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## THE ELECTROPHYSIOLOGICAL ANALYSIS OF THE FUNDAMENTAL PROBLEM OF COLOUR RECEPTION

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### § 1. INTRODUCTION

IN a memorable lecture at the Royal Society in 1801 Thomas Young expressed his well-known views on the mechanism of colour reception. This was done almost in passing, and accompanied by the comment that he regarded them as something of a corollary to Newton's great discovery. It was impossible, he said, to conceive of the many spectral colours as being represented by an equally great number of optic nerve fibres of different type. For this reason he suggested that the number is limited. He fixed the number of fibre types at three, but this limitation is less essential than the three main generalizations implied in his thesis: (i) that the analysing mechanism is placed in the peripheral visual apparatus, (ii) that the number of colour-sensitive elements is relatively limited, (iii) that these elements represent widely different regions of the visible spectrum. Certain fundamental aspects of the problems contained in these assumptions can now be investigated with the aid of very direct methods. It has become possible to record the impulses in single fibres of the optic nerve of animals.

It is well known to most physicists that Professor Adrian in this country first showed that all sense organs respond to stimulation by discharging trains of impulses of constant size through their nerve fibres. The electrical nature of the nerve impulse as a conducted wave of negativity has been known since the work of Du Bois Reymond in 1849, but by introducing electrical amplification and by cutting down the nerves from certain receptors until only single fibres were left, Adrian succeeded in demonstrating that the response to variations in stimulus intensity is a variation in frequency of an impulse of constant size in the individual fibres (Adrian, 1932). This result is the basis of modern physiological analysis of all sensory mechanisms. The retina was also included in Adrian's pioneer programme of research (1927), and several important results were obtained. But at that time, in the late twenties, the new technique opened up so many prospects to physiology that the seemingly hopeless and formidable problem of isolating single fibres among the several hundred thousands of the optic nerve was left unsolved.

The American physiologist Hartline (1938) solved this technical problem for the first time by a very painstaking method of microdissection. He used the excised eye of the frog, removed lens and cornea and lifted up fibres from the retina on to his electrode in the region where they converge to form the blind spot. This technique is extremely laborious, and I remember Dr. Hartline telling me once that every eighth experiment succeeded, provided, of course, that the experimenter had acquired sufficient skill to succeed at all. (For a review of Hartline's work, see *J. opt. Soc. Amer.* 1940.)

## § 2. MEASUREMENTS ON ISOLATED FIBRES

Our own microelectrode technique is a great deal simpler. For work on colour reception it is essential that the technique for isolation of fibres should not be too difficult. It must be applicable not only to excised eyes but also to mammalian eyes in the living narcotized or decerebrated animal. The microelectrode is a thin platinum wire, isolated with glass down to the tip. It is applied to the inside of an eye from which cornea and lens have been removed. The microelectrode touches the fibres running along the retina to the blind spot. A schematic picture is shown in figure 1, referring to the rat's retina. This picture

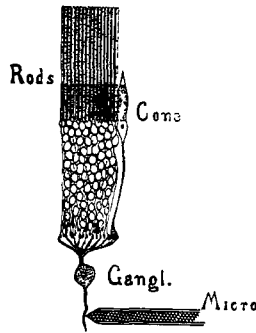


Figure 1. Diagram illustrating microelectrode on optic nerve fibre of rat. Several receptors and bipolars converge to form the unit recorded from. (Granit, *Acta Physiol. Scand.* 2, 1941 a.)

also illustrates the fact that several receptors converge towards the single fibre isolated. There are few cones in the rat's retina. One cone and a much greater number of rods make up the convergence unit assumed to be isolated by the microelectrode. Such isolated fibres have very different properties. The records in figure 2 illustrate the simplest type: the isolated unit responds to an increase in intensity from the threshold upwards, with an increasing number of impulses at an increasing rate of discharge. These particular records are from the eye of a guinea pig in which such units form the great majority; it was maximally sensitive to green light around  $530\text{ m}\mu$ , as shown by figure 3. The ordinate of this curve is the inverse value of the relative quantum intensity necessary to elicit one impulse, as in the uppermost record of figure 2. The animal was light-adapted.

This experiment illustrates the main principles of the microelectrode experiment on colour reception. It is a technique for measuring the absolute threshold

to spectral light. In actual practice such experiments are not carried out photographically, but the impulses, or, as we say, the *spikes*, are amplified and led to a loud-speaker. The spectral energy is increased by means of a calibrated wedge until a sharp report is heard in the loud-speaker. Single fibres are not always

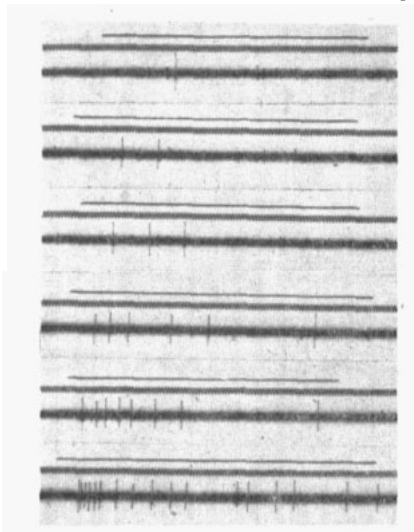


Figure 2. Guinea pig. Isolated unit with maximal sensitivity in  $530\text{ m}\mu$  responding to different intensities, increasing from record to record downwards. Uppermost line in each record = light signal. Time in  $1/50$  sec. between this and spike records. Uppermost record at threshold strength, lowermost record at  $10.7$  times threshold energy. (Granit, *Acta Physiol. Scand.* 3, 1942.)

obtained, and quite often one has to be content with a highly restricted discharge. Since the threshold method always picks up the most sensitive fibre of all, this limitation is less serious than might have been imagined. In my latest experiments with the cat's retina, single fibres were obtained in 60% of the cases.

