

## Light, colour and vision\*

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Our eyes enable us to perceive the world around us, and they are, therefore, amongst our most precious possessions. What they accomplish is such a familiar experience that we cease to be conscious of the remarkable nature of the services which they render. I propose, in this lecture, firstly, to draw your attention to some of the outstanding features of our visual powers, and then to recount to you how they have been sought to be explained. The subject is so extensive in its scope that I cannot hope in the course of an hour's lecture, to do more than sketch very briefly, the explorations that have been made in this field of knowledge in past years and continue to be made at the present time.

Surveying the facts of visual experience, we may group them under three heads: firstly, we may remark upon the enormous range of the intensities of light to which the eye can adapt itself and yet function with comfort. From the brightest sunshine the dim starlight of a clear but moon-less night is a step-down in intensity by a factor of a hundred million, but one can nevertheless see well enough in either case, to keep to the path on a countryside walk. Indeed, the measurements, which have been made of the power of the eye to detect feeble light have shown that for very brief exposures, the human eye is several thousand times more sensitive than the fastest photographic emulsions so far produced. Secondly, we may remark upon the power of our eyes to adjust themselves for viewing objects which are either far or near, upon their power to judge the form and distance of the objects appearing in the field of vision, and to estimate their positions relatively to each other, as also to detect their movements. Then again, when attention is fixed on any limited area in the visual field, our eyes can perceive and recognize very fine details. Thirdly, we may remark upon the ability of our eyes to recognize and distinguish the characters of an illuminated object which may be described respectively as its brightness, its hue or colour, and the degree of saturation or purity of that colour. If all these three attributes are taken simultaneously into consideration, the number of possibilities between which our eyes can discriminate is extremely large.

The incidence of light from external objects on our eyes and our perception of these objects are the two ends of a connected set of processes: firstly, the

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\*Gandhi Memorial Lecture delivered on Friday, the 2nd October 1959, at the Raman Research Institute, Bangalore.

functioning of the eye as an optical instrument which forms images of external objects on the retina; secondly the functioning of the retina as a receptor of radiant energy; thirdly, the transmission of the messages originating at the structures of the retina to the visual centres in the brain, and finally the integration of the messages received from the retinae of both the eyes into a visual picture exhibiting various characteristic features, viz., form, depth, detail, brightness, colour, and movement. The importance of the role which binocularity plays in the phenomena of vision needs to be stressed. It is very strikingly illustrated by the known facts of colour vision; when a picture of an object printed in complementary colours in stereoscopically displaced positions is viewed through complementary filters placed before the two eyes, one perceives a single picture in relief, but exhibiting no colour whatever.

## 2. The eye as an optical instrument

Leonardo da Vinci was the first to propose a rational theory of the functioning of the eye. He compared it with that of the *camera obscura* and assumed that an image rendered sharp by the lens was formed on the internal cavity of the eye. Indeed, it is the case that the eye is built in several respects like a photographic camera. It is approximately spherical in shape, and is covered by a fibrous tunic which is white and opaque for the most part, but has a transparent protuberance in front which is of greater convexity than the rest. These two parts of the eye are known respectively as the sclera and the cornea. The darkening of the interior necessary in a camera is secured by the presence of the chorioid coat which is a membrane traversed by numerous blood vessels and abundantly pigmented. The chorioid clings closely to the sclera and absorbs the unwanted rays. Against the inner surface of the chorioid coat lies the part of the retina which is sensitive to light. A further analogy with a camera is provided by the eyelids, which, acting like a shutter, can be closed to exclude light. Likewise, when light is admitted, it is regulated in amount by the variation of the size of the pupil which corresponds to the variable aperture of a photographic camera.

