THE COLOUR RECEPTORS OF THE MAMMALIAN RETINA

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IN A SERIES OF PAPERS (3–12) the spectral properties of vertebrate colour receptors have been analyzed with the aid of the micro-electrode technique and an equal energy spectrum. An early summary appeared in 1941 (5), a later summary in 1943 (11). This work has now been supplemented with experiments of a new type, to be described below. These represent the final general solution of the problem.

In the early work different types of retinae were used in the hope of finding preparations in which perhaps one type of colour-sensitive element would be emphasized at the expense of others and so help to define the spectral region specifically concerned in mediating wave-length differentiation. This surmise proved correct, and a brief summary of the earlier results will now serve to present the problem in the form that it had assumed before ripe for the new mode of attack, developed in this paper.

The method of experiment was to measure the energy necessary for a threshold response in the various wave-lengths and plot the results in the shape of curves showing sensitivity—defined as reciprocal of energy necessary for a response—in per cent of the maximum of sensitivity for any given type of element. As stated above, the abscissae were obtained directly as the wave-lengths of an equal energy spectrum but more often the readings were corrected so as to refer to a spectrum of equal quantum intensity, a correction necessary for comparisons with photochemical results. Data for the human eye are generally given in terms of an equal energy spectrum. If the retinae contained rods they had to be light-adapted. The rod-free retina of the snake (*Tropidonotus*) served as a check on the conclusions reached with mixed light-adapted retinae. In the cone-eye of the snake there was no element containing the highly sensitive visual purple that could interfere with the measurements of the spectral sensitivity of the cones. These statements do not imply that the rods necessarily would be incapable of mediating responses from other regions of the spectrum than those covered by the visual purple distribution of sensitivity. They merely emphasize that rods charged with visual purple reproduce the sensitivity distribution of this substance so that no substance of lesser sensitivity has a chance of turning up, except at the base of the curve.

Background of present problem. Most elements in light adapted mixed retinae as well as in the cone-retina of the snake gave the broad type of distribution of sensitivity with maximum around 0.560μ, shown in Fig. 1 and called the *photopic dominator*. The curves refer to frog and snake. If a mixed eye was dark adapted the maximum shifted to the region of 0.500μ and the photopic dominator then served as *scotopic dominator.* These dominators are therefore the carriers of the Purkinje shift. When below, for brevity's sake, the term "dominator" is used alone it always stands for "photopic dominator." Since the same single spike, isolated by the micro-electrode, is shifting its sensitivity with state of adaptation it is clear that rods and cones either converge towards the fibre giving this spike or else that rods have different spectral properties depending upon whether they are charged with visual purple or not. Now the presence of the dominator in the cone-eye of the snake shows that it is represented by cones. The same is shown by the fact that the photopic luminosity curve of the human fovea corresponds to the dominator distribution of sensitivity. The dominator therefore must be a cone, the more so as it is absent in the rod eyes of rat and guinea pig. Therefore the *physiologist* can give no better general definition of what is a cone than to state that *cones are the receptors which give the photopic dominator distribution of sensitivity.* The idea of rods and cones converging towards the same element is thus a better explanation of the Purkinje shift in sensitivity of this element than the alternative suggested above which does not fit the results with rat and guinea pig. Polyak (14) has found that rods and cones actually do converge towards the same ganglion, in my own experiment the one from which the micro-electrode picks up the spike analyzed.

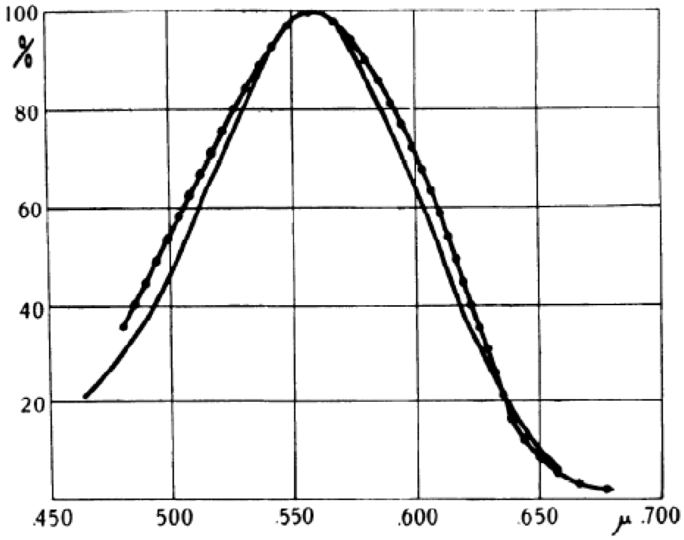

FIG. 1. Distribution of sensitivity of "dominator" element in the retina of the frog (uninterrupted line) and snake (line interrupted by dots). Spectrum of equal quantum intensity.

