COLOR VISION: THE APPROACH THROUGH INCREMENT-THRESHOLD SENSITIVITY

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I am most sensible of the honor of addressing this meeting and of the generosity of the National Academy of Sciences in bringing me here as their guest. The invitation to contribute to the present symposium came just as I had finished a rather elaborate study of the color-matching properties of the average observer. However, that work I believe to be of more colorimetric interest, and I have elected, therefore, to deal with a quite different approach to color vision by a method which does not rest on actual color-matching—the method of increment thresholds.

Consider, to take first the simplest case, a subject whose eyes are fully adapted to a completely dark field. The increment threshold is then just the smallest perceptible quantity of a certain test light which is applied at a particular part of the visual field. For convenience, I use the expression "smallest perceptible quantity," although, of course, thresholds are definable only statistically, for example as critical values of the stimulus variable at which the chance of a perception equals 50 per cent. In the general case, the increment threshold is still the smallest perceptible quantity of a certain test light, but now this is added to another stimulus—the conditioning stimulus—which consists of any distribution of brightness and color to which we may choose to expose the eye. The conditioning stimulus need not be an unvarying one: the increment threshold is, in fact, often measured while the eye is adapting itself to a change from one constant stimulus to another constant stimulus, the whole spatial and temporal pattern of stimulation being considered to form the conditioning stimulus. The increment threshold (or, better, its reciprocal, the threshold sensitivity) is a measure of visual sensitivity which can be varied in different ways to bring out particular properties of the visual response system. We may, for example, vary the angular size and exposure time of the test stimulus, to determine how well the visual system integrates over area and over time. Most important, we may change the spectral composition of the test stimulus, in order to determine the spectral sensitivities that are active in the response system. So far, only changes in the parameters of the test stimulus have been mentioned. In addition, any number of different conditioning stimuli may be used. However, there is evidence that the modifications of the increment threshold by more complex patterns of brightness and color are similar to those obtained with a very simple pattern, namely, a uniform stimulus which extends over and around the area of the field where the test stimulus is applied. We should regard the action of a more stimulus, including stimuli applied at some distance from the test area, as *equivalent* to that of a suitably chosen uniform stimulus of the kind mentioned if, for all possible test stimuli (of various sizes, colors, exposure times, etc.), the observed increment threshold was the same for the two conditions. The equivalence is probably not generally complete, but it has been found to hold approximately in some cases, and we are justified in concentrating, in the first instance, on the simple stimulus pattern. This has the advantage that much

bigger effects on the increment threshold can be obtained with "covering fields" than with conditioning stimuli confined to the surrounding retina.

For probing the color mechanisms of the eye, the method that has been extensively used is to apply, in flashes, a small monochromatic test stimulus of wave length λ to a uniform monochromatic conditioning field of wave length μ and intensity M_μ extending over the test area (the two-color threshold technique). Most work has been done for the case when the eye is fully adapted to the conditioning field, although several recent investigations (particularly by Boynton[1]) as well as some earlier ones have considered non-equilibrium situations. If all the other possible experimental variables (size and exposure time of test stimulus, angles of incidence on the retina of test, and conditioning stimuli, etc.) are kept constant, the increment threshold N_λ, i.e., the smallest perceptible intensity of the test stimulus, will be a function $f(\lambda, \mu, M_\mu)$ of the three variables λ, μ, M_μ. The function f is certainly not simple, and its determination for the whole range of possible values of the three variables is a considerable undertaking. Some progress has been made, however, which suggests that the function may be put in a form involving separate terms identifiable, on certain reasonable assumptions, with the contributions to the increment threshold of component visual mechanisms having different spectral sensitivities and some other differences in their properties. The possibility of "separating" the function f in this way does not, of course, prove that there exist in the eye separate structures and processes corresponding to the different terms. The psychophysical analysis has to be related to objective observations on the visual pigments, on the types of end-organ and the ramifications of the nerve pathways through the higher neurons, on the electrophysiological response, etc., before the "component mechanisms" can begin to acquire a real existence. Despite the wealth of information on the visual system generally that is provided by these objective techniques, there has until recently been little which could be applied directly to the psychophysical data of color vision. The important new development is the objective detection and measurement of bleachable visual pigments, other than rhodopsin, in the living human eye (Rushton).[2] Some repercussions of this work on the increment-threshold analysis will be mentioned later.

The guiding principle in interpreting increment thresholds is that in the retinal area on which the test stimulus is imaged there are several component mechanisms, any one of which may be the means of triggering off the response "seen" when the test flash is applied. Each component mechanism is conceived of as an association of a selected proportion of the end-organs (rods and cones) in the area, the association being effected somewhere in the neural system through which the nervous activity, initiated by light absorption in the end-organs, is transmitted to the brain and finally to the effector nerves of the external response. It is not assumed that the end-organs of a component mechanism are necessarily all of the same kind or contain just one photopigment, nor that end-organs belong exclusively to one component mechanism, but the mechanisms are assumed to have sufficient independence for the idea of a particular component mechanism acting alone to have a meaning. It is assumed, in fact, that the response of all but one component mechanism could be blocked (ideally; it may not be practicable to do

it), leaving the remaining mechanism to respond in its normal way. For a given test stimulus and given conditioning stimulus, the observed increment threshold in the retinal area is assumed to depend only on the respective increment thresholds of the component mechanisms that would be observed under the same conditions if they were acting alone. In particular, it is assumed that the observed increment threshold will not exceed any of the component increment thresholds and will generally approximate to the smallest of these. Finally, each component mechanism is assumed to have a characteristic relative spectral sensitivity function, so that the effect on the mechanism of an intensity I_1 (in energy units) of one wave length λ_1, forming the whole or part of the test or conditioning stimulus, is just the same as that of an intensity I_2 of any other wave length λ_2 that may be substituted for it, provided that I_1 and I_2 are in the inverse ratio of the relative spectral sensitivity values at these wave lengths.