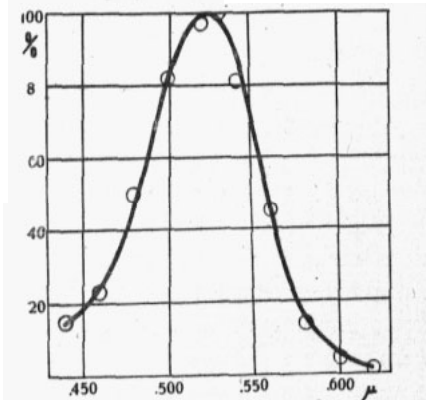


Figure 3. Spectral distribution of sensitivity of spike recorded in figure 2. (Granit, *Acta Physiol. Scand.* 3, 1942.)

Success depends mainly on the success in making the microelectrode, and to some extent, of course, also on patience and practice. The animal must be quiet, for the slightest movement suffices to shift the microelectrode.

I have said that the fibre shown in figure 2 represented a simple type of

response. In the cat's eye, for instance, the fibres respond to an increase of stimulus intensity in a very complex manner. Most fibres discharge to both onset and cessation of illumination. But the relative amount of on- and off-discharges varies a great deal with stimulus intensity. Light may inhibit the on-discharge in a certain intensity range and inhibit the off-discharge in another. The complexity of the response, as soon as the threshold strength has been exceeded, is something stupendous. Hardly two fibres can be said to be exactly alike. An instance is given in figure 4. The figures to the right above each

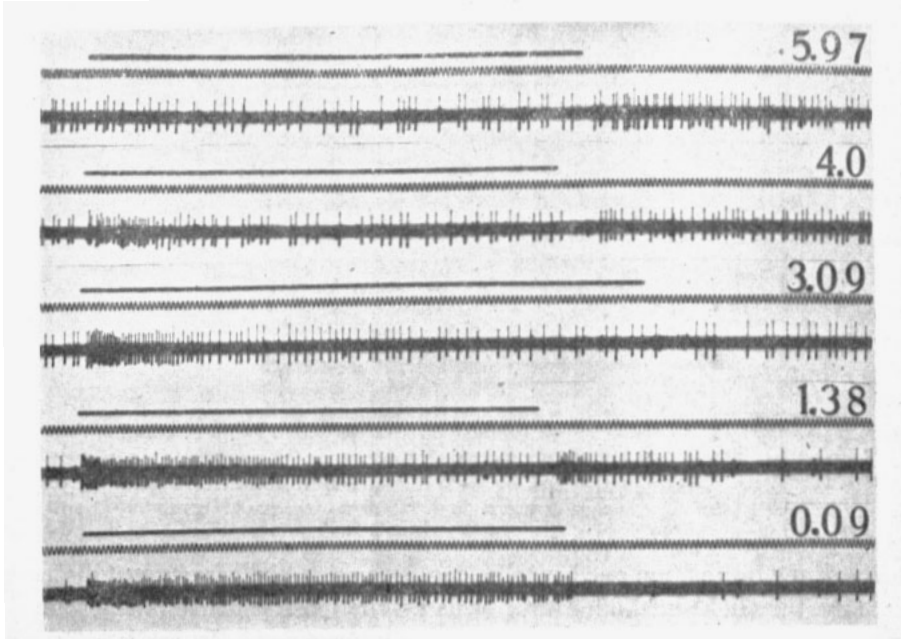


Figure 4. Cat. Isolated spontaneously active element responding to progressively increasing intensities of white light. The numerals to the right show the extinction (densities) of the filter-wedge combination used in front of a light of 892 m.c. Marked as figure 2. (Granit, *J. Physiol.* 103, 1944.)

record show the density of the neutral filter put into the beam of a white light of 892 m.c. In this case the fibre is spontaneously active all the time. The on-discharge increases with stimulus intensity (downwards), the off-effect increases first, is inhibited in record 3.09, increases a second time (record 1.38) and is ultimately completely inhibited at maximal intensity (record 0.09). These complex effects are due to interaction in the extremely complex retinal switchboard of neurons and synapses from which the optic nerve fibres take off. Such phenomena must play an important rôle for discrimination and contrast effects, but they do not concern us here. Figure 4 merely serves as a warning against premature and over-optimistic simplification when one is dealing with a wonderful microcosm of a nervous centre such as the vertebrate retina.

### § 3. THRESHOLD MEASUREMENTS FOR COLOUR-RECEPTION ANALYSIS

From the point of view of the analysis of colour reception we must begin with threshold measurements in the manner just described. For this immediate purpose it is immaterial how the discharge is modified by an increase of stimulus

intensity. We can always determine the energy necessary for a threshold response. This is the method that has been used in my analysis of the fundamental problem of colour reception, the problem raised with such clarity by the far-sighted genius of Thomas Young.

The results of measurements of the energy necessary for a threshold response at various wave-lengths could be very easily interpreted, were it not for the fact that in most of the laboratory animals both rods and cones converge towards the same fibre, as in figure 1. Now the rods contain the extremely light-sensitive substance *visual purple*, which has maximum absorption around 500  $m\mu$  and a quantum yield, as determined by Dartnall, Goodeve and Lythgoe (1936), of 1, so that one quantum of light destroys one molecule of visual purple. Its absorption curve has been fairly well known since the work of Trendelenberg in 1904, and was first accurately determined with up-to-date technique of extraction and photo-chemical analysis by the late Dr. Lythgoe in this country in 1937, and almost simultaneously by several other workers. Schneider, Goodeve and Lythgoe showed in 1939 that the photosensitivity of visual purple agreed with the human scotopic luminosity curve, illustrating the distribution of brightness for a dark-adapted eye to a spectrum of low intensity. (For a full review of this work, see author's summary, Granit, 1946).