In addition to the dominator there are, in the light adapted eye, narrow bands of sensitivity, called *modulators* (Fig. 2). These occupy three preferential regions, red-yellow 0.580–0.600μ, green 0.520–0.540μ, blue 0.450–

0.470μ. In some light adapted rod eyes there was also a narrow band, placed with its top in 0.500μ and thus suggesting a narrow visual purple curve. It is a striking fact that a red modulator with maximum in 0.600μ was found in the rat's eye, in fact, discovered in this eye, and later shown to recur in several other eyes (*e.g.*, frog, snake), in some only as a hump on some other curve (cat definitely, guinea pig less definitely). Green modulators were seen in most eyes, blue modulators in frog and guinea pig, not in the snake. These results are summarized in Fig. 2. For details the original papers should be consulted. It should be emphasized that well isolated modulators always are narrow bands so that their maxima for this reason are well defined though varying from case to case within the regions mentioned. In the snake the maxima were in 0.600 and in 0.520μ. Whereas this shows that modulators are found in pure cone eyes, there is no evidence to exclude the possibility of modulators also being rods—in the anatomical sense.

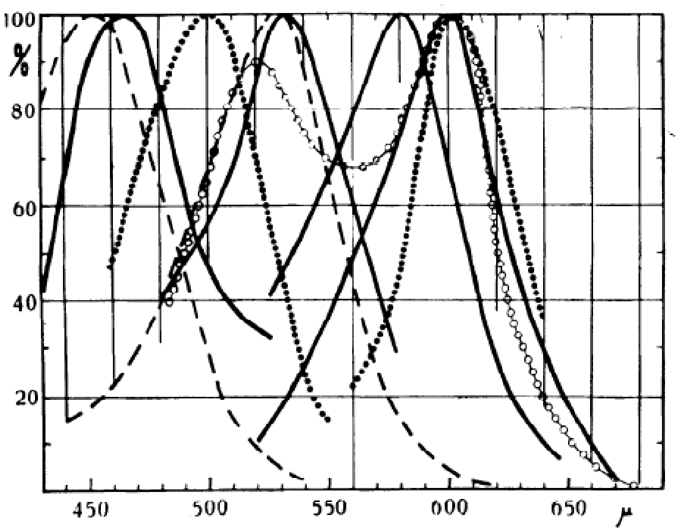

FIG. 2. Distribution of sensitivity of "modulator" elements from eyes of *rat* (dots), *guinea pig* (broken line), *frog* (line in full), and *snake* (line interrupted by circles). Note that a number of ordinates on either side of 0.560μ are drawn down to indicate "dominator" values. Spectrum of equal quantum intensity.

Statement of present problem. In the earlier work, summarized above, the study of the modulators was based on the chance of finding such relatively simple "colour units" and the experimental work was thus extremely tedious, though a necessary preliminary to any analysis of the mechanism of colour reception. It seemed desirable to minimize this element of chance and at the same time devise a method for answering a fundamental question: can the dominator possibly be regarded as the sum of a larger number of modulators? And, if so, what are the spectral properties of these modulators? The use of a mammalian retina (cat) will at the same time force those engaged in studying human colour vision to face a number of new facts.

Consider the situation created by the micro-electrode technique applied to the cat's retina, as schematically indicated in the diagram to the right in Fig. 3. Several receptors converge to form the element isolated by the microelectrode on the optic nerve, probably a much larger number than is indicated in the diagram. The eight rods are assumed to be receptors which in the dark adapted state are dominated by visual purple. After light adaptation they may or may not be above threshold. The two cone-like structures need not necessarily be cones, although some of them certainly are cones by the definition given above and because a dominator has been found in the cat's eye (10). In the fully dark adapted cat's retina visual purple dominates in the rods and gives them a high sensitivity to light such as no other structures possess. The large circles represent averages, based on 1326 readings with fully dark adapted eyes summarized in 179 determinations ultimately averaged to give these circles. As to details of technique see below.

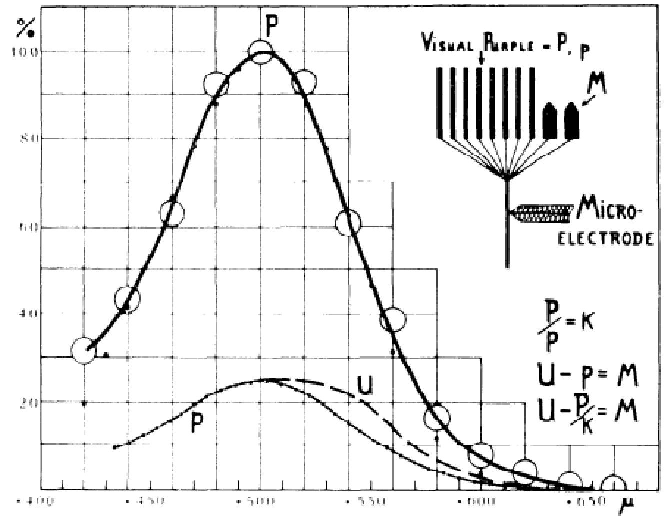

FIG. 3. Dark adapted cat. Large circles, averages for scotopic dominator. Small black circles, Lythgoe's corrected curve for visual purple absorption. As to significance of symbols and p- and U-curves, see text. Spectrum of equal quantum intensity.

Diagram to the right illustrates convergence element picked up by micro-electrode on the optic nerve.

The small black points are Lythgoe's (13) corrected values for visual purple absorption in solution. His corrected curve of 1937 is a little too low in the short wave-lengths, as proved by direct measurements of the photosensitivity of this substance by Schneider, Goodeve and Lythgoe (15). My curve is a little too high between 0.560 and 0.600μ, no doubt owing to the fact that in this region of low visual purple sensitivity the photopic dominator with maximum in 0.560μ has some slight influence on the experimental readings.

