NATIONAL PHYSICAL LABORATORY

SYMPOSIUM No. 8

Visual Problems of Colour

VOLUME II

LONDON: HER MAJESTY'S STATIONERY OFFICE

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SESSION IV

SUBJECTIVE COLOUR MEASUREMENT, TEMPORAL EFFECTS, DEFECTIVE COLOUR VISION

Chairman: PROFESSOR Y. LE GRAND, MUSÉUM NATIONAL D'HISTOIRE NATURELLE, PARIS

*Unfortunately, the manuscript of this paper was not available at the time of printing.

PAPER 13

THE NEEDS AND PROSPECTS OF SUBJECTIVE COLOUR MEASUREMENT

By W. D. WRIGHT

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13. THE NEEDS AND PROSPECTS OF SUBJECTIVE COLOUR MEASUREMENT

By W. D. WRIGHT

SUMMARY

THE extent to which a normal C.I.E. specification can be said to define the appearance of a stimulus is first discussed. Examples are then given of a variety of phenomena in which a higher order of subjective colour measurement is required. These include problems of design, visual effects of adaptation, contrast, after-images, retinal position and Maxwell's spot, and technical problems of colour rendering and colour reproduction. Finally, the establishment of a scale of subjective colour measurement by the adoption of a standard viewing situation is considered, and the proposals to this end put forward by the author in 1951 are recalled.

THE SUBJECTIVE ELEMENT IN A TRISTIMULUS SPECIFICATION

THE definition of a colour C by the equation

$$C \equiv + X(X) + Y(Y) + Z(Z)$$

expresses the fact that a certain mixture of three reference stimuli will produce the same colour sensation as C, when both are seen under the same viewing conditions. Although this specification involves an observer and is therefore a subjective relationship, it does not in itself define the appearance of C, since this will change with change in viewing situation, whereas the specification is more or less independent of the observing conditions.

Nevertheless, the widespread use of the C.I.E. chromaticity chart as a kind of colour map demonstrates that at least some correlation between specification and appearance can be established; thus, we expect to find blues in the bottom left-hand corner of the chart, whites in the middle, greens at the top, and so on. Indeed, with experience, more specific descriptions may come to be associated with particular areas of the chart.

Surface colours constitute a special case, in that their chromaticity is a function of the spectral composition of the illuminant as well as the spectral reflection of the surface, while their colour appearance is

relatively constant with change in quality of illumination. For example, a white surface under illuminant S_C will be located at $x = 0.31$, $y = 0.32$ and under illuminant S_A at $x = 0.45$, $y = 0.41$, yet in each case the surface will look white. This phenomenon of colour constancy can be attributed primarily to the effect of adaptation in compensating for excess energy at the short or long wave end of the spectrum. It means, however, that any deduction about the appearance of a surface colour from its chromaticity must also take account of the chromaticity of the illuminant for which the surface colour has been evaluated and under which it is to be seen. Indeed, in some charts such as the Hunter, α, β-diagram *(ref. 1)* or the Adams chromatic-value diagram *(ref. 2)*, the illuminant is located at the origin of the co-ordinate system, in which case the appearance of the surface colour can be more readily visualised from its location in the diagram.

This is even more obvious in the case of colour atlases such as the Munsell or the Ostwald system, based as they are on a colour solid with a black-white central axis. Since the samples in these atlases have been calibrated colorimetrically, it is possible to describe a specimen in terms of, say, its Munsell hue, value and chroma from a knowledge of its tri-stimulus specification, and hence, so it would appear, to give quite a precise description of its appearance. The incompleteness of this statement will be apparent from the next section.

SOME PROBLEMS DEMANDING A HIGHER ORDER OF SUBJECTIVE COLOUR MEASUREMENT

THE description of colour appearance by identification with an actual sample is ambiguous unless the viewing conditions under which the sample is seen are also defined, notably the area of the sample and the quality and level of the surround illumination. Almost any problem in colour design is in effect an exercise in colour appearance, and while the elements in a colour scheme might be described by their tristimulus specifications or by their Munsell co-ordinates, their actual appearance will be affected by contrast between one area and another, by the size of each area and so on. Durrant *(ref. 3)*, for example, refers to the inadequacy of colorimetry in the development of schemes of decorative lighting and to the radical changes in appearance in a given colour depending on the colours immediately surrounding it. If a practical system of subjective colour measurement were eventually developed, its most lively application would most probably be found in the realm of design.

Some very intriguing problems in textile design have been discussed and illustrated by Warburton and Lund *(ref. 4)*, and by Warburton and Oliver *(ref. 5)*. Here simultaneous contrast, and also the reversed contrast effect sometimes known as the Van Bezold "spreading effect", have a vital influence on the appearance of the design, which normal colorimetry is quite

incapable of recording. Yet their investigation is worthy of study not only because of their importance in design but because of their inherent interest in our understanding of the visual processes. As Evans *(ref. 6)* has said in relation to the spreading effect, "until this effect can be explained without elaborate assumptions we cannot say that we understand the way in which the visual process operates". (Note: It is hoped that by the time of the meeting in September 1957 it will be possible to report some subjective measurements on this effect.)

Sometimes subjective colour measurements are desirable purely as a tool in visual research. The study of adaptation by binocular matching *(ref. 7)* is one example; the study of after-images *(ref. 8)* is another. It would be of great interest to record the subjective appearance of Maxwell's spot (the entoptic projection of the macula), which has been the subject of intensive study by Walls and Mathews *(ref. 9)* and of further analysis by Judd *(ref. 10)*. More precise information about its colour appearance might well help to decide between the receptor theory and the pigment theory of its origin. In experiments on the stabilised retinal image, some very interesting colour changes have been reported *(ref. 11)*, but if the qualitative descriptions of these changes could be supplemented with quantitative measurements, some quite exciting deductions might follow. In the experiments by Moreland *(ref. 12)* on peripheral vision, a form of subjective colour measurement has been employed, in which a test stimulus viewed peripherally was matched against the red-green-blue mixture of a colorimeter field, viewed foveally. In this way a dramatic demonstration was given of the collapse of the spectrum locus in the chromaticity chart with increasing distance from the fovea. Many more measurements of this type remain to be made.

However, the most vigorous application of subjective colour measurement has so far been in the realm of colour rendering and colour reproduction. The introduction of the fluorescent lamp has directed the attention of the illuminating engineer very forcibly to the distortions which can occur in the colour appearance of illuminated objects, when the spectral composition of a light source departs significantly from that of a temperature radiator. As mentioned earlier, adaptation commonly corrects for most of the change in chromaticity that occurs with change in colour temperature of a Planckian illuminant. With sources of less orthodox energy distribution, the chromaticity displacements are such that they may not be adequately corrected by adaptation to the overall quality of the light.