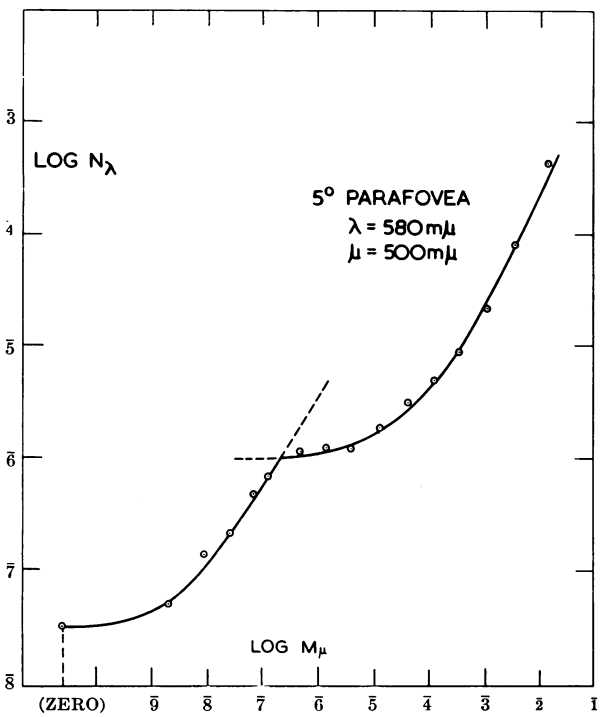

FIG. 1.—Increment threshold, $N\lambda$, versus field intensity, M_μ, for 5°′ extrafoveal vision. Test stimulus: 1°, 0.06 sec. Subject: W. S. S. ($N\lambda$ and M_μ expressed in erg sec^{-1} [deg. of arc] $^{-2}$.)

The analysis of increment-threshold measurements on the above lines may be illustrated by examining briefly the case of extrafoveal vision, for which there is the ample evidence of the duplicity theory of vision for the operation, in some sense, of distinct rod and cone mechanisms. Figure 1 gives an example of a so-called threshold-versus-intensity (t.v.i.) curve, in which the logarithm of the increment threshold is plotted against the logarithm of the uniform conditioning stimulus for a particular pair of test and conditioning wave lengths, λ = 580 mμ, μ = 500 mμ. In this case the test stimulus (1°, 0.06 sec.) was imaged 5° from the

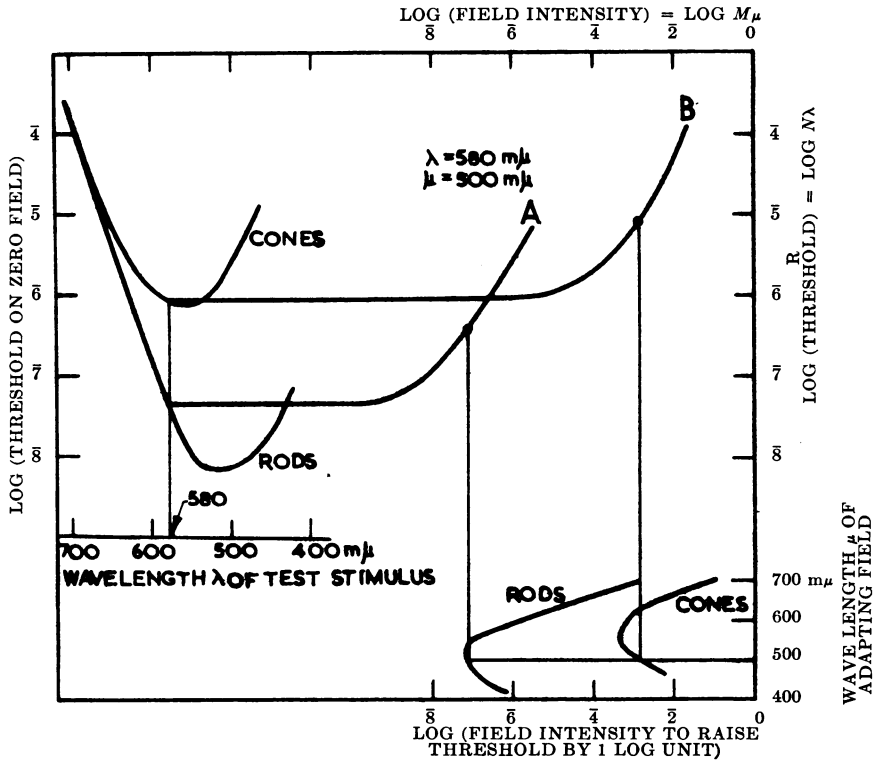

FIG. 2.—Diagram illustrating how t.v.i. curves like that of Fig. 1 result from the t.v.i. curves of two component mechanisms, A (rod) and B (cone), whose positions with respect to the axes of log $N\lambda$ and log M_μ for any test and field wave lengths λ and μ are determined by the respective spectral sensitivity curves of the mechanisms shown in the auxiliary diagrams.

fovea. Figure 2 shows diagrammatically the tentative interpretation of the curve of Figure 1 in terms of two component mechanisms of the kind contemplated above.[3] Curves A and B (Fig. 2) represent, respectively, the t.v.i. curves assumed for the A (rod) and B (cone) component mechanisms when acting alone. At each field intensity the observed increment threshold is put equal to the lower of the values appropriate to the A and B curves. The crucial question now is What happens if λ and μ are changed? According to the assumption about the spectral sensitivity curve of a component mechanism, a change in λ, keeping μ constant, should merely displace the curves A and B—without change of shape—parallel to the ordinate axis, by amounts determined by their respective relative spectral sensitivities. A change in μ, keeping λ constant, should, on the other hand, displace the curves parallel to the axis of abscissae by amounts also fixed by the respective spectral sensitivity curves. The spectral sensitivity curves are also shown in the diagram, and it is easy to visualize the effects of changing λ and μ. The experimental t.v.i. curves obtained for various combinations of test and field wave lengths show that the branch of the curve attributed to the A mechanism conforms satisfactorily to these *displacement rules*, the displacements parallel to the two axes being controlled by the same spectral sensitivity curve. For the B branch, how-

ever, the displacement rules fail to hold, and it is impossible to represent the increment threshold for extrafoveal vision as arising from just two component mechanisms in the way proposed. The next step would be to see whether the B branch could be represented as the resultant of two or more branches, but this is difficult because the form of the B branch for many of the interesting (λ, μ) combinations is not accessible to observation: it is masked by the A branch, which has the lower threshold.