Let my curve for dark adapted elements be described by P, a function of wave-length, practically identical with visual purple photosensitivity. Now visual purple is a homogenous substance so that adaptation of the eye to any colour will reduce visual purple sensitivity by proportionate ordinates in all wave-lengths. Hence, if the converging receptors contained visual purple alone, red, green etc. adaptations would reduce the curve to p (point and broken line in Fig. 3) so that

$$\text{(i)}\ P/p = k$$

Since, however, the convergence element analyzed with the aid of the micro-electrode may contain other colour sensitive receptors, the curve P will, in point of fact, in many cases not be reduced by selective adaptation to p but to some other curve U (see Fig. 3). The same would happen if other colour sensitive substances were formed by illumination of visual purple. If this curve U contains modulators, the ordinates for the modulators M will be the difference between U and p, as clearly seen from the diagram, or

$$\text{(ii)}\ M = U - p$$

This also means that after selective adaptation p may be unknown and only U experimentally obtainable. It is therefore necessary to supplant p by P/k from equation (i). The final formula is thus

$$\text{(iii)}\ M = U - P/k.$$

U and P are experimental quantities, obtained respectively *before* and *after* selective adaptation of the eye. If k could be determined, equation (iii) could be solved and the modulators, if present, defined. Now it is possible to determine k by selecting for solution of equation (i) that region of the spectrum in which is found the largest drop in sensitivity from P (*before*) to p (*after* selective adaptation). This criterion means that in this region there was no other photosensitive substance than visual purple to resist selective adaptation. As a rule this spectral region lies where the letter p is placed in the diagram of Fig. 3. All quantities of equation (iii) are now defined and measurable and we can proceed to test by experimentation the arguments developed.

METHOD

For stimulation a special colorimeter was designed by Dr. W. D. Wright of the Imperial Institute of Science and Technology, London, on the principle of his own well-known colorimeter (18). The calculations and drawings for the instrument were made by Mr. G. C. Newton under whose direction the parts were assembled and sent over from London just before the war. It was set up here and calibrated by the physicist of this laboratory, Mr. K. T. Helme, Mag. Phil. A Phillips tungsten filament lamp, fed by high capacity storage batteries, was used at a colour temperature of 2800° K. In the previous work the Hilger spectrometer was employed but Wright's instrument with its double prisms and consequent greater purity extended the range within which measurements could be made further into the short wave-lengths. With the Hilger instrument stray light was considered to be a source of error beyond 0.450μ. On the other hand there was less energy available even in this large model Wright colorimeter so that it proved difficult to use anaesthetized animals which have raised thresholds of stimulation. But decerebrate cats with a few cc. of 20 per cent of urethane injected intraperitoneally turned out to be excellent preparations for the present purpose. The urethane was necessary to suppress minor movements of the animal or its eye.

The cornea was cut away, the lens removed and a platinum wire micro-electrode, covered with glass down to the tip, inserted. The animal was then left to dark adapt in its box for not less than half an hour and generally nearly an hour before the experiment started.

The discharge was led to cathode ray and loudspeaker in the usual manner. It has proved valuable to run the power stage to the loudspeaker slightly off the straight part of its characteristic curve. Thus, in experiments with less successful isolation of single spikes, only spikes above a certain size become audible. A sharp report is then heard at the threshold. The energy for a threshold response was determined from the calibrated wedge-filter combination used to adjust stimulus intensity.

RESULTS

Description of the experiment. In the beginning the P curve of the dark adapted eye was determined each time and the calculations made on the basis of this curve. But when a sufficient number of such curves had been assembled they were averaged into the curve P, shown in Fig. 3 and this average curve used. The first experiments were then recomputed in terms of the average curve for P so that the whole material now is uniformly treated. With this curve available it was merely necessary to determine its top (before coloured adaptation was begun) in order to calculate the constant k.

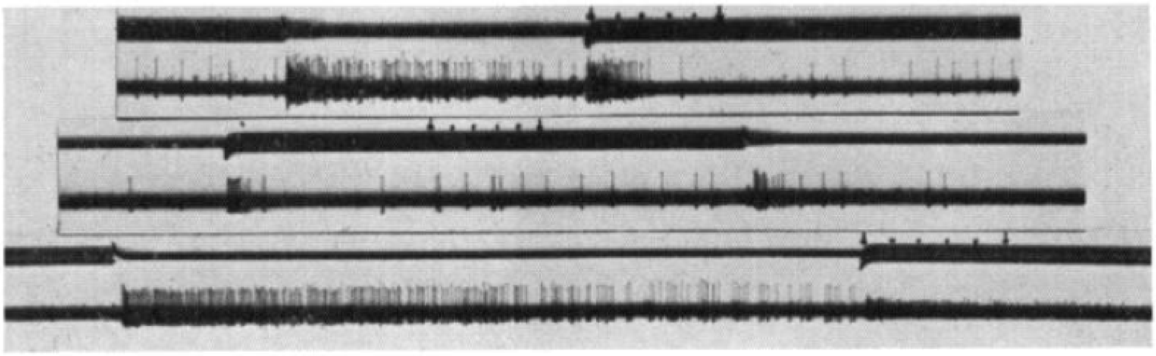

FIG. 4. Three different experiments showing different types of single spikes, the lowermost type lacking an off-effect. Illumination with adapting light the switch of which is connected to time marking beam so that the 50 period excursions are contracted during illumination. One second marked by dots in each record.