The interior of the eye is not empty, but is filled with transparent media known as the aqueous humour and the vitreous body which fill respectively the front and the back of the cavity. Their refractive indices (1.336) differ very little from that of pure water. Behind the iris lies the lens of the eye. Both of its surfaces are convex, the front less so than the rear. The refractive index of the lens varies from the centre to the periphery; its effective value is 1.42. Since however, the lens is immersed in a medium of which the index is 1.336, its converging action on the light is greatly reduced thereby, and only supplements that produced by the front surface of the cornea. The principal function of the lens is to enable the eye to accommodate itself for near or distant vision as required. This is brought about by the action of the ciliary muscles on the capsule which is an elastic membrane

completely enclosing the lens; the force thus exerted on the material of the lens enables the curvature of its front surface to be increased for near vision as compared with the normal state of the eye when viewing distant objects.

The shape of the eye-ball is maintained by the action of what is known as the intra-ocular pressure, viz., the hydrostatic pressure of the fluid filling the cavity of the eye. Fresh fluid is continually added to the aqueous humour and is continually drained away from it into the blood stream by a complex arrangement which is so regulated that the pressure of the fluid within the eye remains roughly constant. Since, as already remarked, the external surface of the cornea plays the leading role in the work of the eye as an optical instrument, it is not surprising to find that provision exists for protecting the corneal surface and maintaining it in good condition. This, indeed, is the function of the eyelids and the lacrimal apparatus. The periodic blinking of the eyes serves the purpose of cleaning and wetting the cornea.

The effective functioning of our eyes is to a very great extent dependent upon certain accessory structures associated with them. The eye-ball is located within the cavity known as the orbit and its movements are controlled by three pairs of muscles which enable the eye to be directed towards any particular object in the field of vision. The construction of the eye makes it possible to have a very large angular field of vision. This, for each eye separately, is about  $160^\circ$  laterally and  $120^\circ$  vertically, and for both eyes together, somewhat more than two right angles from left to right. It is, of course, not to be expected that the image of external objects formed on the surface of the retina would everywhere be sharply focussed. Indeed it is only over a very small fraction of the whole field of view that the image on the retina is well defined and sharp. When we direct our eyes towards an object, we make use of this well-defined part, which, as we shall see presently, falls on the region of the retina which is best equipped for the discrimination of fine detail in the image.

A question of some interest is the reason why the effects of chromatic aberration on our vision are scarcely noticeable in normal circumstances. The explanation is that the refractive media of the eye have very small dispersive powers. Further, the sensitivity of the eye to radiation exhibits a maximum spread over a narrow region of the visible spectrum. This circumstance would tend to minimise any visible manifestations of chromatic aberration. They can however be observed when a small, bright source of light is viewed through a colour filter which transmits only the two ends of the visible spectrum, viz., red and violet respectively.

### 3. The structure of the retina

The retina is a delicate membrane which is specially adapted for the reception of light stimuli. In the fresh state it is soft, translucent, and of a purple tint, owing to

the presence of a colouring material named rhodopsin or visual purple. Near the centre of the retina there is an oval yellowish area, named the *macula lutea* where the visual sense is most perfect. This shows a central depression which is termed the *fovea centralis*, where the retina is exceedingly thin, some of its layers having practically disappeared, and the dark colour of the chorioid is distinctly seen through it. About three millimetres to the nasal side of the *macula lutea*, the optic nerve pierces the retina at the optic disc which has a diameter of about 1.5 millimetres. The centre of the disc is pierced by the central artery and the vein of the retina. The optic disc is insensitive to light and is termed as the blind spot.

The retina itself consists of several layers of cells. The first is the pigmented epithelium which is firmly joined to the inner surface of the chorioid coat. Next comes the retina proper or the visual layer containing the receptor cells and their nuclei. The receptors are recognized as being of two kinds known respectively as the rods and the cones. They both consist of elongated cells which point towards the chorioid coat, and the light entering the eye has accordingly to pass through the remainder of the retina to reach them. The impulses originating at the visual layer are then transmitted to the optic nerve through the outer layers termed collectively as the bipolar and ganglionic layers. The outermost layer of the retina in contact with the vitreous body is the *stratum opticum*. It consists of the nerve fibres formed by the expansion of the optic nerve over the surface of the retina. They are connected with the visual cells through the bipolar and the ganglionic layers. The human retina contains some six million cones and over a hundred million rods, whereas the optic nerve contains only some 8,00,000 nerve fibres. It follows that some tens and sometimes even hundreds of receptor cells must be connected to a single ganglion cell by way of the bipolars. An exception, however, appears to exist in respect of the *fovea centralis*. Here there are no rods and the cones are longer and thinner than in the other parts of the retina. Each cone in this area is connected separately by way of a monosynaptic bipolar to an individual ganglion cell and this enables it by means of the corresponding fibre of the optic nerve (which is simply the axon of the ganglion cell) to act individually at the cortical centre. It is in this manner that the high degree of visual acuity or power of discrimination possessed by the central area of the retina has been explained.