We now examine the various component mechanisms which we are led to postulate for the fovea, the area of the retina where color discrimination is most highly developed and where the absence of rod end-organs eliminates (probably) any participation of a "rod" component mechanism. (This last simplification is not quite a certain a priori, as the adapting field extends into the retinal area containing rods, but it seems to be so in fact.) Consider, first, the t.v.i. curves obtained with test stimuli of short wave length ($\lambda < 510$ mμ) and with conditioning stimuli of medium or long wave length ($\mu > 520$ mμ). These show a division into two branches ($\mu <$ about 560 mμ) or of three branches ($\mu > 560$ mμ), an example of the latter being given in Figure 3. The three branches are provisionally ascribed to three component mechanisms, denoted by the neutral symbols π_4, π_1, π_3 marked in the figure. The changes in the t.v.i. curve when λ and μ are altered establish that the branch π_1 obeys the displacement rules. But if λ becomes too large or μ too small, the π_1 branch is masked by the π_4 branch; thus the displacements observable by changing λ and μ correspond to non-overlapping spectral ranges of the spectral sensitivity curve of the mechanism, and it is not possible immediately to check that a single spectral sensitivity curve determines displacement of both kinds. The difficulty can be largely overcome by the "auxiliary field method." In this we use as conditioning stimulus a mixture of a fixed auxiliary field of long wave length sufficiently intense to bring the increment threshold to the π_1 branch of the curve, and a main field of wave length μ, which may be as short as desired. The comparative effects of main fields of different wave length in moving the increment threshold higher up the π_1 branch can then be determined.[4] It is found that in the overlapping region ($\lambda < 500$ mμ) the λ and μ displacements correspond to a common relative spectral sensitivity curve and that this curve has a maximum at approximately 440 mμ (energy expressed in quantum units). The evidence on the π_3 branch is more limited because of the difficulty in obtaining the very high field intensities needed to reach it. The results again indicate a branch obeying approximately the displacement rules and with consistent λ and μ displacements in the overlap region

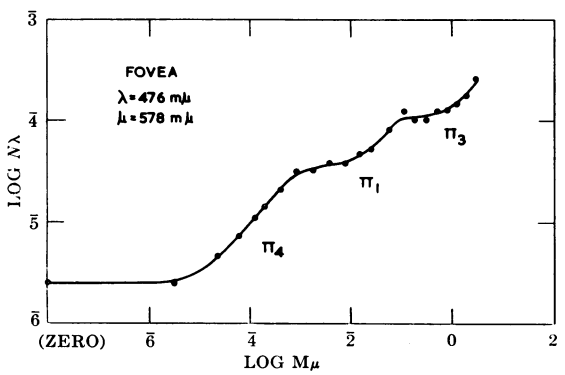

FIG. 3.—Foveal t.v.i. curve. Test stimulus: 1°, 0.2 sec. Subject: E. K. ($N\lambda$ and $M\mu$ in erg sec^{-1} [deg. of arc]$^{-2}$.)

($\lambda < 500$ mμ). As can be seen in Figure 4, the spectral sensitivities of the π_1 and π_3 component mechanisms (derived from μ-variation displacements) agree closely in shape in the region of their maxima ($\lambda < 500$ mμ) and differ only at long wave lengths. (The curves of Figure 4 and later figures refer to the mean results of the same four subjects.) But for test stimuli in the short-wave region the two mechanisms still differ in their absolute thresholds, i.e., the values to which their increment thresholds tend as the conditioning stimulus is reduced to zero: the absolute threshold for π_3 is about four times that for π_1. It was unexpected to find two component mechanisms with maximal and closely similar spectral sensitivities in the blue. But there is also some evidence of a third component mechanism (π_2) with maximal sensitivity in the same spectral region. This is indicated by a breakdown in the displacement rules for the branch π_4 when, for conditioning fields of long wave length (e.g., 600 mμ), the wave length of the test stimulus is reduced below about 460 mμ. The discrepancy would be consistent with a π_2 mechanism with the spectral sensitivity curve (by the μ-variation method) in the range 510–700 mμ, as shown in Figure 4. For $\mu <$ 510 mμ, the curve must lie above the points of the arrows shown in the figure. Unfortunately, the auxiliary field device is not applicable in this case, and the form of the curve has not been determined in the neighborhood of the maximum, although the latter can hardly lie outside the range 440–480 mμ.

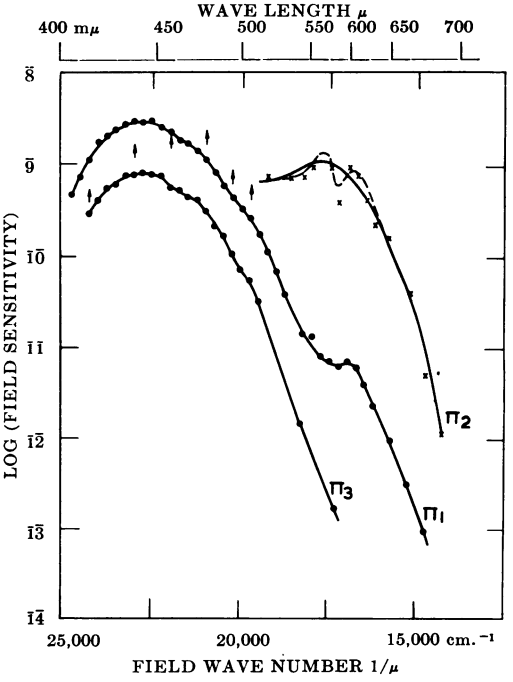

FIG. 4.—Field spectral sensitivity of foveal cone mechanisms π_1, π_2, and π_3. Field sensitivity is defined as the reciprocal of the field intensity in quanta sec^{-1} (deg. of arc)$^{-2}$ required to raise the increment threshold of the mechanism to ten times its zero-field value. For $\lambda < 510$ mμ, the arrow points indicate values below which the undetermined part of the π_2 curve cannot fall. Means for four subjects, π_1 and π_3; for three subjects, π_2.