The Wright colorimeter contains a special switch by means of which another beam of light, the adapting beam, can be thrown in and out. This switch was connected to the second—timemarker—beam of the double ray cathode ray oscillograph. When, as in the examples shown in Fig. 4, the adapting beam was switched on, the time marker beam (above the spike record) was compressed and so signalled the change on the film. A second tungsten lamp (2800° K) in the beam of which could be placed Ilford Spectral filters served as adapting light. As to their extinction curves, see Wright (19). Thus the eye could be illuminated with red, green, blue etc. adapting light, this light be instantaneously interrupted, and the test light from the spectrum flashed in 3 sec. after interruption of coloured adaptation. This time was chosen in order to give the off-effect time to pass or to diminish in frequency (see Fig. 4) so as to make it possible to hear whether the test light caused a fresh discharge and thus was above the threshold. 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 after adaptation. Working through the spectrum in this manner the U curve was determined, always, of course, with a repeated control wavelength as a check on the general level of sensitivity. At least 5 uninterrupted minutes of coloured adaptation was allowed before the experiment was begun.

The coloured adaptation suppresses the sensitivity, by definition maximally k times, since $P/p = k$. Often k can be taken as an average for several wave-lengths, but nearly always 0.480μ will be found to be in the region where k is maximum. The values for k for a given coloured filter varied greatly from experiment to experiment. They do not depend merely upon the intensity of the coloured stimulus but also upon the state of the retina, how much decerebration has interfered with the animal (even though the carotid was left untied on the side used for experimentation), how much urethane it has been necessary to give in order to keep it quiet, etc. These values for k, when given below, are merely to be regarded as rough averages.

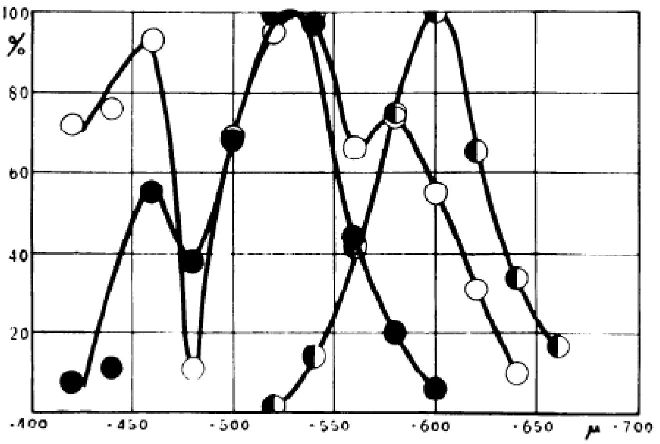

FIG. 5. Average effects of selective adaptation, as described in text. ● *Red* adaptation, ○ *green* adaptation, ◐ *blue* adaptation. Spectrum of equal energy.

Systematic determinations of the U curves was carried out in 34 experiments, 10 adaptations with each of the red, green and blue Ilford Spectral filters, 2 with the yellow and 2 with the violet Spectral filter. The number of observations totalled 3988, collected in 601 readings, meaning that each of the 601 points was based on, on an average, 6 to 7 observations around the threshold. The experiments with the yellow and violet filters were controls carried out merely in order to find out whether change of quality of the adapting light would add any new information to the results obtained in the 30 main series (red, blue, green). This was not the case and so presentation of the results will be limited to the U curves in the main series. In the work 60 per cent of the U curves were based on observations with isolated spikes such as those shown in Fig. 4, in the rest restricted activity was studied. In 29 per cent of the U series equation (iii) came out zero. This means that the micro-electrode had struck an element (or a small group of elements) connected to pure visual purple receptors, since it presupposes $U = p$. In such cases the M values oscillated around plus and minus.

Analysis of main series. When the modulator curve M had been determined from equation (iii) its maximum was given the value 100 and the values in the other wave-lengths in per cent of the maximum. For a general survey of the results Fig. 5 should be consulted. This does not show any individual modulators but the general effect of adaptation to red, green and blue light as gross averages of the M curves obtained, independently of where in the spectrum these modulators have been found. They therefore give an idea of the chance for a given point to reach a certain magnitude.

Blue adaptation gave the most uniform results and will be discussed first. In four cases, $U = p$ and hence equation (iii) was zero. In the six remaining cases red modulators were obtained as shown by the curve. The average value for k was 1500. *Red adaptation* suppressed red modulators, but green and blue modulators made themselves felt as shown by the curve. In one case $M = 0$. Average $k = 450$. Whereas blue and red adaptations suppressed the modulators in these regions, this was not the case with *green adaptation*. As shown by the curve there are humps in both the green, blue and red-yellow regions of the spectrum. In three cases $M = 0$. Average $k = 630$. This curve well illustrates one of the difficulties of the present method. When two adjacent modulators, such as the blue and green, are simultaneously present they probably overlap around 0.480–0.490μ but this region has to be used for determination of k, meaning that equation (iii) will be zero at this point, and so excessively low values in this region and steep slopes towards it are derived. The accuracy with which M curves can be obtained diminishes from red to blue end of the spectrum.

