavelengths less than 5000 Å and greater than 6000 Å, in other words in the blue and the red regions of the spectrum. The former is evidently lutein and there is good reason for identifying the latter with the blood-pigment methaemoglobin, more appropriately designated above as ferrihaemoglobin to indicate its chemical relationship with ferrohaemoglobin, the ordinary form of haemoglobin. Since the red cells in blood are provided with mechanisms both for the formation of ferrihaemoglobin by the oxidation of ferrohaemoglobin and for its reduction back to the ferrous state, there are good grounds for assuming the presence of ferrihaemoglobin in the retina where it is needed and has a specific role to perform.

8. Hue discrimination in the spectrum

The major features of the distribution of luminosity and colour in the spectrum can be ascertained in a very simple manner merely by viewing the white-hot straight filament of a tungsten lamp through a diffraction grating. It then becomes evident that the most luminous part of the spectrum is in the greenish-yellow region and that on either side of it the luminosity falls off unsymmetrically, in other words, more slowly on the side of longer wavelengths. The observable colour alters with change of wavelength but such change is most rapid at certain points in the spectrum, and relatively slow in the intermediate regions. In particular the change-over from blue to green and from yellow to orange is particularly rapid, while the change from green to yellow is quite gradual. The change from violet to blue occurs in a narrow region of the spectrum, and there are also indications that the change from orange to red is rather abrupt.

The facts stated above find quantitative expression in the hue discrimination curve which has been studied by several investigators. They receive a satisfactory explanation on the basis of the data regarding the retinal pigments and their spectroscopic behaviour. It was remarked earlier that lutein changes over from complete transparency to nearly complete opacity abruptly in the region of wavelengths around 4900 Å. This, it may be remarked, is precisely the place where the hue discrimination curve dips down very steeply. Then again, ferrohaemoglobin changes over from almost complete transparency to nearly complete opacity in the region of wavelengths around 5900 Å. This again is the wavelength at which the hue discrimination curve dips down to its lowest point. In other words, the change from blue to green is rather abrupt for the reason that lutein functions very efficiently at wavelengths less than 4900 but ceases to function at greater wavelengths, its place being taken over by ferrohaemoglobin. Similarly the change from yellow to orange is abrupt for the reason that ferrohaemoglobin functions efficiently at wavelengths below 5900 Å but ceases to do so at greater wavelengths and its place is taken by ferrihaemoglobin. On the other hand, the transition from green to yellow is quite smooth for the reason that ferrohaemoglobin functions over the whole range under consideration. The minor features in the hue discrimination curve noticed in the blue and red regions can likewise be explained in terms of the striking changes with wavelength in the form of the absorption curves of lutein and ferrihaemoglobin which are the pigments functioning in those regions.

9. The results of colour mixture

As stated earlier, the sensation produced by non-homogeneous light may be equated to that resulting from an admixture of white light with an appropriately chosen "pure colour", the latter term including the pure colours of the spectrum as well as the pure purples produced by the superposition of light from the extreme red and violet ends of the spectrum. This fact emerges from the numerous investigations on colorimetry made in the past, the results of which are embodied in the so-called chromaticity diagrams of which there are various forms. We shall here refer to and briefly describe the XYZ type of representation which at the present time is most generally accepted and used.

The XYZ chromaticity diagram takes the form of a closed figure which is roughly triangular in shape with a rounded vertex and a straight base which represents the line of pure purples. The rest of the perimeter of the figure represents the pure spectral colours arranged on it in a manner which will presently be stated. All observable colours (including white light) are represented by points lying within the closed figure, the point representing white light appearing somewhere near its centre. The pure spectral colours ranging from the extreme red end of the spectrum up to and including a part of the green up to 5350 Å appear on one side of the triangle arranged on what is practically a straight line. The pure spectral colours from 5350 to 5050 Å appear as the rounded-off vertex of the triangle. The third side of the triangle is a curved arc on which the spectral colours from 5050 Å up to the extreme violet end appear. The wavelengths are however distributed on this arc very non-uniformly. Practically the whole of its length is taken up by the wavelengths from 5050 to 4600 Å, while the rest of the spectrum from 4600 to 3800 (the extreme violet end) is compressed into a very short arc which forms the tip of the perimeter where it joins the line of purples.

The form of the chromaticity diagram as described above has a striking and indeed obvious relationship to the spectroscopic behaviour of the retinal pigments described earlier. The curved arc running from 5050 to the violet end of the spectrum is the region of wavelengths where lutein exercises a marked absorption, and it is therefore not surprising to find that practically the whole of the arc is taken up by the wavelengths at which such absorption is greatest. *Per contra,* lutein is completely transparent to all the wavelengths which appear on the straight line forming the other side of the triangle. This region is covered by the absorption spectra of the blood-pigments where such absorption is strongest, while the rounded-off vertex of the triangle represents the part of the spectrum in which the strength of their absorption falls off rapidly, as is shown by the absorption-curves themselves and is independently confirmed by the rapid drop in the luminous efficiency of the spectrum between 5350 and 5050 Å. The form of the chromaticity diagram thus indicates that the three receptors contemplated in the trichromatic theory of vision may be identified respectively with the three retinal pigments lutein, ferrohaemoglobin (including its oxygenated form) and ferrihaemoglobin operating in their respective regions of absorption in the spectrum.

10. Anomalies in colour vision

The blood-pigment ferrohaemoglobin is readily oxidisable to ferrihaemoglobin, but such oxidation is ordinarily inhibited by the circumstance that it can form the molecular compound with oxygen known as oxyhaemoglobin which circulates through the body in arterial blood and is returned after de-oxygenation through the veins. Normally, therefore, ferrihaemoglobin is not present in human blood in any appreciable quantity, though in certain pathological conditions it is known to form a substantial proportion of the blood-pigment. The presence of ferrihaemoglobin as a receptor for colour vision in the retina must therefore be regarded as a special provision to meet the need for a pigment which has a strong absorption in the region of wavelengths greater than 6000 Å. The possibility therefore arises that the quantity of it in the retina may in certain cases be either greater or less than that normally present and that it may even indeed be totally absent in some cases. In the latter event, the person concerned would be red-blind. On the other hand, a deficiency would result in colour vision of the type known as protoanomalous, while an excess would result in deuteranomalous vision. In the former case, the result would be a closing up of the luminous efficiency curve away from the red so that its asymmetry of form becomes less pronounced. In the latter case the luminous efficiency curve would open out towards the red and its asymmetry of form become more pronounced.

As was remarked earlier, the dip in the hue discrimination curve normally observed at 5900 Å arises from the large fall in the strength of the absorption of light by ferrohaemoglobin which occurs in the region, while at greater wavelengths, the operative pigment is ferrihaemoglobin. If, however, the latter is not present in sufficient quantity, the change in hue with change of wavelength would be less rapid, in other words, the hue discrimination curve would move upwards. These results are in agreement with the ascertained facts of the subject.