As the wave length λ of the test stimulus is increased above about 450 mμ, the branches of the t.v.i. curve associated with mechanisms having maximal sensitivity in the blue move upward with respect to the π_4 branch, and for λ greater than 520 mμ they move completely above it and are inaccessible to measurement, whatever the wave length of the conditioning stimulus. For these test stimuli of longer wave length, the π_4 branch does not obey the displacement rules, although the well-marked transitions obtained at shorter wave lengths are not in evidence. It was originally thought that the results would be explained by admitting that there were, in fact, two branches—a π_4 and a π_5 branch—with associated spectral sensitivities not very widely separated along the spectrum, so that sharp transitions from one

branch to the other would not be expected. Further measurements indicated, however, that, while this explanation is fairly satisfactory if attention is confined to conditioning stimuli below about 150 trolands, it leads to discrepancies with observations made at higher intensities. The spectral sensitivities of π_4 and π_5 derived by the μ-variation method from measurements in the lower-intensity range are shown in Figure 5. These sensitivities, like those of Figure 4, represent at each wave length the reciprocal of the field intensity (in quantum units) required to raise the increment threshold of the particular mechanism to ten times its zero-field value. If we also know the shape of the branch of the t.v.i. curve appropriate to the mechanism and the absolute threshold of the mechanism for some test wave length, we can derive the curve showing the variation of the increment threshold or its reciprocal, the threshold sensitivity, with test wave length for any intensity and wave length of the field. This calculation has been made in Figure 6 for the five component mechanisms π_1–π_5 for the case of a field of wave length 667 mμ and intensity 29 trolands. The observed threshold sensitivity at each test wave length should equal approximately the highest of the component threshold sensitivities, and it is apparent that only π_4 and π_5 are concerned in this instance. The circle points represent the directly observed threshold sensitivities and are in satisfactory agreement with the prediction. The comparison of the predicted and observed curves when the field intensity is raised by a factor of nearly 100 is shown in Figure 7. The discrepancy is not only in the absolute values (which might arise from uncertainty in the shape of the π_4 branch) but also in the shape of the observed curve in the wave-length range where it should be at least parallel to π_4. The indication is that, with a high-intensity red field, the π_4 mechanism is relatively more sensitive on the short-wave side of about 580 mμ than the calculation treating π_4 as a single component mechanism with its low-intensity properties would predict. This deviation is independently confirmed by t.v.i. curves taken to high intensities. An analogous, although smaller, effect for π_5 is shown by observations with low- and high-intensity green conditioning fields (Figs. 8 and 9) and is again confirmed independently by t.v.i. curves. The π_5 mechanism under high green stimulation is relatively more sensitive on the long-wave side of about 580 mμ than

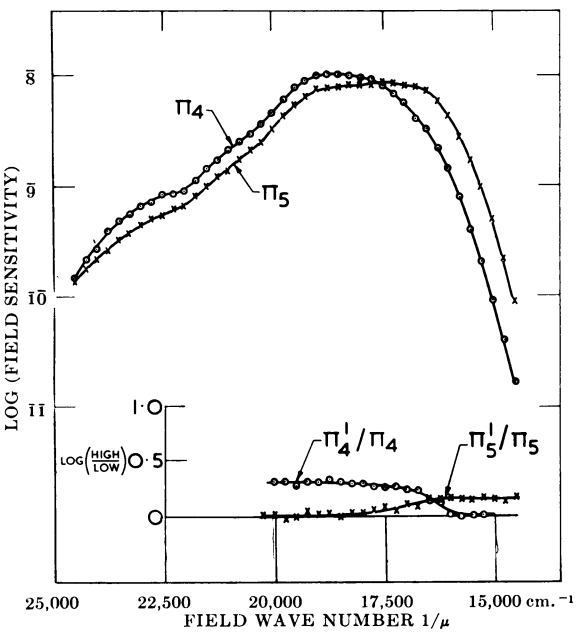

FIG. 5.—Field spectral sensitivities as in Fig. 4 for cone mechanisms π_4 and π_5. The inset diagram shows the log (ratio of the sensitivities: high-intensity level/low-intensity level) for the π_4 and π_5 mechanisms. Means for four subjects.

the calculation treating π_5 as a single component mechanism with its low-intensity properties would predict. Insufficient is yet known of these deviations from single component properties of π_4 and π_5 to say whether they could be explained by assuming additional component mechanisms. For the present, it is advisable merely to recognize modified high-intensity conditions of these mechanisms, denoted by π_4' and π_5', respectively. The differences in spectral sensitivity in the low- and high-intensity conditions of π_4 or π_5 are not large compared with the differences between π_4 and π_5. A first determination of the ratio of the high- to the low-intensity spectral sensitivity is shown in the inset diagram of Figure 5. A tentative deduction

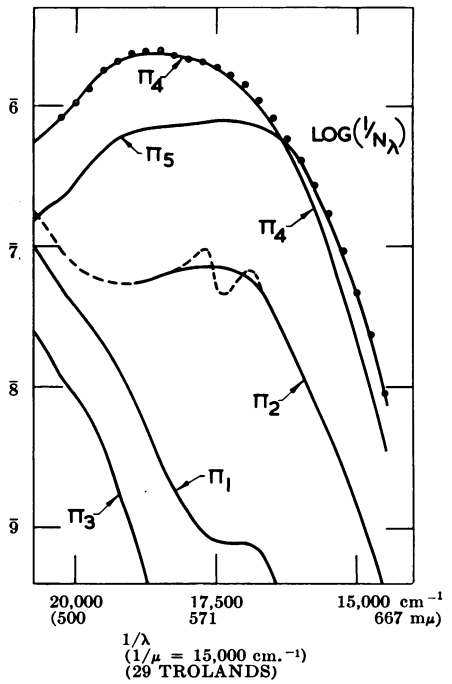

Fig. 6.—*Points:* Increment-threshold sensitivity by $1/N\lambda$ versus test stimulus wave number 15,000 cm^{-1} (wave length 667 mμ) and intensity 29 trolands. Test stimulus: 1°, 0.2 sec. Means of four subjects. *Curves:* predicted threshold sensitivity versus wave-number curves at this conditioning stimulus for the component mechanisms π_1–π_5.