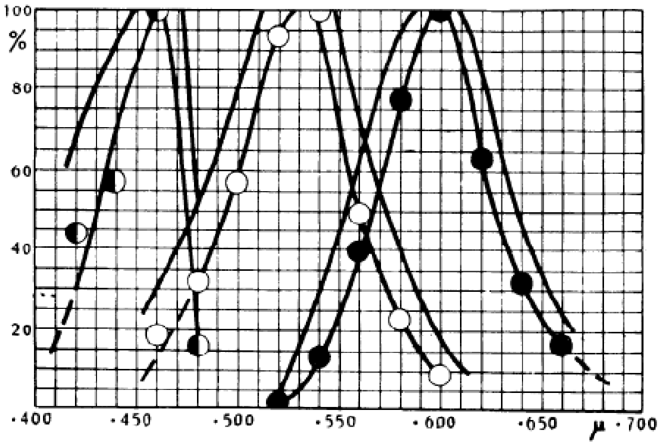

FIG. 6. Averages of individual modulators as obtained by selective adaptation. ● *Red* modulators, ○ *green* modulators, ◐ *blue* modulators. Outer contours indicate dispersion. See text. Spectrum of equal energy.

In Fig. 6 the results are presented in a different manner. The individual modulator curves have been averaged independently of the kind of selective adaptation by which they have been obtained. The circles marking the readings show the averages, the outer margins are drawn to indicate the dispersion (δ). It will be shown below why these lines are of special significance.

There were seven red modulators available, six referring to single spikes, six blue-adapted, one green-adapted. Average $k = 2000$. One modulator had its maximum in 0.580 (yellow), six in 0.600μ (red). It might be added that in a series, adapted to violet, a second yellow modulator with maximum in 0.580μ was obtained. A similar yellow modulator has also been found in the frog's eye (6). The individual red modulators were narrow bands. The steep fall of the red modulator curve towards the yellow may be accentuated by haemoglobin absorption in the retinal vessels.

The green modulator curve is an average of nine curves, five red-adapted, four green-adapted. Single spikes in 4 cases. Average $k = 430$. Five of these green modulators had their maxima in 0.540μ, two in 0.520μ, and two were of the narrow visual purple type with maximum in 0.500μ. All have been seen before in various animals. The maximum of the green modulators were thus spread out over a larger part of the spectrum than the other ones. But some of the individual modulators were broad and overlapped to a considerable degree.

The blue modulator curve is an average of eight curves, three red-adapted, five green-adapted, four of which were single spikes. Average $k = 690$. Only one of the blue modulators (not a single spike) was pure in the sense that there was no rise in the green region of the spectrum. One of the blue modulators had its maximum in 0.440μ, the other ones in 0.460μ. Thus, like the red modulators, their range of variation is relatively small, and the modulators were narrow even though their narrowness towards the long wave-lengths probably is overemphasized by the method of analysis.

The organization of colour reception in the mammalian retina on the basis of narrow modulator bands in three main regions of the spectrum thus again conforms to the principles discovered by the earlier "chance method" of testing the spectra of elements located in various eyes. And these new results have emerged from several stages of calculation (of energy, reciprocal of energy, determination of k, solution of equation $M = U - P/k$) which, until a large experience had been gathered, made it impossible to anticipate the final outcome of an experiment at the time of its performance.

Synthesis of the cat's dominator. In this work visual purple has not been completely removed by the relatively moderate adaptations to coloured lights. It has been removed by elimination with the aid of equation (iii). If light adaptation had been carried very far by using strong lights it is probable that the dominator would have been obtained despite selective adaptation. One has to count upon the probability that modulators by strong light adaptation may become synchronized into dominators, which may be single spikes given by modulator fibres co-operating as a unit. From my previous work (10) in which adaptation to 2.400 m.c. "white" light was used it is known that single spikes in the cat's eye give the dominator curves. In this eye it has a definite hump in 0.600μ, as shown by the circles of Fig. 7. These are the averages of 4 dominators in the light adapted cat's retina.

Let us assume that this dominator curve is the sum of a number of modulators, as these experiments make more than probable. The modulators of a given preferential region are spread over a spectral area of greater dimensions than the area covered by any individual modulator. The average modulators in Fig. 6 do not represent this area correctly. The average modulator is a mathematical concept but impulses are also delivered up the optic nerve by any modulator with its legs outside the average. Thus some of the green modulators with maxima from 0.500 to 0.540μ fall outside the average curve. The dispersion gives some idea of the extension of the outer margin of each of the three groups of modulators. In Fig. 8 are given curves indicating the *extreme* values obtained in these experiments for the three preferential regions. These values, on the other hand, include errors of measurement. But together with the curves of Fig. 6, showing the disper-