#### 4. The duality of the visual process

When a person quits the sunshine out of doors and enters a dark room, he can see nothing at first. His eyes then slowly adapt themselves to darkness, and in about half an hour, he becomes fully sensitive to the faint illumination present and can distinguish the various objects around. Conversely, when a person who has been long in darkness comes out into the light, the reverse process of adaptation to a high level of illumination takes place, but this is a much quicker process. These

and other well-established facts indicate that the human eye possesses two retinæ interlaced with each other. One is a day-retina, which has a low sensitivity to light, can perceive differences in colour, and possesses (at least in its central regions) a high degree of visual acuity. The other is a night-retina which has a high sensitivity to light, but lacks appreciation of differences in colour and exhibits a very low visual acuity. So striking are these differences that it is found convenient to give the name of photopic vision to the function of the day-retina and scotopic vision to that of the night-retina.

As remarked above, the sensitivity of the eye to light differs enormously in photopic and scotopic vision. Its variation with wavelength over the visible spectrum has been investigated for both types of vision. A pronounced maximum somewhere in the middle of the spectrum is exhibited in both cases. But the positions of this maximum differ notably, being  $557\text{ m}\mu$  for photopic and  $510\text{ m}\mu$  for scotopic vision. If the two curves of spectral sensitivity are drawn in such manner that the ordinates of the maximum are the same in both, the photopic curve lies well above the scotopic in the red, orange, and yellow regions of the spectrum and well below it in the blue and violet regions. This difference is responsible for the well known and easily observed Purkinje phenomenon which may be stated briefly thus: the relative brightness of two objects, coloured red and blue respectively, changes in a most striking fashion when the light which illuminates them falls off from a high to a low intensity.

It is reasonable to ascribe photopic vision to the activity of the cones in the retina as receptors of light, while scotopic vision represents the functioning of the rods. The characteristic differences between the two types of vision in respect of sensitivity and acuity can be explained on this basis. As already stated, the rods in the retina are far more numerous than the cones and their number is enormously larger than the number of separate nerve fibres connecting the retina with the cerebral centre. Rod vision, therefore, arises from the co-operative effect of a great many of them functioning together and this would, at least in part, explain its characteristic features. The absence of rods in the foveal region of the retina and their presence elsewhere would indicate that sources of light which are too faint to be seen when viewed directly would be visible in averted vision. This, indeed, is a fact of observation, as for example when faint groups of stars are looked for at night in the sky.

## 5. The phenomena of colour vision

Colour plays such an important role in so many different types of human activity that it has naturally been the subject of intensive investigations from many different points of view. The sensations produced by coloured light may be described as presenting three distinct subjective characters, viz., brightness, hue or colour

proper, and the degree of saturation or purity of the colour. The pure colours we are acquainted with are the colours exhibited by a well-resolved spectrum. These range from red to violet but the eye can distinguish a great many different colours between these extremes. The question naturally arises how the colours we meet with in nature or can be artificially produced, are related to the pure spectral colours.

We may begin by stating a few well-established facts of observation. By superposing appropriate amounts of a pure spectral red, say  $700\text{ m}\mu$  and a pure spectral green, say  $546\text{ m}\mu$ , it is possible to reproduce any other colour appearing in the spectrum within this range of wavelengths. Then again, for any given spectral colour lying in the region between the red and the yellow, it is possible to choose a corresponding spectral colour lying in the range between greenish-blue and violet so that appropriate amounts of the two when superposed would result in a pure white. On the other hand, it is not possible to find a spectral colour complementary to radiations in the green region of the spectrum. Then again, by the super-position of spectral colours lying respectively at the red and violet ends of the spectrum, a series of colours are produced which are not observable in a pure spectrum, viz., the purples.