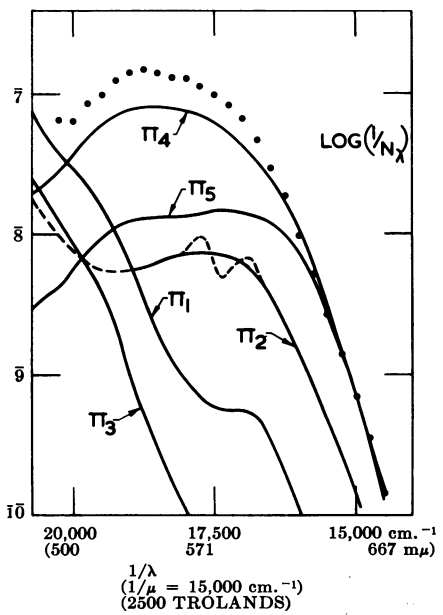

FIG. 7.—As for Fig. 6, but for conditioning field of intensity 2,500 trolands.

from other observations is that the transitions $\pi_4 \rightarrow \pi_4'$ and $\pi_5 \rightarrow \pi_5'$ occur in a range of conditioning intensities of the order of 1 log unit centered on an intensity of about 300 trolands.

The scheme of component visual mechanisms indicated by increment-threshold analysis is summarized in Table 1. The Fechner fraction quoted in the final column is defined as the ratio of the increment threshold to the field intensity when the conditioning field has the same color as the test stimulus ($\lambda = \mu$) and the increment threshold is raised by it to ten times the zero-field value. There are interesting differences between the Fechner fractions of different component mecha-

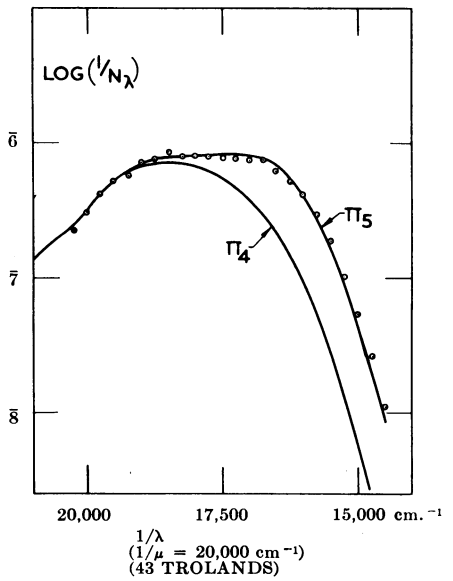

FIG. 8.—As for Fig. 6 but for conditioning field of wave number 20,000 cm^{-1} (wave length 500 mμ) and intensity 43 trolands.

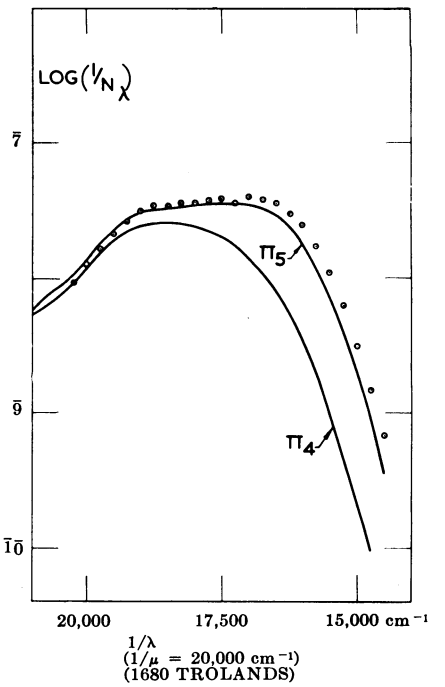

FIG. 9.—As for Fig. 8 but for conditioning field of intensity 1,680 trolands.

nisms: the "blue" cone mechanisms have values four to five times those for the "green" as "red" cone mechanisms. In applying the present ideas of component mechanisms to the explanation of other psychophysical measurements on color discrimination and brightness matching, this difference plays an important part: it corresponds to the small contribution to luminance of short-wave stimuli, despite their strong coloring value.

TABLE 1

Mechanism	Symbol	Remarks	Wave Length of Maximal Sensitivity (mμ)	Fechner Fraction (1°, 0.2 Sec. Test Stimulus)
Rod	π_0	Absent at the fovea	503	(30)
"Blue" cone	π_1	Ratio of blue to yellow sensitivity (440/590) approx. 2.6 log units	440	8.7
	π_2	Ratio of blue to yellow sensitivity (440/590) order of 1 log unit	? (Between 440 and 480 mμ)	? (Probably as for π_1 and π_3)
	π_3	Ratio of blue to yellow sensitivity (440/590) approx. 4.0 log units	440	8.7
"Green" cone	π_4		540	1.9
	π_4'	Modified high-intensity state	540	...
"Red" cone	π_5		575 (very flat max.)	1.8
	π_5'	Modified high-intensity state	587	...