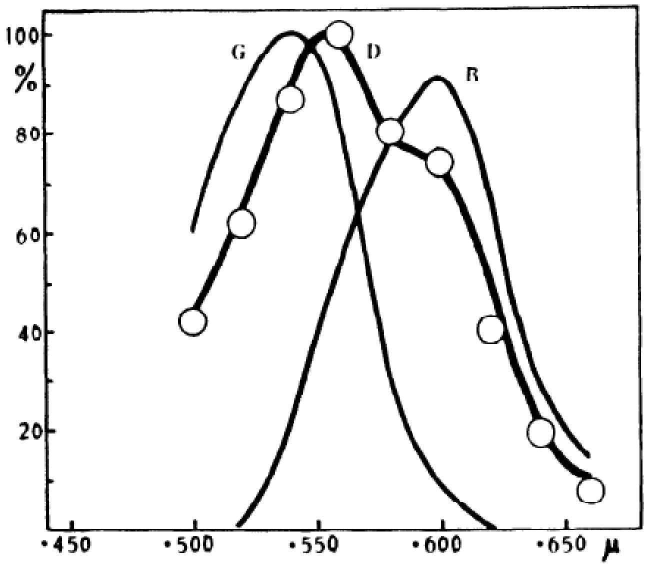

FIG. 7. Circles, averages of 4 photopic dominators of cat. Curve D in heavy lines, synthesis of dominator by adding modulators G and R and plotting their sum in per cent of maximum. Spectrum of equal energy.

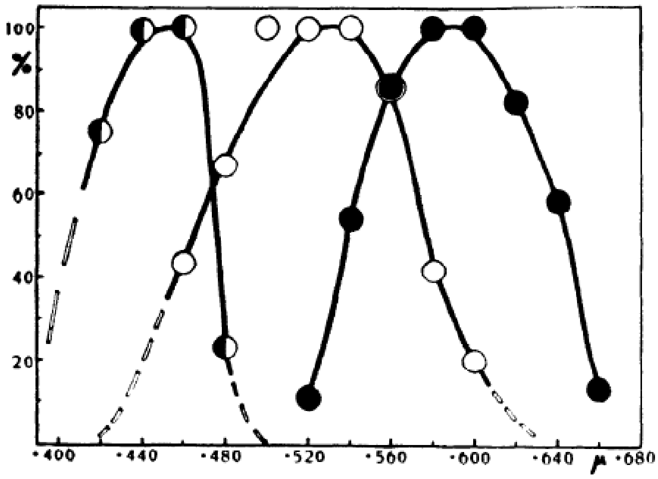

FIG. 8. Extreme values for modulators by selective adaptation as explained in text. Spectrum of equal energy.

sion, they should give some idea of the limits permitted in synthetizing dominators.

Now the dominators of the cat's eye refer to single spikes and thus to a relatively small number of receptors as compared, for instance, with the human photopic luminosity curve. In Fig. 7 the thick line, drawn through the dominator values, is the sum of the relatively narrow red and green curves shown by the thin lines, which still fall within the margin of dispersion of the average modulators of Fig. 6. The fit is quite satisfactory. The dominator (circles) was measured two years ago with the Hilger monochromator (10).

Hoping that an attempt to approximate the conditions for the microelectrode work by using small retinal stimuli would lead to the discovery of humps caused by modulators Wright (20) determined the human photopic luminosity curve with a foveal patch, 21 min. of arc (see also 17). He obtained the curve shown in Fig. 9. The large circles are taken from Fig. 7, showing the cat's dominator, the small black points are my synthesis of this dominator from the same figure. Again agreement is satisfactory. It is thus clear that there is no reason whatever to imagine the human retina to be something very different from other types of retinae. The organization of colour reception, just as the organization of kidney activity follows certain general laws. This truism is expressed here merely because objection has been raised that my results, after all, need not have much to do with human colour vision!

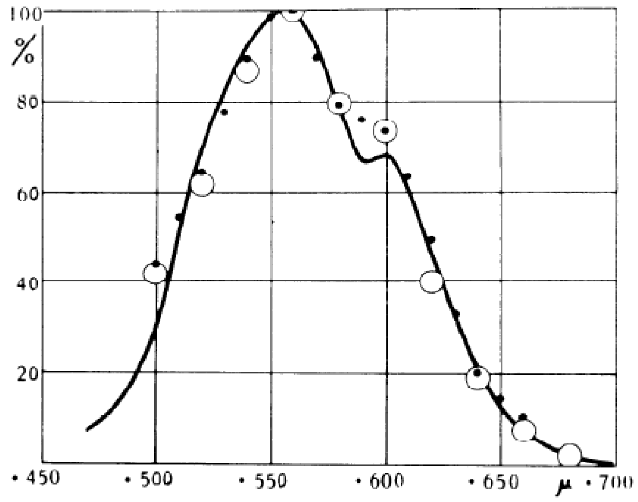

FIG. 9. Wright's (20) photopic luminosity curve for human eye with small foveal patch of 21 min. of arc. Circles, cat's photopic dominator from Fig. 7. Black dots, synthesis of cat's dominator from same figure. Spectrum of equal energy.

The fundamental sensation curves. It is evident that the greater the retinal area contributing to the response analyzed, the greater the chance for modulators placed on either side of the average to contribute to this response. The human photopic luminosity curve will therefore have to be synthetized on the basis of broader curves than the average modulators. This raises the old question of the three fundamental sensation curves of the trichromatic theory. These curves, when added, should give the photopic luminosity curve, practically identical with the average dominators of certain animals (see Fig. 1). It should now be evident that the fundamental sensation curves ("Gründempfindungen," "Elementarempfindungen") of the Young-Helmholtz theory cannot be identical with the modulators which are physiological units, and, probably also, photochemical units of colour reception. The modulators are too narrow for that. On the basis of the known modulators it would be necessary to develop a 6- or 7-colour theory, based on one red and one yellow modulator, two or three green modulators and two blue ones.