A closely analogous problem arises in colour photography and colour television. Here the reproduced picture is almost certain to be viewed under conditions that differ grossly from those of the original scene, especially as regards the luminance and size of the picture, and the quality of the ambient illumination. Moreover, the colour process itself is likely to possess inherent defects which introduce unavoidable distortions.

The problem then arises of specifying the colorimetric requirements of the system to give the most effective and realistic re-creation of the subjective appearance of the original scene.

In tackling these problems we find that the binocular matching technique has been employed in subjective colour measurements by Hunt *(refs. 13,14,15, 16)*, by Winch and Young *(ref. 17)*, by Burnham, Evans, and Newhall *(refs. 18, 19)*, by Burnham and Newhall *(ref. 20)*, and by Wassef *(ref. 21)*. Memory matching on a less quantitative basis has also been used by Bouma and Kruithof *(ref. 22)*, by Helson and Grove *(ref. 23)* and by Helson, Judd and Warren *(ref. 24)*. Quite recently, MacAdam *(ref. 25)* has found it possible to make quantitative studies of the effect of adaptation by fixating on the dividing line between the two halves of a colorimeter field. The two halves of the field were illuminated for nine seconds out of every ten by different adapting lights; for the remaining one second in the cycle, these lights were replaced by the matching stimuli of the colorimeter in one half of the field and by a test stimulus in the other. The matching stimuli were then adjusted to give a match of the test colour when both were seen periodically during the one second exposure; changes in adaptation were thus revealed by changes in the colour match settings.

MacAdam *(ref. 26)* has discussed the results of these experiments in relation to colour pictures seen by projection and by television, just as Newhall *(ref. 27)* has discussed the change in perceived colour with angular size in relation to the angular subtense of a colour picture. Clearly, with these and the other examples in mind, we can say that there is a demonstrable need for subjective colour measurement, and indeed that a very significant amount of such measurement is taking place. Unfortunately, however, unless we adopt some standard system of viewing to which all subjective measurements are referred, it is impossible to correlate the results of one laboratory with those of another. If we wish, for example to make some cross-reference to the measurements of, say, Moreland, MacAdam, Winch, Hunt, and Burnham, Evans and Newhall, we cannot do so because of differences of field size, adaptation level, time of exposure, etc., which they used for the comparison field.

THE ESTABLISHMENT OF A SCALE OF SUBJECTIVE COLOUR MEASUREMENT

IT would seem that the only immediate action required to establish a scale of subjective colour measurement is to agree on a standard set of viewing conditions for the comparison field. The subjective colour would then be expressed by the C.I.E. specification of the stimulus that had the same appearance, when seen under the standard conditions, as the test colour seen in its particular environment. There would be no occasion to adopt one method of comparison in preference to another, at least in the initial stages. Experience might subsequently demonstrate that one technique for

subjective colour matching had marked practical advantages over another, but it would be unwise to restrict the matching to that method alone.

As a basis for discussion at the 1951 meeting of the C.I.E., the following viewing conditions were proposed by the author *(ref. 28)*: angular subtense of comparison field - 4^{o}; angular subtense of surround - 15^{o}; nature of surround - a white or light-grey surface with luminance factor 0.75, illuminated by source S_A to an illumination level of 10 lumens per sq. foot; eye adapted to luminance of surround. The main arguments in support of these conditions were: (a) the comparison field was sufficiently large to avoid small-field effects, but not so large as to play a major role in the adaptation of the eye; (b) the size and luminance of the surround was sufficiently high to produce reasonably quick and complete adaptation; (c) the luminance of the surround was sufficiently high to permit easy representation of dark and near-black colours; and (d) the use of an illuminated *surface* for the surround might contribute to the stability of the viewing conditions through the operation of the phenomenon of colour constancy. The comparison field itself might be derived from the matching stimuli of a colorimeter, the colour samples of an atlas or by any other convenient means of presenting a stimulus or known C.I.E. specification.

The reaction to these proposals has not been particularly startling; in fact, there does not appear to have been any reaction at all! Perhaps if someone would submit a counter-proposal, it would stimulate interest and healthy argument. It is in the hope that the climate of opinion may now be more alive to the importance of subjective colour measurement and the extent to which it is now being practised, that attention has again been drawn to the possibility of establishing a standard procedure.

REFERENCES

1. HUNTER, R.S., *Symposium on Color, Amer. Soc. for Testing Materials*, 1941, p. 61.
2. ADAMS, E. Q., *J. opt. Soc. Amer.*, 1942, **32**, 168.
3. DURRANT, D.W. *Trans. Ill. Eng. Soc. (Lond.)*, 1956, **21**, 117.
4. WARBURTON, P. and LUND, G. V., *J. Text. Inst.*, 1956, **47**, 305, 319 and 347.
5. WARBURTON, P. and OLIVER, P. H., *J. Text. Inst.*, 1956, **47**, 361.
6. EVANS, R. M., *An Introduction to Color*, Wiley: New York; Chapman and Hall: London 1948, p. 181.
7. WRIGHT, W. D., *Researches on Normal and Defective Colour Vision*, Kimpton; London, 1946.
8. PADGHAM, C. A., *Brit. J. Ophth.*, 1953, **37**, 165.
9. WALLS, G. L. and MATHEWS, R.W., *Univ. Calif. Pub. in Psychology*, 1952, **7**, 1.

10. JUDD, D. B., *Coloq. sobre Problemos Opticos de la Vision*, Instituto de Optica; Madrid, 1953, **2**, 197.
11. DITCHBURN, R. W., *Research*, 1956, **9**, 466.
12. MORELAND, J. D., *The Perception of Colour by Extra-foveal and Peripheral Vision*, Ph.D. thesis, Lond. Univ., 1955.
13. HUNT, R. W. G., *Proc. phys. Soc.* B, 1949, **62**., 203.
14. HUNT, R. W. G., *J. opt. Soc. Amer.*, 1950, **40**, 362.
15. HUNT, R. W. G., *J. opt. Soc. Amer.*, 1952, **42**, 190.
16. HUNT, R. W. G., *J. opt. Soc. Amer.*, 1953, **43**, 479.
17. WINCH, G. T. and YOUNG, B. M., Colour and Lighting, Pt. 2., *G.E.C.J.*, 1951, **18**, 88.
18. BURNHAM, R. W., EVANS, R. M. and NEWHALL, S. M., *J. opt. Soc. Amer.*, 1952, **42**, 597.
19. BURNHAM, R. W., EVANS, R. M. and NEWHALL, S. M., *J. opt. Soc. Amer.*, 1957, **47**, 35.
20. BURNHAM, R. W. and NEWHALL, S. M., *J. opt. Soc. Amer.*, 1953, **43**, 899.
21. WASSEF, E., *Binocular Matching Technique and its Application to the Study of Visual Adaptation*, Ph.D. thesis, Lond. Univ., 1952.
22. BOUMA, P. J. and KRUITHOF, A. A., *Phillips Tech. Rev.*, 1947, **9**, 257.
23. HELSON, H. and GROVE, J., *J. opt. Soc. Amer.*, 1947, **37**, 387.
24. HELSON, H. JUDD, D. B. and WARREN, M. H., *Illum. Engrg.*, 1952, **47**, 221.
25. MACADAM, D. L., *J. opt. Soc. Amer.*, 1956, **46**, 500.
26. MACADAM, D. L., *J. Soc. Mot. Pict. Telev. Engrs.* 1956, **65**, 455.
27. NEWHALL, S. M., *J. Soc. Mot. Pict. Telev. Engrs.*, 1956, **65**, 273.
28. WRIGHT, W. D., *Compte Rendu C.I.E.*, 1951, **2**, Paper G.