The discussion so far has been concerned with the breakdown of the three-variable function $f(\lambda, \mu, M_\mu)$, all the parameters of the test stimulus other than color being assumed constant. If one of these is allowed to vary, the effects on the different branches of the t.v.i. curves can be compared, and more information on the properties of the component mechanisms can be obtained. For example, it is known that the response of the cone end-organs of the retina is highly directional, and, by determining the change in increment threshold on altering the angle of incidence on the retina of the rays forming the test stimulus (keeping, of course, the retinal area stimulated the same), differences in the directional properties of different mechanisms can be studied. The differential effects are small, and more measurements are needed, but the early work indicates that π_1 is more directional in its reponse than π_4, that π_4 is more directional than π_5 for stimuli in the green and yellow, but that this position is reversed for red stimuli. Changes in the relative response of different mechanisms as the angle of incidence is varied may be expected to produce changes of color even of monochromatic stimuli. The small changes, observed are, in fact, in general agreement with the relative directional properties of the mechanisms obtained by the threshold observations.

Two outstanding questions are: (*a*) What is the relation of the increment-threshold mechanisms to the three processes of trichromatic color-matching? and (*b*) Do the spectral sensitivities of the component mechanisms represent photosensitivities of visual pigments? We limit ourselves to foveal vision, so that the complication of the rod mechanism does not arise. The two questions are closely related, as the three small-field color-matching functions which sum up the color-matching properties of the foveal retina (conditions of very high intensity excluded) are almost certainly linear combinations of the spectral photosensitivities of three visual pigments, although the coefficients in these combinations are not determinable by straightforward color-matching measurements. Thus, if the spectral sensitivity of a component mechanism could be represented as a linear combination of the color-matching functions, it would also be a linear combination of the pigment photosensitivities. This would indicate that the end-organs of the mechanism contained the pigments represented in the linear combination (i.e., those having non-zero coefficients) and that the effects of light absorption in these different pigments added up linearly. Electrophysiological evidence makes it unlikely that this last state of affairs could come about unless all end-organs of the mechanism contained the pigments in a mixture of the same composition, including the specially simple case of a "mixture" comprising just one pigment. The rigorous application of the argument is hampered by the difficulty of obtaining "hard" data from increment-threshold measurements. However, tests made on the mean spectral sensitivity curves (Figs. 4, 5) indicate that π_4 or π_4' can be expressed fairly well as linear combinations of the small-field color-matching functions. For π_5 the linear representation is less satisfactory, particularly for the high-intensity condition π_5'. For π_3 and for π_1 in the main (short-wave) region of the curve, a linear representation is acceptable, and even with the inclusion of the long-wave lobe on the π_1 sensitivity curve it could not certainly be excluded. The actual shapes of the sensitivity curves also have a bearing here. The spectral absorption and spectral photosensitivity curves that have now been obtained for many visual pigments from animal retinas, by measurements on retinal extracts or complete excised

retinas, differ little in shape from the absorption curve for the pigment of rod vision, rhodopsin; to a first approximation, they correspond to the rhodopsin curve (log absorption factor against wave number) displaced along the wave-number axis so that its maximum occurs at the appropriate position. Before physical absorption and photosensitivity curves can be compared with psychophysical sensitivity curves, the latter must be corrected for the selective light losses in the eye that precede the actual absorption by the photosensitive pigment. The correction is uncertain in the violet but is probably not seriously in error in the blue and green: it is negligible at longer wave lengths. It is found that the corrected π_4, π_4', and π_3 spectral sensitivity curves and the π_1 curve ignoring the long-wave lobe are fairly well represented by displaced rhodopsin absorption curves (Fig. 10: the broken lines are, in fact, the corrected spectral sensitivity curves of the rod mechanism, but the latter has substantially the same shape as the rhodopsin absorption curve in the relevant spectral region). An attempt to represent the complete π_1 curve by the addition of a second rhodopsin-shaped absorption curve whose absorption combines linearly with that of the first is not quite acceptable: the linear summation produces too smooth a transition. But it is for π_5 and π_5' that the representation is least satisfactory: neither a simple rhodopsin-shaped curve nor a linear summation of two such curves (however displaced along the spectrum) will represent the spectral sensitivity of the "red" cone mechanism in low- or high-intensity conditions. It seems certain that the end-organs of π_5 cannot be equipped either with a single rhodopsin-type pigment or with a simple mixture (the same in all end-organs) of two such pigments. It has already been noted that the π_5 and π_5' spectral sensitivities are not adequately represented by linear combinations of the small-field color-matching functions, and the failure to fit rhodopsin-type curves might result from the fact that the increment-threshold spectral sensitivity is not built up linearly from the spectral absorption curves of the pigments contained in the end-organs of the π_5 mechanism. It is most improbable, however, that this

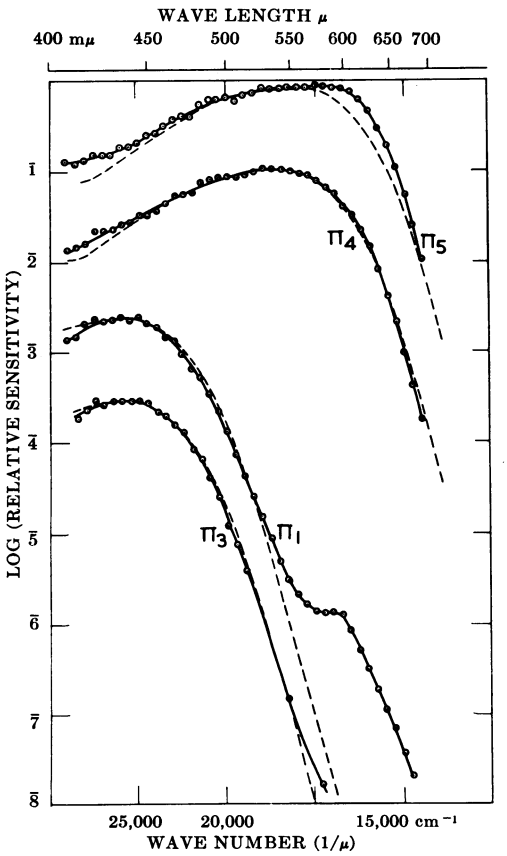

FIG. 10.—Field spectra sensitivity curves of mechanisms π_1, π_3, π_4, π_5 corrected for pre-receptor light losses and compared in each case with the similarly corrected sensitivity curve of rod vision displaced parallel to the two axes to give the best fit.

is the sole cause. Other proposed fundamental (pigment) spectral sensitivities for color vision obtained as strict linear combinations of the color-making functions for which the coefficients have been derived from the properties of the three kinds of dichromatic color defectives and other psychophysical measurements demand a similar non-rhodopsin-type "red" curve, usually including still more striking deviations from the rhodopsin shape at short wave lengths (Fig. 11).