It is therefore not surprising that my method reproduces the same curve if the threshold energy in the spectrum is determined for fully dark-adapted eyes of animals containing rods charged with visual purple. Such measurements will be shown later. At the moment this point is taken up in order to emphasize that the visual purple distribution of spectral sensitivity is a serious complication in work with animals. Visual purple can be removed by light-adaptation, but it regenerates during the time the experiment is carried out in the dark, and so tends to raise the sensitivity in the green around 500  $m\mu$ . This, of course, is a consequence of the convergence of several receptors of mixed nature towards each optic nerve fibre as well as of the extreme sensitivity to light of visual purple. But when we use our own visual purple mechanism in the dark, the spectrum appears colourless. An increased sensitivity to green around 500  $m\mu$  cannot, therefore, in the microelectrode experiment, be ascribed to a hypothetical "green response" of the *cones*. In order to be able to do so we must make certain that we have not been engaged in measuring merely the photosensitivity of visual purple. The experimental work becomes something in the nature of a fight against the absorption curve of visual purple, which tends to cover up the properties of other receptors belonging to the convergence unit which has been isolated by the microelectrode.

#### § 4. THE DOMINATOR AND MODULATORS

In order to illustrate one of the main findings, I shall therefore first draw attention to a curve from the eye of a snake which is lacking visual purple. This animal has a pure cone retina. In figure 5 the curve interrupted by dots refers to the snake (1943 b), the other curve to the frog's eye (1941 c), which has been light-adapted so as to depress the activity of visual purple. The two curves are sufficiently similar to support a conclusion that after light-adaptation the remaining cones of the frog's eye have behaved like the cones of the snake. I shall refer

to this broad cone curve with maximum around  $560\text{ m}\mu$  as the *dominator*. Those familiar with the problems of vision will immediately notice that the dominator curve represents a distribution of sensitivity which is almost identical with the human daylight luminosity curve for cone vision, the so-called *photopic luminosity curve*. Provided that an animal's eye possesses a sufficient number of cones, this

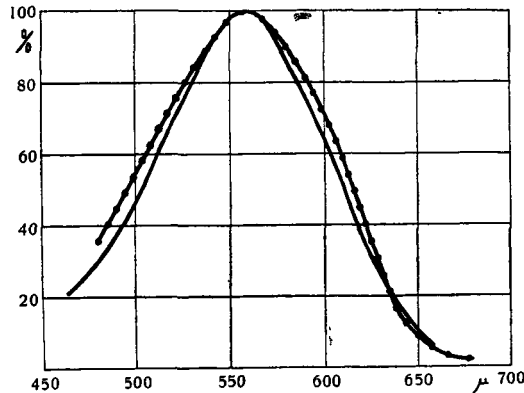


Figure 5. Distribution of sensitivity of dominator element in the retina of snake (line interrupted by dots) and frog (uninterrupted line). (Granit, *Nature, Lond*, 151, 1943.)

curve is always obtained, and represents the most common electrophysiological finding. It is lacking in the eyes of rats and guinea pigs (Granit, 1941 a, 1942). The guinea pig's eye is said to lack cones altogether, the rat's eye is said to contain about 1 % cones, apparently too few to be able to give the dominator.

In a sense the dominator can be described as a physiological unit response, but it is very probable that several receptors have combined to form this unit. We must remember that all optic nerve fibre units are convergence-units, as stated above.

When different optic nerve fibres are picked up, in the manner described, the whole experiment is very much dependent upon statistical chance and good luck. These factors favour the dominator, but other types of curve are also sometimes obtained. These are illustrated in figure 6. The curves are from eyes of different animals : rats (1941 a), guinea pigs (1942), frogs (1941 c), snakes (1943 b). First should be noted that they differ from the dominator curve in two important respects : they are much narrower and are spread over a large fraction of the visible spectrum.

Neglecting for the moment the narrow curve with maximum around  $500\text{ m}\mu$ , which may be described as a narrow visual purple curve, the most striking fact demonstrated by figure 6 is the confinement of the narrow curves to three preferential regions of the spectrum. This is the more remarkable if one considers that they are from different animals. I have called these curves the *modulator curves*.

The most characteristic red modulator had its maximum at  $600\text{ m}\mu$ . It was found in rats (dots), much to my surprise, since I took up the rat's rod eye in order to find out what happens to the visual purple distribution of sensitivity when the eye becomes light-adapted. The result was that I found the red modu-

lator remaining, when the green end of the spectrum, occupied by the visual purple absorption, had disappeared below the instrumental threshold of the Hilger-Tutton monochromator used at that time. After some time in the dark the narrow curve with maximum at  $500\text{ m}\mu$  turned up. Later, during dark-adaptation, it expanded and assumed the shape of the typical visual purple absorption curve. I have since seen the same narrow curve in other rod eyes, but not in the cone eye of the snake. It is difficult to say whether it would play any part in human colour vision or not. Probably not, if central fixation is used. The rat's red modulator may be due to the 1% cones. Histologists, though not all, believe in cones in the rat's eye. There was no dominator in this eye. The red modulator was also seen in the eyes of frogs, in the pure cone eye of the snake, and was indicated as a hump on the green curve in some very rare cases in the guinea pig. In the frog I found some modulators with maximum at  $580\text{ m}\mu$ . These will be called yellow modulators.