PROFESSOR W. D. WRIGHT summarised his paper (13). He added that Mr. Belcher, at the Imperial College, was at that time making some subjective measurements on the colours of small patterns seen against coloured backgrounds. The slight colour changes seen in large contrasting test patches became very considerable at small angular subtenses. It was thought that any or all of entoptically scattered light, simultaneous contrast, and eye movements might be contributory factors in the phenomenon. So far, measurements had been done by comparisons with Munsell patterns seen under standard conditions, but it was intended also to use the Wright colorimeter.

DR. J. D. MORELAND gave further details of his subjective measurements on peripheral colour vision mentioned in Professor Wright's paper. He showed, on the Breckenridge-Schaub diagram, the collapse of the spectrum locus as the test field was placed successively at eccentricities of 15°, 30° (where an almost straight locus indicated dichromatic vision), and 40° (where an almost point locus indicated monochromatic vision). By assuming that the number of colours discriminated was proportional to the area enclosed by the spectrum locus, and that the number of cones covered by the test field was that given by Polyak, it had been possible to derive an almost linear relationship between these two quantities and to deduce that the minimum number of cones required for the beginning of discrimination was 300, or, allowing for lateral convergence and like effect, perhaps 30.

DR. M. H. PIRENNE referred to a classroom experiment in which an incandescent filament with red and green filters was viewed at an eccentricity of 90°. The colours could be distinguished, which suggested that the periphery was not monochromatic. But the observation was not conclusive, as other sensory clues might help the judgment. THE CHAIRMAN (PROF. Y. LE GRAND) suggested that stray light reaching the fovea was perhaps a sufficient explanation.

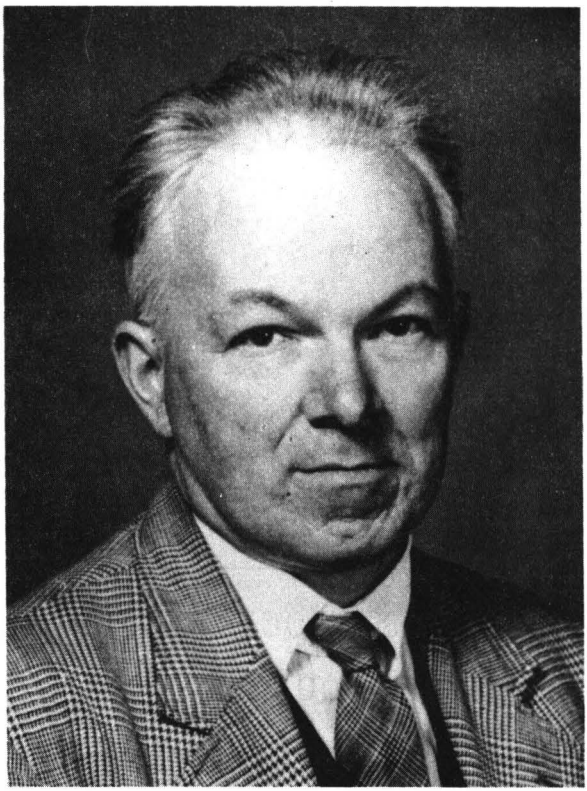
Detailed criticisms of the standard conditions proposed by Professor Wright for subjective colour measurement came from DR. R. W. G. HUNT and DR. D. B. JUDD.

DR. HUNT considered that the comparison brightness level of Professor Wright's proposed standard conditions was not quite high enough and DR. JUDD wondered why illuminant *A* rather than illuminant *C* was proposed. To the latter question, PROFESSOR WRIGHT replied that the greater practical convenience of source *A* had influenced him, but any suggestions which would forward the main idea he welcomed.

PAPER 14

THE PHYSIOLOGY AND PSYCHOLOGY OF COLOUR RENDERING

By B. H. CRAWFORD



Dr. B. H. Crawford is at present in the Light Division of the N.P.L., Teddington, which he entered in 1929. His work during this period has been almost entirely research in physiological optics, recognised in 1946 by the University of London by the award of a D.Sc. degree. He was educated at the Lower School of John Lyon, Harrow, and studied physics at University College, London; he carried out research in the Rodenside Laboratory of Messrs. Ilford, Ltd., for two and a half years before coming to the N.P.L.

14. THE PHYSIOLOGY AND PSYCHOLOGY OF COLOUR RENDERING

By B. H. CRAWFORD

PHYSIOLOGY is placed before psychology because physiology, in the sense of a vital mechanism, must exist before psychology, in the sense of perceptual processes, can come into action. But in the study of colour rendering it would seem that psychology bulks larger than physiology, although the physiology of colour rendering is not quite what can be predicted from previous knowledge of the colour mechanism of the eye. Before going into the details, however, of how much is physiological and how much psychological, it is necessary to be as definite as possible as to what colour rendering is. The general definition of colour rendering may be taken as the appearance of objects, in general coloured, under a given illuminant. We now have to define, or at least try to understand, what we mean by appearance. Appearance is usually qualified in some way, pleasant, unpleasant, like this, like that, truthful, distorted, and so on. In other words, appearance ends up in the brain in a state of being compared with something else, either directly or indirectly. So we now have reached the point that appearance is to be judged by comparison: it only remains to decide on the manner of the comparison, or, if necessary, to classify the sorts of comparison which are appropriate to the various practical problems of colour rendering.

The following classification of visual comparisons is proposed:

(a) Purely spatial comparisons. This is the sort of comparison which is made in visual photometry and colorimetry, in which two small fields are closely juxtaposed with an imperceptible line of division. Under these conditions an observer is able to make comparisons with the minimum uncertainty and maximum precision. The human processes involved are as much as possible physiological, any psychological effort being reduced to a minimum.