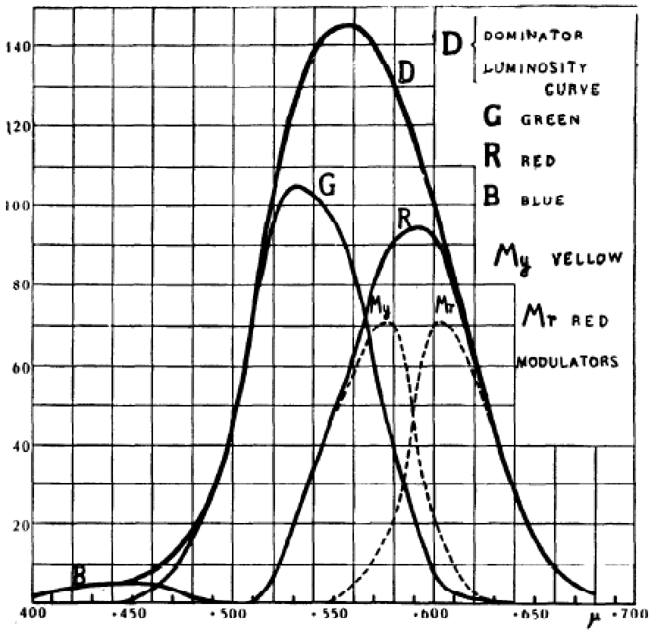

FIG. 10. Synthesis of human photopic luminosity curve (D), as determined on 125 observers by Coblentz and Emerson (1917), on the basis of three fundamental sensation curve, B, G and R, the latter composed of two modulators M_y and M_r adding up to R. Spectrum of equal energy.

But considering that the modulators are centred around three spectral regions it may be worth while to adhere to the structure of the trichromatic theory and find three fundamental sensation curves centred to these regions. In Fig. 10 an attempt has been made to split the human luminosity curve, as determined by Coblentz and Emerson (1), into three component sensation curves. The individual modulators are indicated in the figure for the red sensation curve. They give the *R* curve when added. Since the results probably will be tested by sensory experiments on colour matching, the coefficients used in constructing Fig. 10 have been given in Table 1.

It is hardly necessary to point out that these data can be combined into a number of slightly different synthetic pictures, for instance, a *G* curve somewhat broader towards the red side with the *R* curve somewhat narrower towards the green side in which case M_r would be higher than M_y and the R curve not necessarily smooth. Nevertheless, because of the limitations set by the modulators, it is clear that the data obtained serve to restrict to a considerable degree the limits within which such constructions can be made.

Table 1. Fundamental colour sensations of man

Wave-length	Red (R)	Green (G)	Blue (B)	Dominator (D)	Dominator in per cent	Coblentz & Emerson Luminosity curve
400	—	—	1.45	1.45	1.0	1.0
410	—	—	2.46	2.46	1.7	1.7
420	—	—	3.48	3.48	2.4	2.4
430	—	—	4.2	4.2	2.9	2.9
440	—	0.08	4.7	4.78	3.3	3.3
450	—	0.95	5.0	5.95	4.1	4.1
460	—	3.24	4.88	8.12	5.6	5.6
470	—	8.54	3.48	12.02	8.3	8.3
480	—	16.9	1.25	18.15	12.5	12.5
490	—	27.8	0.32	28.12	19.4	19.4
500	—	45.7	0.10	45.8	31.6	31.6
510	0.5	72.5	—	73	50.3	50.3
520	7.0	96	—	103	71.0	71.0
530	20	105	—	125	86.2	86.2
540	34	102	—	138	95.2	95.4
550	48	96	—	144	99.4	99.4
560	63	82	—	145	100	99.8
570	81	59	—	140	96.5	96.7
580	91	39	—	130	89.7	89.8
590	94	22	—	116	80.0	80.0
600	92	8	—	100	69.0	68.7
610	78	3	—	81	55.9	55.7
620	61	1	—	62	42.7	42.7
630	43	0.5	—	43.5	30.0	30.2
640	28	0.05	—	28.1	19.4	19.4
650	16.7	—	—	16.7	11.5	11.5
660	9.36	—	—	9.36	6.45	6.45
670	4.9	—	—	4.9	3.38	3.38
680	2.58	—	—	2.58	1.78	1.78

DISCUSSION

The attempts to describe the fundamental sensation curves, from Maxwell onwards, have recently been summarized by Walters (16), who himself has contributed an analysis by developing Wright's method of selective adaptation. Of all curves, hitherto published, those of Walters are in best agreement with my own. He has not given the blue end for which both electro-physiological and sensory data are less reliable than elsewhere, when regarded from a strictly quantitative standpoint.