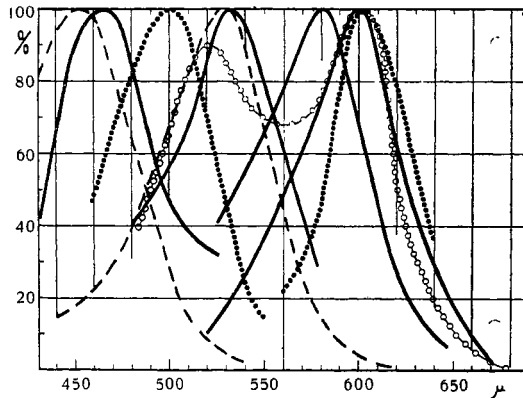


Figure 6. Distribution of sensitivity of modulator elements from eyes of rat (dots), guinea pig (broken line), frog (line in full) and snake (line interrupted by circles). In this figure and in figure 5 spectra of equal quantum intensity. The ordinates on either side of  $560\text{ m}\mu$  drawn down to indicate dominator values. (Grant, *Nature, Lond.*, 151, 1943.)

Green modulators are found in all eyes between  $520$  and  $540\text{ m}\mu$ , even in the cone eye of the snake, but in this animal it proved impossible to separate them from the red modulator. Blue modulators around  $460\text{ m}\mu$  were found in the frog's eye and in the pure rod eye of the guinea pig, but not in the cone eye of the snake.

The general biological implications of these findings are clear enough. Nature has not taken the trouble to invent new mechanisms of colour analysis for every new species. It has, as it were, decided upon the principles to be used and then proceeded to use them with what, from our point of view, we might call a greater or lesser degree of perfection. The eyes of the different animals are probably adapted to the life and habits of the species concerned. With regard to modulators, the boundaries between rods and cones do not seem to be very strict. It seems certain that dominators only are found in eyes with a large number of cones. It is possible and even probable that red modulators are cones in the histological sense, but modulators in the short wave-lengths need not be cones.

Blue modulators must be rods in the histological sense, and it is doubtful whether blue modulators can ever be anything else. The experiments suggest that, on the whole, more attention should be paid to photochemistry than to histology. Histological and photochemical definitions as to what is a cone or a rod may disagree. Unfortunately cone photochemistry is still at the stage when it is no exaggeration to state that the less said about it the better. It is, of course, very difficult to extract substances from receptors which to all appearance are practically colourless.

If I may state my own belief it is that the cone substances are modifications due to changes in the bonds linking the visual purple chromophore to its protein body. There is some evidence for this view which cannot be discussed in this connection (see Granit, 1941 b). Some day those working on the photochemistry of visual purple will provide us with important clues to the solution of this riddle. Lythgoe made a beginning when, shortly before his death, he found that visual purple, regenerating from its photoproduct "transient orange", had its absorption curve shifted towards the long wave-lengths. This work was never published.

#### § 5 NATURE OF THE DOMINATOR

The microelectrode experiments now described did not suffice to create that feeling of satisfaction with which the completion of a work properly should end. The element of statistical chance involved made them not only extremely tedious but also unsatisfactory; and what was the meaning of the dominator, which was the most common finding in eyes containing a great number of cones? Could it be regarded as being formed by grouped modulators? Those questions

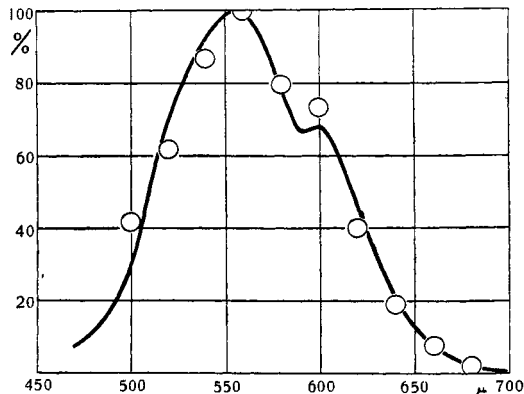


Figure 7. Luminosity curve determined by Wright (*Nature, Lond.*, 151, 1943) with a small fovea patch of low brightness. The circles illustrate the cat dominator from Granit (*Acta Physiol. Scand.* 5, 1943 a.) Equal-energy spectrum.

became more pressing when it was found that in some cases the dominator of the snake eye had a hump around 600  $m\mu$  and that all dominators in the cat's eye had this same hump. Despite this it proved impossible to obtain red modulators in the cat's eye, although this eye is more like the human peripheral retina than any other eye used in my work.

At that time Dr. Wright published in *Nature* (1943) a brief note reporting the results of an experiment in which he had tried to imitate the microelectrode

method by measuring the luminosity curve of a very small patch of light. He also found a hump on the foveal luminosity curve in the red around 600 m $\mu$ . Figure 7 shows Wright's curve. The circles refer to my own measurements of the cat's dominator. This parallelism between two independent measurements with very different techniques suggested that the dominator might be a composite curve, besides suggesting that the human and the feline mechanism of colour reception cannot be fundamentally different. It therefore became imperative to develop a method by means of which it would be possible to split the dominator, if it could be split. Considering that about 36% of the isolated fibres in the light-adapted cat's eye gave the dominator, a successful splitting of the dominator would minimize the statistical element of chance involved in the process of hunting for simpler units of colour reception. For the new experiments I used Dr. Wright's well-known colorimeter (1934), drawn and constructed for this work by Mr. G. C. Newton.

The principle of the experiment is illustrated in figure 8. The animal is

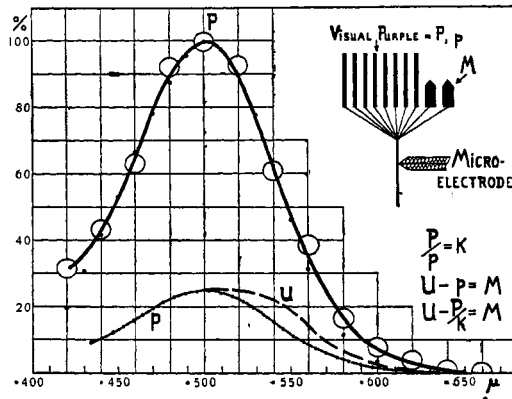


Figure 8. Dark adapted cat. Large circles = average distribution of sensitivity of isolated fibres in the optic nerve. Small black circles = Lythgoe's corrected curve for visual purple absorption from *J Physiol* 89, 1937. Spectrum of equal quantum intensity. As to significance of diagram and symbols, see text. (Granit, *J. Neurophysiol.* 8, 1945.)

fully dark-adapted so that the highly sensitive visual purple completely dominates and gives the curve *P*. This is based on some 1320 readings, averaged into 179 values, again averaged to give the large circles around the curve. The small black points are Lythgoe's corrected curve for visual purple absorption, which is a little too low in the violet, as shown by Schneider, Goodeve and Lythgoe (1939). A slight effect of the dominator makes my curve a little too high in the yellow-red region.