(b) Spatio-temporal comparisons. In this class I include all comparisons in which the visual fields to be compared are separated spatially, by an amount large or small, so that the observer's eyes, or even his whole person, must travel from one field to the other over an intervening space, which in itself may be either neutral or distracting. It is obvious that a tremendous range of conditions is included within this class. At one extreme it can be exemplified by the photometry of point sources by direct comparison of one with another at a small angular separation on an otherwise uniform field of view. The precision of such a comparison

is somewhat less that that of a class (a) comparison, owing to the fact that the intensities of the point sources have to be remembered, albeit for a brief interval only. It is plain that the importance of the psychological factor may be continuously increased by increasing the angular distance between the things compared (e.g., lighthouses on opposite compass bearings), or even making it necessary for the observer to move bodily from one place to another in order to make his comparison (e.g., comparing the lighting in two different rooms not simultaneously visible from the same place): memory, the psychological factor, comes more and more into play. In fact, the spatial separation can be made so wide that the comparison merges into class (c).

(c) Pure memory comparisons. It is difficult to find a neat and accurate name for this class of comparison, but it is intended to include only those cases in which the observer first looks at, and becomes statically adapted to, one field, then repeats the process for another field, with a sufficient interval between the two observations to remove all sense of temporal or spatial change. Or, in other words, the observer is required to compare the two fields by an effort of memory only; the psychological factor is now a maximum, the precision of the comparison a minimum. This is the principal domain of colour rendering. It has been investigated very little so far. The precision of measurement being so low makes the investigations the more difficult, of course, and for this reason, perhaps, unattractive, but the precision is by no means zero, and with patience and the necessary precautions useful measurements can be made.

Having classified comparisons from the aspect of their psychological content, we must now come to some decision regarding the classes of comparison which are significant in colour rendering. It would seem justifiable in the first place to exclude class (a) as this is used for hardly anything else but photometric and colour matching, usually as part of a measurement technique. One possible exception might be a camouflage scheme, but this is very specialised and may be left out of a general consideration of colour rendering.

Passing over class (b) for the moment, it is obvious that class (c) comparisons are of major significance in colour rendering, as they represent the case of most general interest, that of living under a given lighting installation and finding it satisfactory, or not, for itself alone in the absence of another installation for comparison. What might be termed "absolute satisfaction" is involved, with memory as the only criterion.

Class (b) comparisons, comprising as they do all the intermediate gradations between (a) and (c), form a very debatable group. It is likely that no agreement will ever be reached on precisely how much of class (b) falls within the purview of colour rendering, but at least one should be prepared for all eventualities by realising how the various possible practical conditions can resemble each other and yet differ from each other.

For every practical problem of colour rendering it must be presumed to be possible to determine a set of tolerances within which a lighting installation must lie in order to conform to its type or be suited to its purpose. As the problem changes, so the tolerances will change, but they will always exist, though they may be difficult to determine. It is this existence of a set of tolerances which connects together all conditions of colour rendering observation. The differences will lie in the magnitude and also in the character of the tolerances. Magnitude is an obvious difference; the more indirect and remote the comparisons involved in the problem, the greater will be the tolerances. A less self-evident difference is the character of the tolerances, for instance, the degree of mutual dependence between them. A certain amount of evidence, both technical and scientific, already exists regarding mutual dependence between tolerances, but not enough yet to enable generalisations to be formulated. Whether this mutual dependence is psychological or physiological is not yet clear; it may well be the latter, and this brings us to a consideration of the general physiological aspect of colour rendering.

It is almost axiomatic that the known colour reception mechanisms of the eye are operative in colour rendering, but there is evidence that these mechanisms are at least modified in colour rendering. For example, the tolerances of colour rendering may be expressed as a sort of hue discrimination diagram, but the minima are not in the usual places. There may be a purely logical reason for this, but at least it shows that the physiological mechanisms of colour rendering cannot necessarily be predicted from existing knowledge.

Again, the mutual interdependence of colour rendering tolerances, referred to above, hints at a mechanism, physiological or psychological, which is not evident in colour matching, though it has been assumed in various systems of colour nomenclature, namely, the circle of hues of Ostwald and later workers. This gives the same reality to purples, as sensations, as to all the other hues which exist as spectral colours; colour rendering experiments for their part show that red and violet are mutually interacting to the same extent as the other pairs of hues which are actual neighbours in the spectrum. This would indicate that the realm of purples between spectral red and violet is just as real psychologically, perhaps physiologically, as any of the spectral regions.

Such results hold out the hope that colour rendering experiments are not only of practical use in the design of lighting installations and the specification of illuminants, but will also contribute to our knowledge of the visual mechanism.

PAPER 23

COLOUR THRESHOLDS WITH MONOCHROMATIC STIMULI IN THE SPECTRAL REGION 530-630 mμ

By M. DAGHER, A. CRUZ and L. PLAZA

L. Plaza

A. Cruz M. Dagher

L. Plaza is Vice-Director of the Instituto de Optica "Daza de Valdés" in Madrid and is in charge of its Photometry and Colorimetry Section. He came to the Institute in 1944, having graduated in Physics at Barcelona University. For a time, he was a guest-worker at the Bureau of Standards in Washington, studying Colorimetry with Dr. Judd. He holds the degree of Ph.D. of Madrid University and is also Professor of Photometry and Colorimetry there.

A. Cruz, born in Madrid in 1925, is a graduate of Madrid University and holds the Optical Engineering Diploma of the Instituto de Optica "Daza de Valdés" in Madrid. He has been at the Institute since 1949, working on photometric and colorimetric problems. In 1953, he attended a course at Imperial College, London, under Professor W. D. Wright.

M. Dagher, born in Latakia, Syria, in 1929, graduated in Physics from Damascus University in 1951. He has been a Professor of Physics at the High School of Damascus. In 1955, he obtained a scholarship to study in Spain, since when he has been doing research work at the Instituto de Optica "Daza de Valdés" in Madrid.

23. COLOUR THRESHOLDS WITH MONOCHROMATIC STIMULI IN THE SPECTRAL REGION 530-630 mμ

By M. DAGHER, A. CRUZ and L. PLAZA

SUMMARY

A technique is described for determining the thresholds of colour perception with monochromatic stimuli. With this technique the thresholds for three observers with normal colour vision have been measured for spectral stimuli from 530 to 630 mμ (at each 2 mμ) and for stimulus sizes, 2° and 15'.

The absolute thresholds for the same observers and for wavelengths in the same part of the spectrum have also been determined. By comparing the two sets of data the photochromatic interval or factor has been obtained for each observer.

The perception of chromaticness for each observer is given as a function of the wavelength and the relative energy of the stimulus, for the 2° and 15' stimuli.