Rushton's[2] objective measurements of bleachable pigments in the human fovea have established the presence in protanopes, deuteranopes, and color normals of a pigment he has named *chlorolabe* with a difference spectrum and action spectrum having a maximum at 540 mμ. As he has pointed out, the spectral sensitivity of the π_4 mechanism is a fair approximation to the spectrum of chlorolabe. The

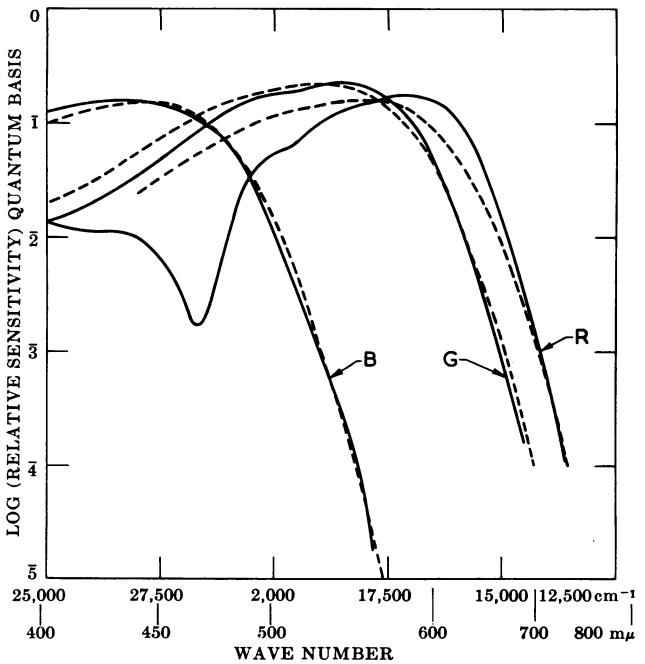

FIG. 11.—Thomson-Wright colour fundamentals corrected for light losses and compared with the displaced rod curve as in Fig. 10.

π_4' spectral sensitivity curve lies still closer to the objective curve. In fact, we have here a convergence, onto a common curve of rhodopsin type, of four spectral sensitivities: the objective spectrum of chlorolabe, the "green" fundamental derivable from the small-field color-matching functions of normal and dichromatic subjects,[5] the increment-threshold sensitivity π_4', and, finally, the sensitivity of a normal eye in a state of "artificial monochromasy" produced by exposure to very intense violet and red stimuli (Brindley[6]). The implication for the "green" cone mechanism is that, in the high-intensity condition, its end-organs contain, or at least are activated by the light absorption of, just one pigment—chlorolabe. Why, then, should the spectral sensitivity π_4, attributed to the mechanism in the low-intensity condition, be different? If exactly the same end-organs were concerned

at all intensity levels, either these would have to contain—probably in relatively small amount—a second pigment more red-sensitive than chlorolabe, or, alternatively, the effective spectral absorption curve of the latter pigment in its situation within the end-organs would have to vary with the intensity of stimulation. A variation of the kind required would occur if at low levels of stimulation the optical density of the pigment in the end-organ was high enough for self-screening to occur and if the reduction of density by bleaching at high levels of stimulation substantially reduced the self-screening. "Self-screening" denotes here the selective filtering of the light reaching the deeper pigment layers in the end-organ, in its passage through the upper pigment layers. Brindley has considered the possibility that the breakdown of metameric color-matches after the eye has been exposed to high intensities may be explained by the reduction of self-screening present at low and moderate intensities.[6] The difference between the π_4 and π_4' spectral sensitivities would correspond—very approximately—to a change in self-screening if in the low-intensity condition the chlorolabe in the end-organs had an optical density at the maximum wave length 540 mμ of about 1.0 and if this was reduced to about 0.2 in the high-intensity condition. However, the existence of self-screening in the end-organs of the green cone mechanism is contrary to all the evidence: Brindley's results show that the breakdown in metameric color-matches in the green-yellow-red range is associated with an anomaly not of the "green" process but of the "red" process only; the transition from π_4 to π_4' occurs in an intensity range lower than that required to produce appreciable breakdown in color-matches; the requisite density of the chlorolabe under zero-field conditions and the necessary degree of bleaching in passing from the π_4 to the π_4' intensity level are both improbably high, according to Rushton's objective data on chlorolabe. As a more red-sensitive pigment, *erythrolabe*, has been shown objectively to be present in the retina (Rushton),[2] the suggestion that the end-organs of the "green" cone mechanism might contain a small proportion of it mixed with chlorolabe is, at first sight, promising. The difficulty here is to understand why the red-sensitive pigment should be bleached or rendered ineffective by an increase in intensity corresponding to the transition π_4 to π_4'. The objective data on erythrolabe would poind to a comparatively small reduction—not more than 10 per cent—in its density by bleaching in this intensity range. We are led, therefore, to the other main possibility that, at low intensities, additional end-organs, not containing only chlorolabe, have contributed to the spectral sensitivity derived for the "green" cone mechanism. Many ways can be imagined in which this might come about, but it would be pointless to enlarge on them, as there is at present little evidence to distinguish different suggestions. One general observation may be made: whatever the way in which the non-chlorolabe end-organs are associated with the chlorolabe end-organs in determining π_4, the association is broken as a result of increasing the level of stimulation.