If the eye be adapted to red, blue or green light the curve *P* is reduced to *p*, by proportionate ordinates at all wave-lengths, since *P* represents the homogeneous substance visual purple. Hence

$$P/p = k. \quad \dots\dots(1)$$

But if there are any other colour-sensitive substances (*M*), *performed* or produced by visual purple, curve *P* does not drop to *p* but to some other curve, *U*

(figure 8). The modulators  $M$  are given by the difference between  $U$  and  $p$ , as evident from the diagram, or

$$M = U - p. \quad \dots\dots(2)$$

In this case  $p$  is unknown, but the equation can be solved by giving it the form

$$M = U - P/k. \quad \dots\dots(3)$$

$P$  is obtained *before*,  $U$  *after*, selective adaptation, and  $k$  can be obtained from (1) by finding the spectral region in which selective adaptation has caused the largest drop of sensitivity, since in this region there was no other substance than visual purple left to resist light-adaptation. This region will generally be found in the place where the letter  $p$  is inserted in the diagram (figure 8). All quantities of (3) are now known, and the argument can be tested by experiment.

Equation (3) was solved in 34 experiments on the basis of some 4000 observations collected in 601 points on  $U$ -curves. Some 60% of the  $U$ -series referred to isolated fibres, the rest to restricted activity. In 29% the equation came out zero ( $U = p$ ), and hence the microelectrode had struck a unit with pure visual purple receptors. In the rest of the series complex curves were obtained.

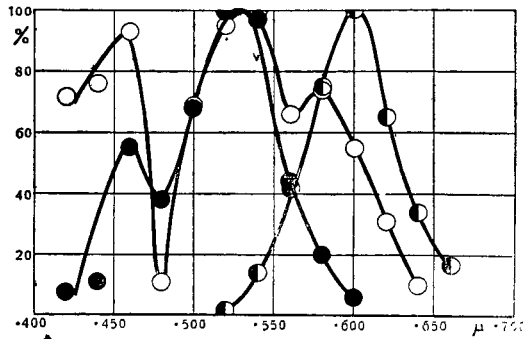


Figure 9. Average effects of selective adaptation of cat's eye, as described in text. ● = red adaptation, ○ = green adaptation, ● = blue adaptation. Spectrum of equal energy. (Granit, *J. Neurophysiol.* 8, 1945.)

Coloured adaptation was used because it was hoped that, for instance, red adaptation would suppress red-sensitive elements and give elements sensitive to other colours a chance to appear. The eye was left in coloured light for some time, this light then instantaneously interrupted, and a test light from the spectrum flashed in, 3 sec. after interruption of the coloured adaptation. This time was chosen in order to give the off-effect time to disappear or to diminish in frequency, so as to make it possible to hear whether the test light caused a fresh discharge or not. When the test had been carried out, the adapting light was again switched on for a while until the eye was ready for a new test with some other spectral wave-length. For adaptation the Ilford spectral filters red, green and blue were used in the main series. A minor number of experiments were carried out with the yellow and violet filters.

For a general survey of the  $M$ -curves from equation (3), figure 9 should be studied. This does not show any individual modulators, but merely the general

effect of adaptation to red, green and blue light as gross averages of the  $M$ -curves obtained. The maximum for each individual experiment has always been given the value 100, so that the curves give an idea of the chance for a given point to reach a certain magnitude.

It is seen that blue adaptation gave the most uniform results, so that only curves with maximum in the red were obtained. Red adaptation actually suppressed red modulators, but green and blue modulators made themselves felt. The adaptation to green had a still less selective character. There were humps in both the red, green and blue regions of the spectrum.

Let us now present the same results in a manner which is easier to follow. The individual modulators from the three preferential regions have been picked out and averaged, independently of the kind of coloured adaptation by which they have been obtained. The results are shown in figure 10, in which, also, the dispersion is indicated (outer contours). The narrow red modulators were of two types with maxima respectively at  $600\text{ m}\mu$  (red) and  $580\text{ m}\mu$  (yellow), the former type being the more common. Most green modulators overlapped and had

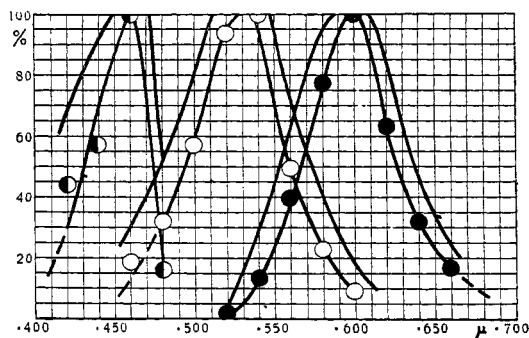


Figure 10. Averaged individual modulators (cat) as obtained by selective adaptation. ●=red modulators, ○=green modulators, ●=blue modulators. Outer contours indicate dispersion, see text Spectrum of equal energy. (Granit, *J. Neurophysiol.* 8, 1945.)

maxima at  $540\text{ m}\mu$ , some at  $520\text{ m}\mu$ , and two of them were of the type previously described as narrow visual purple curves. These may be lacking in pure cone eyes. These modulators were the ones seen before in different types of retinae, analysed by the earlier "chance" method. The blue region could be better analysed with Wright's colorimeter. Most blue modulators had their maxima at  $460\text{ m}\mu$  (blue), one at  $440\text{ m}\mu$  (violet). They were very narrow bands. Errors of measurement increase from the red to the blue end. On account of the steepness of the modulator curves the maxima are fairly well definable.