I. INTRODUCTION

IN the literature there are not many papers on the determination of the photochromatic interval or factor *(refs.1,2,3)* and thinking it would be interesting to obtain more data on the subject, some experiments using direct measurement were done at the Instituto in 1948 *(ref.4)*. At the same time, and using the same experimental conditions, the hues of the sensations when the energy of the stimulus was near the threshold were determined for a few wavelengths.

These experiments were repeated in 1953 with more wavelengths and using a new and more refined apparatus. The results were presented at the International Colloquium on "Problemas Opticos de la Vision" held in Madrid in April of that year. This paper was not published because the results showed firstly, the necessity for a better control of the size and presentation time of the stimulus, and secondly the possibility of more accuracy in the naming of the perceived colours.

A year ago new experiments of this kind were started, and in this paper are presented the results obtained for the first region of the spectrum examined.

II. TECHNIQUE

THE experimental problem is this: to present to an observer (in determined conditions of adaptation and fixation) a monochromatic stimulus of known wavelength and energy, and to record the colour perceived. The experiment is to be repeated, with the greatest possible number of wavelengths and energy levels, and with different stimulus sizes.

(A) Stimulus.

The apparatus used to obtain the stimulus is shown in *fig. 1.* A double monochromator of subtractive dispersion is the principal element. Its entrance slit, R_1, receives light from a ribbon filament lamp, M_1, of 6v. 100w., through the condenser C_1. At the other end of the monochromator a condenser, C_2, forms an image of the exit slit, R_3, on the point O, where the pupil of the observer is situated, so that he receives a Maxwellian view of the condenser C_2. The condensers C_1 and C_2 have the same aperture as the collimator lenses L_1, L_2, L_3, L_4. The three slits of the monochromator were always of the same width and for the experiments this was such that the purity of the stimulus varied only from 3 to 6 mμ.

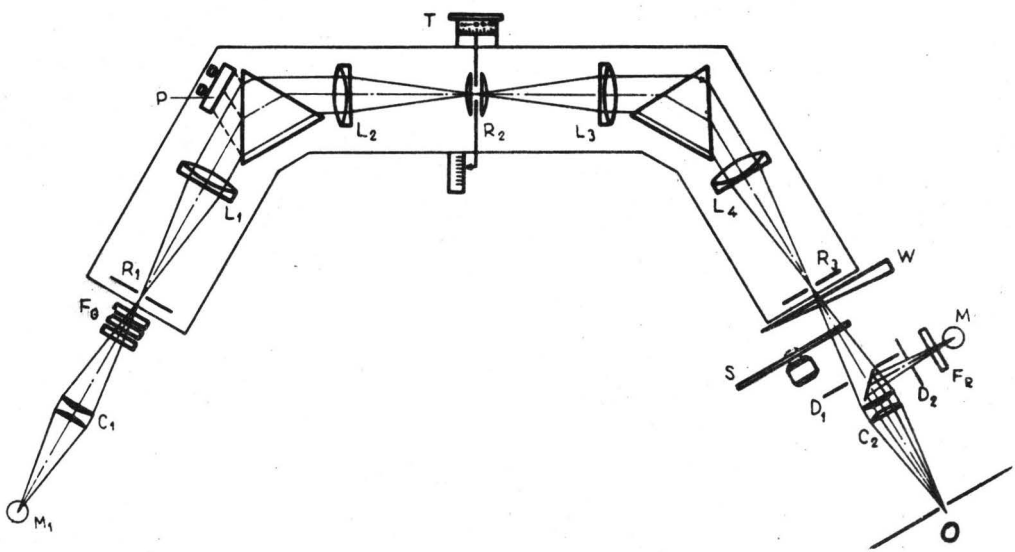


Fig.1.

(i) Variation of the stimulus wavelength.

This is done by the displacement of the central slit, R_2, through the primary spectrum. A linear scale and the drum T measure this displacement.

Wavelength calibration was carried out with spectral lamps of Hg, Na, Cd, Kr and Ne. More than 50 spectral lines of known wavelength were used. An initial calibration was made visually, but later a photoelectric cell was placed at the exit slit and the scales were read at the point of maximum response for each line. The calibration curve obtained was checked against other known spectral lines and the results show that the maximum deviation for the spectral region studied is 0.2 mμ.

(ii) Variation of the stimulus energy.

The range of variation of the energy of the stimulus must be very big (from less than the absolute thresholds to more than the saturated spectral colours) and it was necessary to use 7 neutral filters, F_G, about 0.1 transmittance each, placed before the entrance slit of the monochromator. For the continuous variation of the energy between the steps corresponding to the filters, a photometric wedge, W, was used. It is placed immediately after the exit slit and its lateral position is measured on a linear scale.

The calibration of energy proceeded by the following steps.

Determination of the relative energy that would reach the eye of the observer if there were neither filters nor a wedge. This calibration was made placing a thermopile at the point O. Its response was amplified by a primary galvanometer and two thermocouples in opposition, and finally recorded with a second galvanometer. This calibration was repeated several times to check on any variation during the period of several months occupied by the experiments. The total energy that passed through the entrance slit was controlled by the photoelectric cell P, and the voltage applied to the lamp was constant and also checked continuously.

Determination of the spectral transmittance of each of the 7 filters and of the wedge. These measurements were made with a Beckman spectrophotometer with a modified sampleholder in the case of the wedge.

(iii) Variation of the stimulus size.

This was obtained by placing circular diaphragms D_1, before the condenser C_2, and two of them were used such that the stimulus size was 2° or 15'.

(iv) Region of the retina stimulated.

A system of fixation assured that the fovea was always the region stimulated. The system is composed of a lamp M_2, a red filter F_R, a stop D_2 with 4 holes in it, a very thin glass plate and the condenser C_2. The image of the lamp filament is formed at the same point O as the image of the exit slit and the sizes of both images are about the same (so that when the

observer sees the fixation points he is sure that the energy of the test stimulus will also reach his retina). The 4 fixation points appear to the observer around the test stimulus and their intensity is regulated by the same observer.

(v) Duration and frequency of presentation of stimulus.

As the thresholds depend on the duration of the stimulus, this must be constant through all the experiments. It should be short to avoid, as much as possible, the effects of chromatic adaptation, but must be long enough to permit perception of chromaticness. A duration of 3 seconds was used.

On the other hand all reasons are in favour of a long interval between the presentation of two stimuli, but one too long would not allow many observations to be made in one session and the experiment would be too tiresome. A period of 9 seconds was selected.

In practice this was done by means of the sector S, the aperture and velocity of which were regulated to obtain the times of 3 and 9 seconds, respectively.

(B) Observers.

The authors were the observers and all three show normal colour vision with the Ishihara test, and are trained for this sort of observation. M.D. is 28 years old, A.C., and L.P., 34.

(C) Experimental procedure.

A session began with half an hour of dark adaptation and then about an hour of observations. Sometimes the observer rested in the middle of the session for a while to avoid fatigue.