It is to be noted that the trichromatic theory is a diagrammatic presentation of colour vision, based on colour matching, and that *fundamental sensation curves cannot be shown to exist,* except as mathematical entities. The message to the brain, as picked up by micro-electrodes on the optic nerve, is composed of modulators and dominators, the former being the units of wave-length reception. During several years of analysis of colour reception I have never seen curves that could be described as equivalents of the fundamental sensation curves. They are theoretical postulates which can merely be satisfied by adding modulators within the three preferential regions. The details of the mechanism of colour reception must therefore be described in terms of modulators and dominators.

From this point of view colour discrimination can be considered, as illustrated in Fig. 11 from the work of Wright and Pitt (21). This function is optimal in 0.580–0.600μ where the two red modulators, the red proper and the yellow one overlap (in Fig. 10 in 0.590μ). It is quite good in the green in which the individual modulators are broader and less well separated from each other. There is a second optimum in 0.480–0.510μ where the narrow visual purple modulator (green), the yellow modulator and the blue modulator arise and partly intersect. The blue modulator may contribute more to this region than is indicated in the diagram. Finally there is a third, lesser optimum between 0.450 and 0.440μ, suggesting, as did my experiments, that two blue modulators overlap in this region. One of them probably corresponds to the sensation of violet (the modulator with maximum in 0.440μ). In fact the third optimum postulates a violet modulator in the human eye.

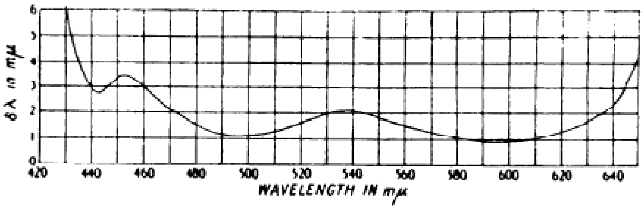

FIG. 11. Human colour discrimination, as determined by Wright and Pitt (21).

Individual modulators thus provide the cue for colour discrimination. They occur in different proportions in different retinae and thus, even in man, account for variations in the colour sense, from anomalies to complete colour blindness (11). It is generally stated that all colours can be mixed by a match of three primaries, but this is not strictly true. The matches in certain regions are and will always remain approximations. The reason for this is that nature uses, at least, 6 or 7 primaries and thus achieves perfection.

In certain *functional units of reception* several receptors of modulator type are combined so as to converge into an element giving the dominator distribution of sensitivity. This unit covers too wide an area in the spectrum for colour discrimation and can only correspond to the sensation of white, as given also by the similar photopic luminosity curve. Elsewhere (11) it has been pointed out that the existence of a functional unit corresponding to a sensation of white explains a number of difficulties facing the theories of colour vision. The separate existence of this functional unit also explains the typical cases of red-green colour blindness (protanopes, deuteranopes) in which the sensation of white is retained despite absence or diminished number of certain modulators with individual paths to the brain. The modulators may combine into slightly different dominators, thus explaining the difference between protanopic and deuteranopic luminosity curves. Also in diseases affecting colour vision the white sensation is generally retained despite absence of colour sense so that it must be concluded that the individual modulator paths are more sensitive to disturbing agents than the dominator paths. A simple explanation, supported by electrophysiological evidence, would be that there is a much greater number of dominator elements than of the individual, isolated modulator elements, necessary for discrimination.

Application of the dominator-modulator concept to the problems of colour vision thus involves a theoretical structure which is not identical with that of the trichromatic theory. The latter is dealing with gross averages, the dominator-modulator theory with the units of colour reception discharging to the brain. But the location of the modulators to three preferential regions of the spectrum makes it possible to give a good approximation to a theory by using three fundamental sensation curves, as in the diagram of Fig. 10.

The physiological mechanisms of wave length discrimination of the eye and the ear (2) have now been shown to be organized on the same principles. In both cases the micro-electrode technique has been used for picking up the discharge in the corresponding nerves. Quality (colour, pitch) is a kind of "local sign," something connected to "place," a certain receptor joined to a fixed path so that probably the discharge ultimately is landed in a fixed place in the center.

SUMMARY

Determinations of the spectral sensitivity of fibres, isolated in the cat's optic nerve with the aid of micro-electrodes, have been made during selective adaptation of the retina with red, blue and green lights.

The adapting light suppresses sensitivity in its own spectral range and so facilitates discovery of units stimulated by other parts of the spectrum.

Such units of colour reception, called *modulators*, are found in three preferential regions, 0.600–0.580μ (red-yellow), 0.540–0.500μ (green), 0.460–0.440μ (blue-violet).

The modulators are narrow bands of sensitivity, especially narrow at the two ends of the spectrum. There are two typical red modulators with maxima in respectively 0.600μ (red) and 0.580μ (yellow), three overlapping green modulators with maxima in 0.540, 0.520, or 0.500μ, the latter a narrow visual purple curve. This may be lacking in pure cone eyes. The greatest number of green modulators had their maxima about 0.520–0.540μ.

There are finally two blue modulators with maxima in 0.460μ (blue) or 0.440μ (violet).

It is shown that detailed understanding of the mechanism of colour discrimination requires, at least, a 6- or 7-colour theory in terms of these modulators but that the modulators in the three preferential regions can be averaged into three "fundamental sensation curves" such as postulated by the trichromatic theory. Such curves have never been found in the microelectrode experiments and can only have a limited applicability in analyzing phenomena of colour vision.

A tentative set of "fundamental sensation curves," located to the preferential regions of the modulators, is given in the paper.

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