The average modulators of figure 10 are too narrow to add up to a cat dominator. It is clear that impulses also must be delivered up the optic nerve by modulators with "legs" outside the averages. The dispersion gives some idea of the extension of the outer margin of each of the three groups of modulators. In figure 11 the extreme values obtained in these experiments are given. Together with the curves of figure 10, showing the dispersion, they should give some idea of the limits permitted in synthesizing the dominator.

In figure 12 is shown the synthesis of the cat's dominator (Granit, 1943 c)

from figure 7. The thick line, drawn through the readings, is the sum of the red and green curves, R and G. In the light of these experiments it seems permissible to maintain that the dominator is a composite curve consisting of modulators. Nevertheless the dominator must be regarded as a *biological unit*. It cannot be neglected in theories of colour vision even though the modulators are

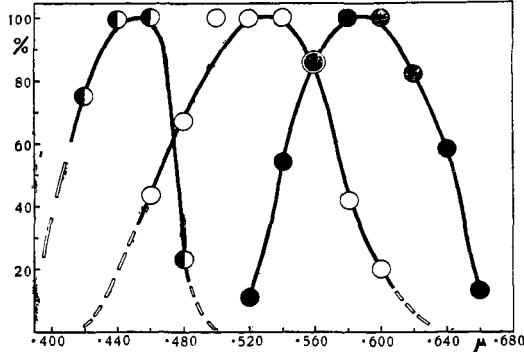


Figure 11. Extreme values obtained for cat modulators by selective adaptation, as described in text. Equal-energy spectrum. (Granit, *J. Neurophysiol.* 8, 1945.)

the *ultimate physiological units*, the units of first order. It should be emphasized that modulators in the pure state were also obtained without coloured adaptation in some animals.

Why have modulators never been found in the human eye with sensory methods? The main reason would seem to be that the analytical unit-field

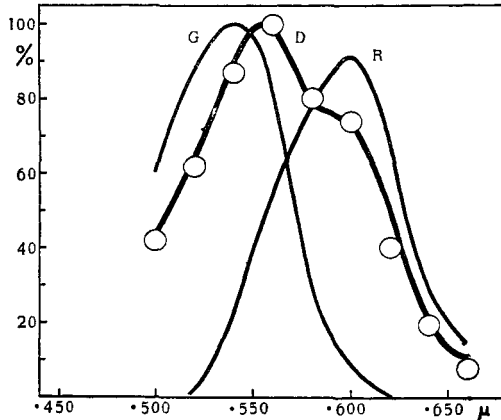


Figure 12. Circles = averages of four photopic dominators of cat. Curve D in heavy lines = synthesis of this dominator by adding modulator areas G and R and plotting their sum in percent of maximum. Equal-energy spectrum (Granit, *J. Neurophysiol.* 8, 1945)

contains too many elements, perhaps up to a hundred thousand nerve fibres. I should also like to draw attention to the fact that the microelectrode technique is a threshold measurement. Wright's and Walters and Wright's (1943) promising results suggest that experiments with small areas and low intensities, perhaps aided by selective adaptation, might open up new possibilities. Some-

thing might also be gained by studying the peripheral field of vision (see Walters and Wright, 1943).

In figure 13 I have synthesized the human photopic luminosity curve on the basis of the results obtained with the cat's optic nerve. The daylight spectrum or cone spectrum of the human eye agrees very well with the dominator (D) of the electrophysiological experiment. The three preferential regions within which modulators are found are given by the R, G and B curves, forming the three fundamental sensation curves of the Young-Helmholtz trichromatic theory.

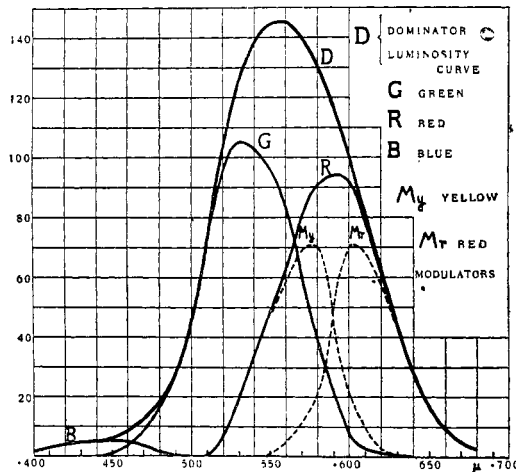


Figure 13. Synthesis of human photopic luminosity curve (D), as determined by Coblentz and Emerson (*Bull. Bur. Stand., Wash.*, no. 303, 1917), on the basis of three fundamental sensation curves, R, G and B. The R-curve indicated to be the sum of two modulators  $M_y$  and  $M_r$ . Equal-energy spectrum (Granit, *J. Neurophysiol.* 8, 1945)

Their sum is the dominator. For the R-curve I have indicated the two modulators  $M_r$  and  $M_y$ . It would, no doubt, be possible to combine the modulators in a slightly different manner, for instance an R-curve with a hump at 600  $m\mu$ . But the last word on this question must remain with those who are experts on human colour psychophysics. It should be remembered that threshold measurements, such as are used in electrophysiological measurements, record the narrowest curve that can be obtained. It seems possible that the greater the level of intensity, the greater the width of the modulator curve. The retina, after all, is a complex nervous centre with mechanisms of facilitation.