About 12 wavelengths were selected for each session. The presentation was in random order, first with a very low level of energy that was raised a little after each run of wavelengths. In order to connect the results of the different sessions (changes in retinal sensitivity), a determination of the absolute threshold for one or two wavelengths was also made in each session.

The head of the observer was fixed with a chin and head holder (it was not possible to use a dental impression because the observer had to name the colour that he saw). The observer could, at his will, make the red fixation points disappear. A system of sound signals was used to indicate the moment just before the stimulus began (at that moment, the observer made the fixation points appear) and the moment it finished the observer made the fixation points disappear so as to remain in complete darkness for the next 9 seconds. Fifty-one wavelengths were used (each 2 mμ), 15 to 20 levels of energy were necessary for each wavelength and the experiments were repeated several times for each observer (each wavelength at least 6 times in a session). Taking all into account, 5,500 observations were made

for each observer and each size of stimulus.

Apart from the determinations of absolute threshold made during the ordinary sessions as a control, the values of the curves given in the results were obtained in special sessions. Wavelengths were used in these measurements (each 10 mμ) and each wavelength was presented at least 50 times at each of the 4 levels of energy to allow the application of the statistical method of fixing the thresholds. The complete experiment was repeated 3 times.

III. RESULTS

FIGS. 2, 3 and *4* represent the results for each observer. The left-hand side corresponds to the 2° stimulus size and the right-hand side to the 15' one.

The curves of absolute threshold are an average of those obtained in each of the three independent experiments.

The thresholds of chromaticness have been derived from the data of the 6 experiments with a criterion of 50%. For example: at the wavelength of 570 mμ the point of separation of the two zones A and yg has been taken at the level of energy in which the observer said three times "achromatic" and three times "yellowish-greenish". In general there is a good agreement between the response to the same stimulus in different sessions.

In the zones marked with the initials of the colour perceived, the saturation increases with the energy. The dotted lines of the figures mark the energy level at which the observer considered the colour was saturated.

The photochromatic interval was computed as the difference between the first threshold of chromaticness and the absolute threshold and in *fig. 5* is represented for each observer and stimulus size.

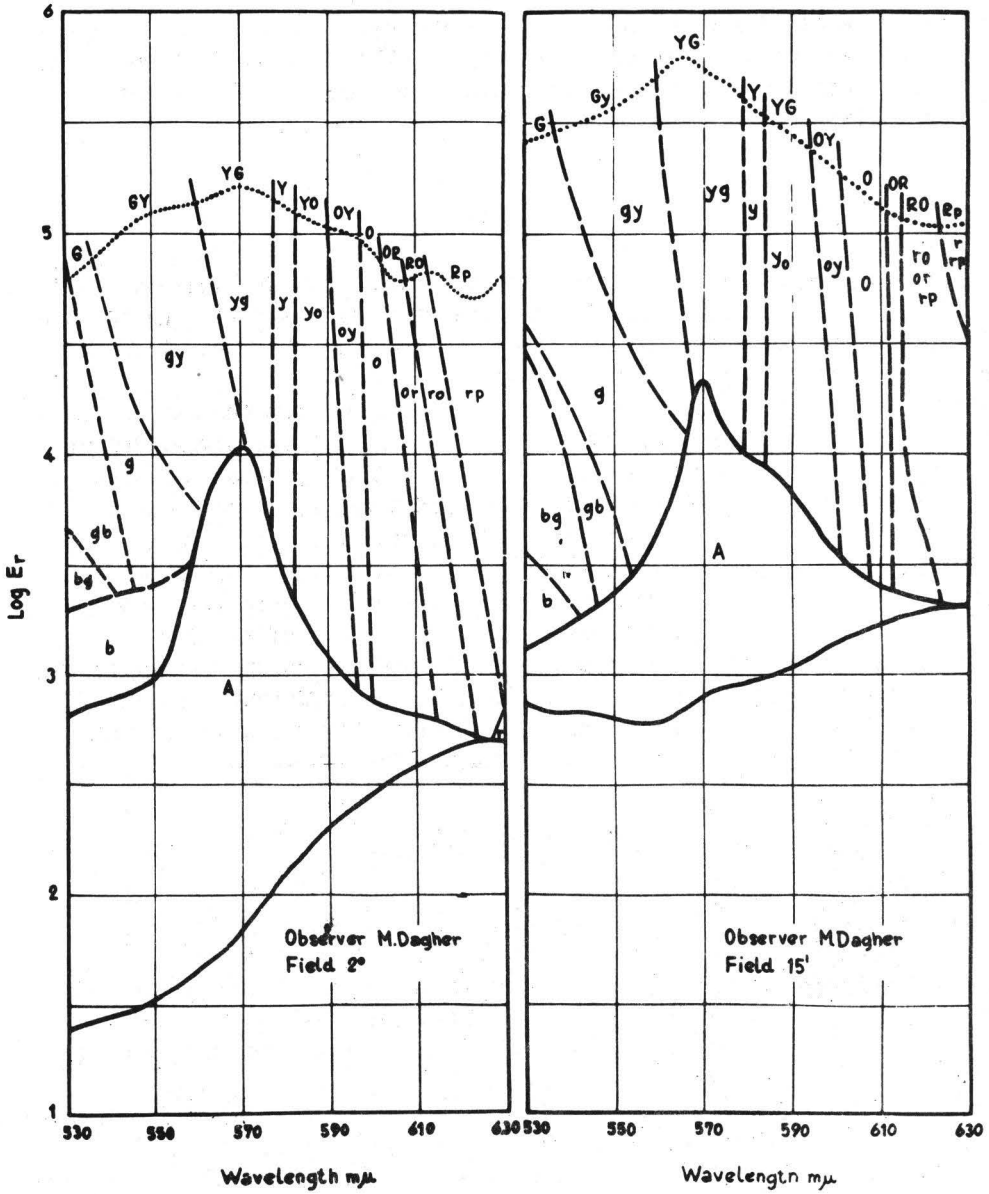
IV. COMMENTS ON THE RESULTS

THE complete discussion will be made when the results for all the spectrum have been obtained. For the moment it is interesting to note:

1. The results of two of the observers (M.D. and L.P.) are in generally good agreement and present the following characteristics:

   (a) The curves of absolute threshold for 15' have the characteristics of cone vision, but those corresponding to the 2° stimulus seem more like rod vision.