Finally, it may be remarked that by mixing *three* selected spectral colours in definite proportions, we may match any desired colour sensation. This is the fundamental law of colour vision which has however to be understood in a special sense, viz., that in certain cases the addition is to be replaced by a subtraction. Why this is so can be readily understood if we represent the three selected spectral colours by the vertices of a triangle and the colours obtained by superposing them by points inside the triangle. Taking the three selected spectral colours to be  $700\text{ m}\mu$  (red),  $546\text{ m}\mu$  (green), and  $436\text{ m}\mu$  (blue), pure white would correspond to a point at the centre of the triangle, while other colours drift away from the centre in a direction represented by the dominant hue and to an extent which expresses its purity or saturation. But colours closely approximating in purity to the colours lying between the green and violet in the spectrum would lie outside such a triangle. Hence one would have to add to the colour under study a suitable amount of its complementary and thereby diminish the saturation or purity of the resultant to make it the same as the mixture of two colours compared with it.

The foregoing statements refer to the facts of colour vision as normally observed. Anomalies of colour vision are however exhibited by certain individuals, and these have been very thoroughly investigated by reason of their interest in relation to theories of colour vision. Persons whose colour vision is anomalous may be classified into three groups, viz., anomalous trichromats, dichromats, and monochromats. Anomalous trichromats are those who need, in general, three component stimuli to match any given colour, but their proportions are different from those for normal observers. Dichromats are those who require only two component stimuli; while monochromats are subjects who see only variations of brightness and are unable to recognize any colour.

## 6. Photochemistry of the retina

The principal characteristic of the reaction of the retina to light is its extreme selectivity as regards wavelength. In view of this, the only reasonable explanation of the sensitivity of the retina to light that has been proposed is one based upon the photochemical action of light. In other words, light is absorbed by a coloured substance associated with the receptor cells and induces a change in the substance; this in its turn sets up or gives rise to an electrical displacement or potential which is taken up and transmitted by the nerves as an impulse to the cortical centre. For such a theory to be sustainable, the photosensitive substance has to satisfy a number of requirements. It must be stable in the dark and after being altered or destroyed by light should be capable of being regenerated so that the receptor could continue to be light-sensitive.

As mentioned earlier, the retina in the fresh state exhibits a purple tint. But when exposed to light it becomes clouded, opaque, and bleached. Thus it is natural to assume that the colouring matter present in the fresh retina known as rhodopsin or visual purple is the photosensitive substance which enables the transformation of light into some other form of energy capable of acting directly on the nerves. A substantial proof of the correctness of this view came to hand when the light-absorption curve of human visual purple was determined and its resemblance to the scotopic curve of luminous efficiency in the spectrum was revealed. In other words, rhodopsin or the visual purple is indicated as the agent responsible for the activity of the rods in the retina as receptors of light radiation. The loss of the sensitivity of the eye to weak illumination in bright daylight and its restoration when the subject remains in the dark for long periods is explained on the basis that the exposure to strong light bleaches out the rhodopsin and that this is regenerated in darkness after a sufficient period of time.

Quite naturally, therefore, one is led to suppose that the sensitivity of the cones in the retina also arises from the presence of other photosensitive pigments in them. Experimental evidence supporting this view has been adduced by W H Rushton in a recent remarkable investigation. He has developed a technique for measuring the pigment present in the fovea by analyzing the light reflected from it and observed in an ophthalmoscope. Observations were made by him with normal trichromatic individuals and as also with a dichromat who was rather insensitive to red light. It was found that the fovea on exposure to bright light bleaches and darkens again during the next few minutes. Evidence is forthcoming from the observations that the normal fovea contains two visual pigments, one of which is green-sensitive and the other is red-sensitive; the former alone was found to be present in the fovea of the dichromat.