§ 6. COLOUR VISION

It should be emphasized that the electrophysiological experiments have not provided any evidence for the existence of three fundamental response curves. From the physiological point of view, colour vision must be understood in terms of modulators and dominators. The three fundamental response curves must be regarded as approximations depicting the areas covered by the modulators in the three preferential regions. But it is interesting to note that my schematic response curves agree fairly well with those obtained by Walters (1942) in experi-

ments developing Wright's (1934) method of selective adaptation. Walters' curves are shown in figure 14.

Recent work by Pitt (1944) on the three response curves has not yet become available to me, but from a summary by Stiles (1944) I infer that Walters' results have been confirmed by Pitt by a different method. Pitt's curves extend further down into the blue part of the spectrum.

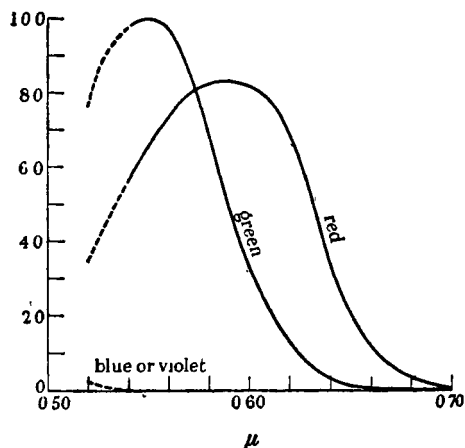


Figure 14. Fundamental sensation curves determined by Walters (*Proc. Roy. Soc. B.*, 131, 1942).

The fineness of hue discrimination would seem to be well explained by the narrow modulator curves. Figure 15 is taken from the work of Wright and Pitt (1934). The ordinates show the shift in wave-length, necessary for discrimination of hue at adjacent wave-lengths, so that minima in the curve signify maxima of discrimination. In the region between 580 and 600  $m\mu$ , where the red and the yellow modulators intersect, one can distinguish wave-lengths separated by as little as 1  $m\mu$ . From figure 13 it is clear that precisely in this region a slight shift of wave-length suffices to redistribute the nerve fibre signals between

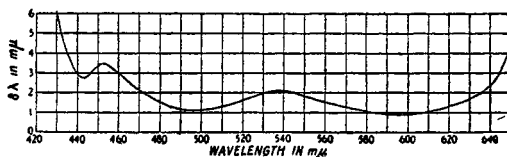


Figure 15. Human hue discrimination according to Wright and Pitt (*Proc. Phys. Soc.* 46, 1934).

the red and the yellow modulator. The second optimum between 480 and 510  $m\mu$  is found in a place where the blue and red modulators meet and intersect with the green ones. Rather remarkable is the third (less marked) optimum between 450 and 440  $m\mu$ , which suggests, as did my experiments, that two blue modulators overlap in this region, the blue proper with maximum at 460 and the violet one with maximum at 440  $m\mu$ .

## § 7. THE NATURE OF WHITE AND COLOUR

The existence of the dominator as a physiological unit makes it necessary to consider its sensory equivalent. It is well known that our sensations of light can be divided into two main categories, brightness or luminosity and colour or hue. The luminosity curves of the human eye have several times been referred to. It is well known that corresponding to our two sense-organs in the retina, the rods and the cones, there are two luminosity curves, one for dark-adapted rods charged with visual purple, another for the light-adapted eye and cone vision. These two standard curves are shown in figure 16. The daylight luminosity curve to the right we have identified electrophysiologically as the photopic dominator, the scotopic luminosity curve to the left as a replica of the visual

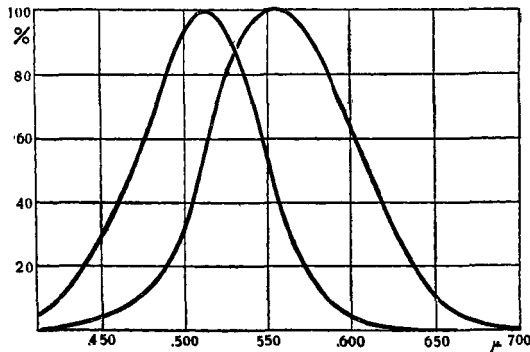


Figure 16. The standard photopic and scotopic luminosity curves of the human eye.

purple absorption curve minus losses of light of short wave-length in the ocular media. If the latter curve is corrected for this and plotted on a quantum basis, it will actually be identical with the curve for visual purple absorption.

Figure 16 is introduced here merely in order to show that a shift of the maximum need not as such cause an impression of colour. Both curves are luminosity curves illustrating the distribution of brightness. From the physiological point of view it seems reasonable to suggest that optic nerve fibres representing wide spectral areas, such as those of figure 16, cannot cause any other impression than that of brightness or whiteness. For discrimination of wave-length, nature has developed a very different type of mechanism, consisting of narrow modulators in three preferential regions.

According to this view the dominator represents brightness or whiteness. To put it differently, the fundamental visual equivalent to impulse frequency is a neutral white. Colour, if I may say so, is a kind of "local sign", carried by the modulators, which are certain receptors or groups of receptors connected to certain fibres so that from the retina up to the brain the same spatial pattern of organization is maintained. Inasmuch as the modulators contribute to impulse frequency they can also contribute to brightness.

Galambos and Davis (1942) have recently applied the microelectrode technique also to the acoustic nerve. There too it was found that the different acoustic frequency bands were represented by different fibres, rather narrow bands at that. In the ear too the perception of quality or pitch is something

related to space, just as in the eye. Loudness, however, is almost certainly a function of total impulse quantity, just as brightness in the eye. Colour and pitch are determined by some kind of local sign.

What makes the eye particularly interesting is that the spectral distribution of brightness is also found to be represented by individual optic nerve fibres. In my opinion this must be regarded as evidence for the view that white has the character of a separate sensation. It has long been known that brightness and colour have maintained a certain amount of independence. This is particularly obvious in defective colour vision. Thus the deuteranope is a red-green blind observer with a normal distribution of luminosity. I do not see how this can be explained by the trichromatic theory, according to which white must be regarded as the sum of the red and green fundamental response curves with a minor contribution from the blue curve. If the red and green curves are lacking, one must expect a grossly abnormal distribution of luminosity instead of the normal one found. This difficulty does not exist for the dominator-modulator concept.