   (b) The curves corresponding to the first perception of chromaticness all have a maximum around 570 mμ (tritanopic vision for levels of energy below this maximum). The energy of this maximum is higher for the 15' stimulus but the difference is not very significant.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630
Wavelength mμ
Observer M.Dagher
Field 2°
Gy
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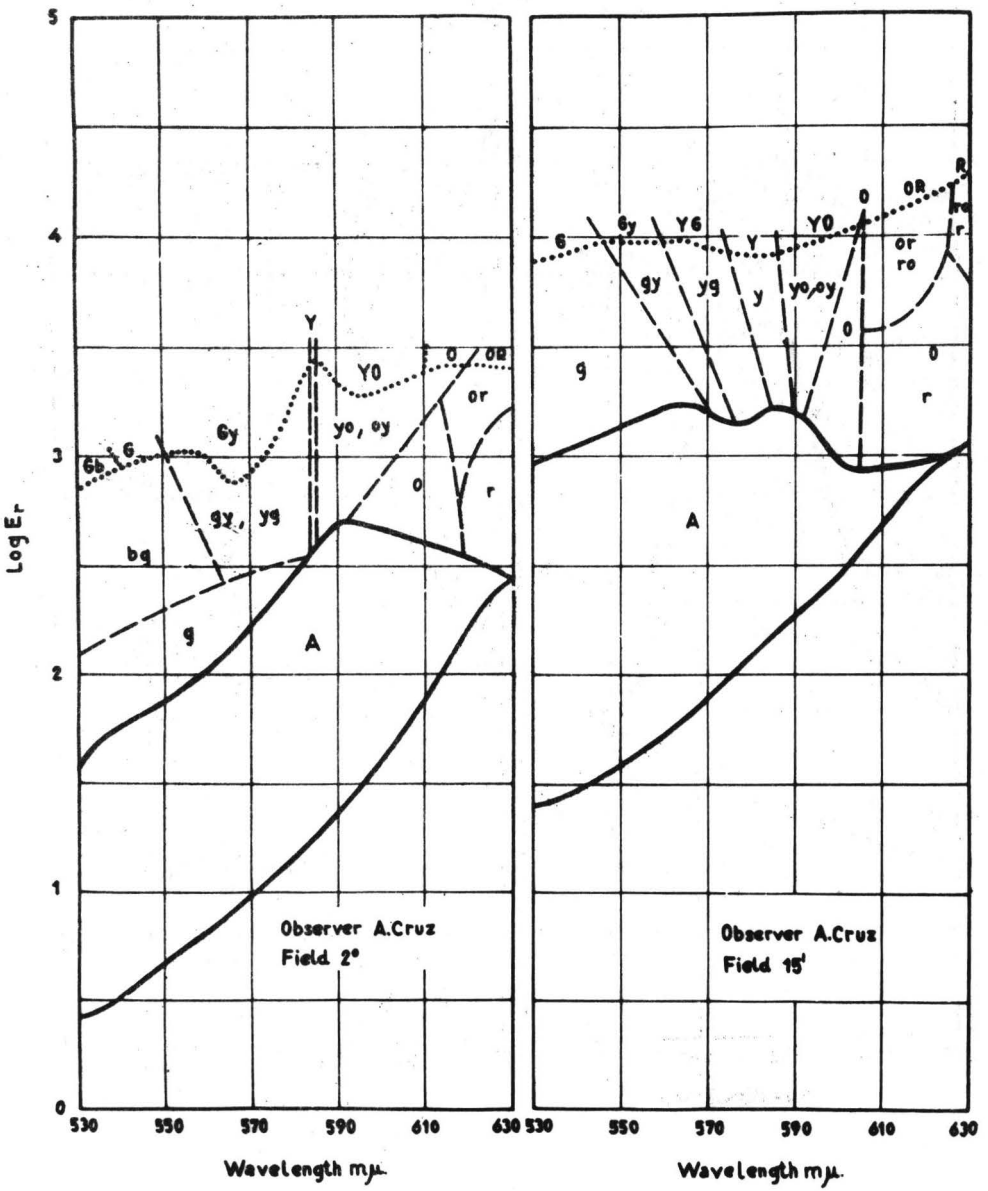
Wavelength mμ
Observer M.Dagher
Field 15'

Fig.2.


Log Er
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Wavelength mμ
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yo, oy
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Observer A.Cruz
Field 2°
Observer A.Cruz
Field 15'

Fig.3

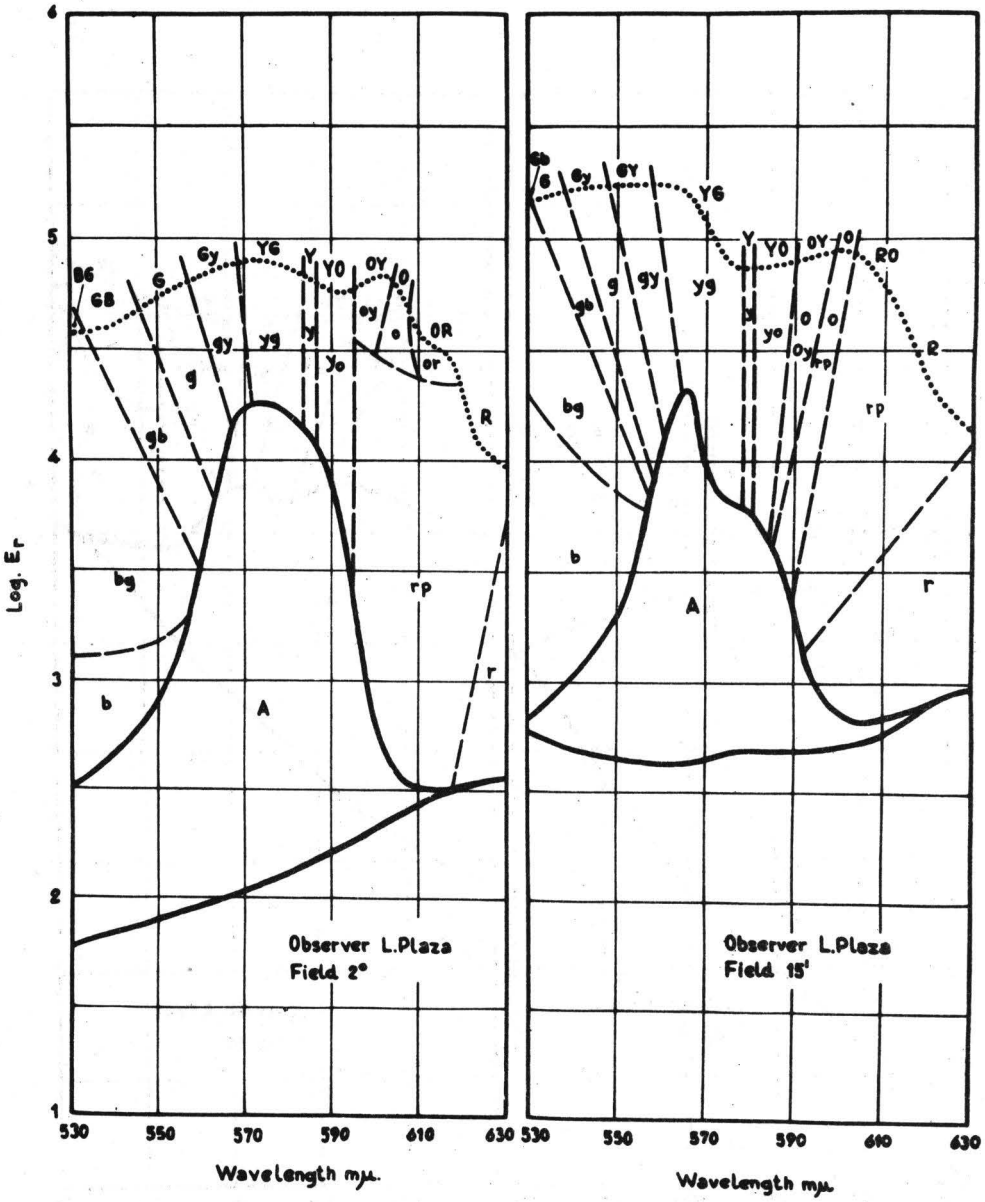
Log. Er
Wavelength mμ.
Observer L.Plaza
Field 2°
Observer L.Plaza
Field 15'
BG
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Fig.4