It is possible that in three blue-sensitive mechanisms—π_2, π_1, π_3—we have something like the same principle in operation. If we accept π_3 as the "blue" cone mechanism with end-organs containing just one blue-sensitive pigment of rhodopsin type (cyanolabe? not yet detected objectively), the spectral sensitivities of the other mechanisms would correspond to associations of cyanolabe with non-cyanolabe end-organs, these associations being broken at higher levels of stimulation by long-wave light. On this view, only one of the three mechanisms would be in

being at any moment, and this represents formally a radical change in our working hypothesis. But, while it can be shown from the steady-state increment-threshold measurements that the mechanisms π_1 and π_4 are present together, the relationship of the spectral sensitivity curves of π_1, π_2, and π_3 prevents a similar proof that any two of these are simultaneously present.

Comments generally similar to those made on π_4 and π_4' apply to the change from π_5 to π_5', but there are some differences. There is an additional objection to the use of self-screening as an explanation of the change; bleaching of the self-screening pigment would lead to a change in the spectral sensitivity curve even qualitatively different from that observed. This is not necessarily in conflict with Brindley's conclusion that, at higher-intensity levels, a change in self-screening of the end-sensitive pigment accounts for the breakdown of metameric color-matches, although the objective data on the erythrolabe in the retina do not support this theory. There is no convergence of the different spectral sensitivities with maxima at long wave length on a common rhodopsin-type curve. The π_5 curve does not agree with the objective spectrum of erythrolabe: Rushton has shown that π_5 can be fitted by the absorption curve of a mixture of erythrolabe and chlorolabe in the proportion 1:0.6.[2] For π_5', the corresponding proportion would be about 1:0.3, so that π_5' is nearer the objective curve of erythrolabe. The fact that both erythrolabe and chlorolabe have been shown to be present in the deuteranopic eye favors the Fick hypothesis of red-green fusion for the explanation of deuteranopia. The character of dichromatic color vision as a reduction form of normal color vision means that the spectral sensitivity of the red-green fusion in the deuteranope must be a linear combination of the normal's color-matching functions and hence almost certainly of the spectral absorption (strictly photosensitivity) functions of the normal's pigments. Deuteranopia would then be explained by the presence in all the end-organs of the fused red-green system of a mixture in an invariable ratio of the chlorolabe and erythrolabe pigments; any other explanation would encounter linearity difficulties. If, as is sometimes assumed, the normal also has the fusion process of the deuteranope but, in addition, the simple "green" process (and, of course, the "blue" process also possessed by the deuteranope), then the appearance in the normal eye of a π_5–π_5' mechanism supplied by end-organs containing a mixture of chlorolabe and erythrolabe would fit in very well. But there are difficulties: on the one hand, the pigment mixture appears unexpectedly stable when very high-intensity colored stimuli are used in increment-threshold and artificial monochromasy measurements, and, on the other hand, the breakdown of color-matches at high-intensity levels could not correspond merely to an alteration of the composition of a pigment mixture in the end-organs of the "red" cone mechanism.

This review has been devoted mainly to the spectral sensitivities of the color-vision mechanisms of the fovea arrived at by increment-threshold measurements made under steady-state conditions. The spectral sensitivities are perhaps of special interest at this time in the light of the new objective data on cone pigments. The summation properties of different color mechanisms, the way the mechanisms are modified in moving out from the fovea, and their behavior when the conditioning stimulus is suddenly changed have all been studied by the increment-threshold method to a limited extent. There is an interesting field here for further work.

[1] R. M. Boynton, *J. Opt. Soc. Amer.*, **46**, 172, 1956.

[2] W. H. A. Rushton, *Visual Problems of Colour* (N.P.L. Symposium, No. 8) (in Press).
[3] W. S. Stiles, *Documenta Ophthal.*, **3**, 138, 1949.
[4] W. S. Stiles, *Coloquio sobre problemas opticos de la vision* (Madrid: Union Internationale de Physique Pure et Appliquée, 1953), **1**, 65.
[5] L. C. Thomson, and W. D. Wright, *J. Opt. Soc. Amer.*, **43**, 890, 1953.
[6] G. S. Brindley, *J. Physiol.*, **122**, 332, 1953.

VISUAL PIGMENTS IN THE INTACT HUMAN EYE

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It is generally agreed that the first step in the visual process is the absorption of light by one or more photosensitive visual pigments contained in the rods and cones of the retina. The pigment of the *rods* has long been recognized and studied under the name *rhodopsin*, but rod vision is the colorless vision of twilight, and thus, to understand the photochemical basis of color vision, we need to measure the visual pigments in the *cones*. No extract of mammalian eyes has ever yielded a visual pigment other than rhodopsin; this is not surprising in view of the observations of Wald, Brown, and Smith[1] that the chick's eye, where cones relative to rods are a thousand times as abundant as in man, still contains twice as much extractable rhodopsin as iodopsin (the cone pigment). If in man we are to measure the pigments in cones, we must take advantage of two exquisite features of retinal organization. First, there is a tiny area of the retina—the *fovea centralis*—0.6 mm. in diameter, where there are no rods and where the cones are close-packed. If measurements can be confined to this region, contamination by the enormous preponderance of rhodopsin will be absolutely excluded.

The difficulties in dealing with so small a sample are somewhat offset by the second feature of cone structure, for cones are beautifully organized to catch quanta and secure photolysis. By measuring the pigments *in situ* within the cone, we take advantage of this organization and not only detect physically the change in pigment density during bleaching and regeneration but measure this change to an accuracy of about 5 per cent by a procedure which takes about 7 seconds to perform.

In principle, the method is to analyze the light reflected from the eye as seen in a cat's eye on the road by night or in man through an ophthalmoscope. This reflected light has passed twice through the retina and so must have suffered absorption by the retinal pigments traversed. If the incident light falls only upon the tiny *fovea centralis*, the pigments will be cone pigments, and if these are bleached to transparency by a strong dazzling flash, the reflected light will return brighter. Thus measurement of the increase in intensity of lights of various wave lengths will give the *difference spectrum* of the cone pigments involved.

Preliminary reports of equipment and results have already appeared,[2] and some quantitative results upon the kinetics of cone pigments have been published.[3] It will therefore be unnecessary to repeat here the *results* presented at the National Academy, though they show some improvement upon the earlier experiments. But the main conclusions may be summarized.