The various forms of colour blindness I regard as defects in the receptors or elsewhere in the paths representing the modulators. But such defects would have to be of an extreme degree in order to be so complete as to remove the dominators, of which, apparently, there is a very great number, considering how easily they can be detected.

There are, too, several forms of acquired colour blindness. They are characterized by loss of perception of certain hues but not of brightness. In certain forms of colour blindness, such as protanopy, there are minor shifts in the luminosity curve. These can be explained by a minor redistribution of the aggregate modulators forming the dominator.

The distribution of saturation in the spectrum is very characteristic. The ends are saturated and at the same time dark, extreme red and extreme blue being examples of such dark and saturated colours. On the dominator-modulator concept this is explained by the fact that at the ends of the spectrum the dominator values are very low, so that the modulators in these regions are responsible for the greater part of the sensory experience. Again, in the yellow region the large contribution from the dominator makes the spectrum appear relatively white and the colour unsaturated.

#### § 8. CONCLUSION

Let us now return to Thomas Young, in whose honour this lecture is being delivered. It is a characteristic of those whom we revere as classics of science that their ideas have been formulated with a curious insight into how nature might be expected to behave and so have preserved lasting creative power. What greater tribute could one scientist pay to another's memory than to perform an experiment suggested by his ideas, 140 years after they have been formulated, and come to the conclusion that these ideas were fundamentally correct? The mechanism of colour reception is organized by the peripheral visual apparatus, the number of colour-sensitive elements is relatively limited, and these elements represent widely different regions of the visible spectrum. Those were Young's three fundamental assumptions. He was right even in assuming three main types of colour-receiving apparatus. These are the three preferential regions

within which modulators are found. The electrophysiological work may, indeed, be said to have confirmed the view he gave of the framework of a mechanism of colour reception. Its finished picture looks somewhat different, but the old framework was solid enough and shines through.

It has been a great pleasure for me to have had this opportunity of speaking to this distinguished audience in honour of Thomas Young. His original theme was the same as mine, in the sense that he described a peripheral mechanism of wave-length reception in terms of the properties of nerve fibres. Colour vision is a much wider subject, and there are several in this Society who know much more about it than I do. My theoretical attempts to translate the electrophysiological results into the language of colour psychophysics are legitimate, and I believe them to be correct, but further experience may nevertheless necessitate modifications. I can only hope that I shall not have to make these experiences myself, but that somebody else will try his hand at the optic nerve. I also feel just now that it would be interesting to see for a while what photochemistry and colour psychophysics could do for this field before any further labour is invested in electrophysiological work. For the invitation to present the results of this work to the Physical Society I wish to express my sincerest thanks.

## REFERENCES

- ADRIAN, E. D., 1932. *Mechanism of Nervous Action* (Oxford: University Press).  
 ADRIAN, E. D. and MATTHEWS, R., 1927. *J. Physiol.* **63**, 378.  
 COBLENTZ, W. W. and EMERSON, W. B., 1917. *Bull. Bur. Stand., Wash.*, no. 303.  
 DARTNALL, H. J. A., GOODEVE, C. F. and LYTHGOE, R. J., 1936. *Proc. Roy. Soc. A*, **156**, 158.  
 GALAMBOS, R. and DAVIS, H., 1942. *J. Neurophysiol.* **6**, 39.  
 GRANIT, R., 1941 a. *Acta Physiol. Scand.* **2**, 93.  
 GRANIT, R., 1941 b. *Acta Physiol. Scand.* **2**, 334.  
 GRANIT, R., 1941 c. *Acta Physiol. Scand.* **3**, 137.  
 GRANIT, R., 1942. *Acta Physiol. Scand.* **3**, 318.  
 GRANIT, R., 1943 a. *Nature, Lond.*, **151**, 11.  
 GRANIT, R., 1943 b. *Acta Physiol. Scand.* **5**, 108.  
 GRANIT, R., 1943 c. *Acta Physiol. Scand.* **5**, 219.  
 GRANIT, R., 1944. *J. Physiol.* **103**, 103.  
 GRANIT, R., 1945. *J. Neurophysiol.* **8**.  
 GRANIT, R., 1946. *Sensory Mechanisms of the Retina* (Oxford: University Press. In course of publication).  
 HARTLINE, H. K., 1938. *Amer. J. Physiol.* **121**, 400.  
 HARTLINE, H. K., 1940. *J. Opt. Soc. Amer.* **30**, 239.  
 LYTHGOE, R. J., 1937. *J. Physiol.* **89**, 331.  
 SCHNEIDER, E. E., GOODEVE, C. F. and LYTHGOE, R. J., 1939. *Proc. Roy. Soc. A*, **170**, 102.  
 STILES, W. S., 1944. *Proc. Phys. Soc.* **56**, 329.  
 TRENDELENBERG, W., 1904. *Z. Psychol. Physiol. Sinnesorg.* **37**, 1.  
 WALTERS, H. V., 1942. *Proc. Roy. Soc. B*, **131**, 27.  
 WALTERS, H. V. and WRIGHT, W. D., 1943. *Proc. Roy. Soc. B*, **131**, 340.  
 WRIGHT, W. D., 1934. *Proc. Roy. Soc. B*, **115**, 49.  
 WRIGHT, W. D., 1943. *Nature, Lond.*, **151**, 726.  
 WRIGHT, W. D. and PITT, F. H. G., 1934. *Proc. Phys. Soc.* **46**, 459.  
 YOUNG, T., 1855. *Miscellaneous Works of the late Thomas Young*, ed. by George Peacock, vol. 1 (London).