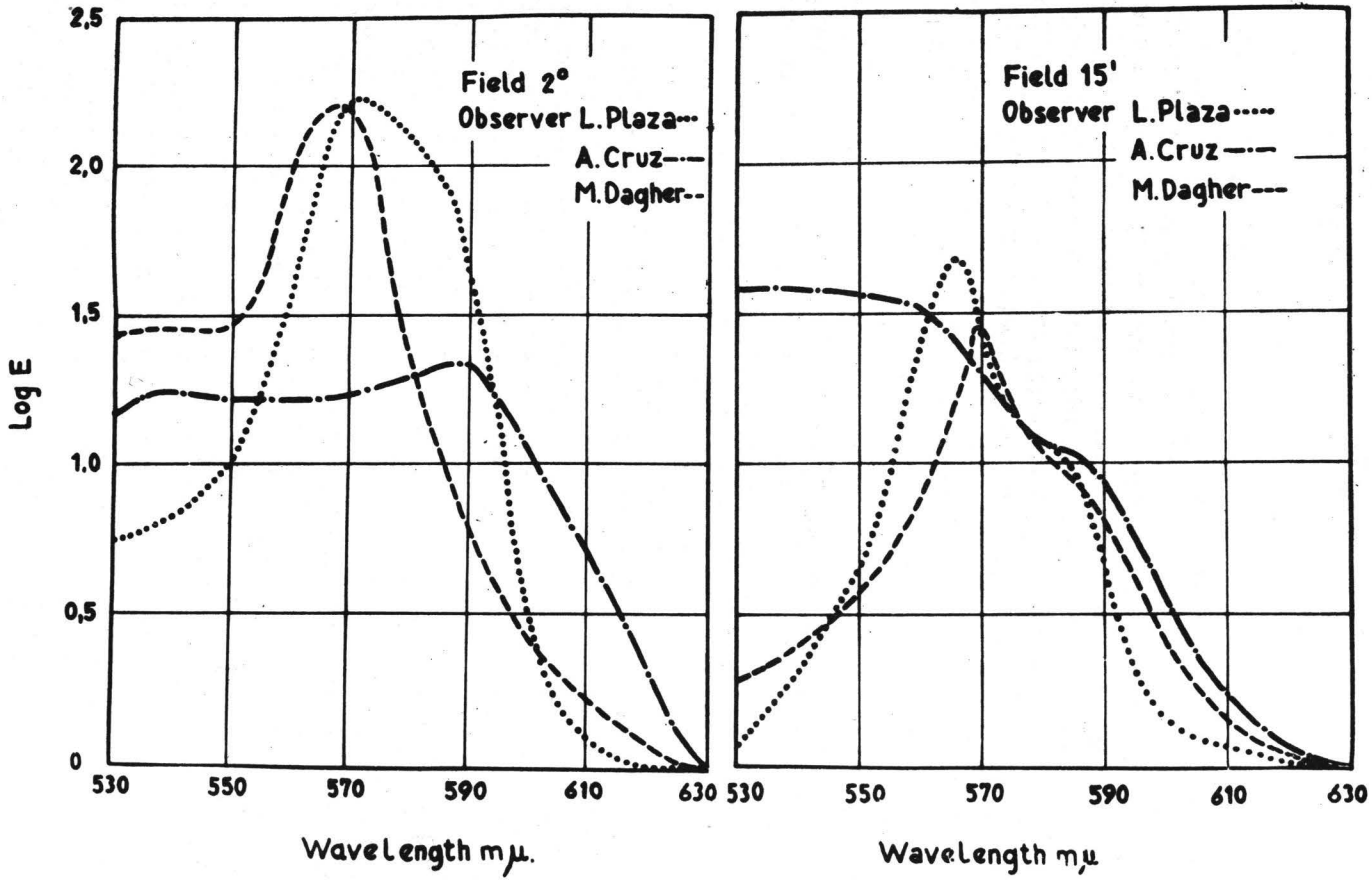

Field 2°
Observer L.Plaza---
A.Cruz—·—
M.Dagher--
Field 15'
Observer L.Plaza·····
A.Cruz—·—
M.Dagher----
Log E
2,5
2,0
1,5
1.0
0,5
0
530
550
570
590
610
630
Wavelength mμ.
Wavelength mμ

Fig.5.

(c) In opposition to the results obtained in 1948 (perhaps because at that time not enough wavelengths were used) the yellow appears as the first colour seen in a narrow band of wavelengths (around 5 mμ wide) near 580 mμ. The yellow zones are vertical and this indicates that for these wavelengths there is no Bezold-Brücke effect.

(d) The photochromatic interval has a maximum around 570 mμ and is zero at 630 mμ. For the 15' stimulus it is very small in the region of 530 mμ. (For the observer L.P. it is almost zero).

2. The third observer, A.C., agrees with the others on the question of the yellow, but presents the following differences:

(a) The curves of absolute threshold are very similar for the 2° and 15' stimuli.

(b) The curves of the threshold of chromaticness do not present a clear maximum.

(c) He is less able to distinguish hue.

(d) In the zone 530 to 570 mμ he needs much less energy to perceive lightness and chromaticness. In that zone the first colour perceived is "greenish" instead of the "bluish" of the other observers.

(e) The photochromatic interval has no maximum. For the 2° stimulus it is practically constant from 530 to 590 mμ.

V. ACKNOWLEDGEMENT

WE wish to thank Mr. J. Juan for his help as experimenter in some of the sessions.

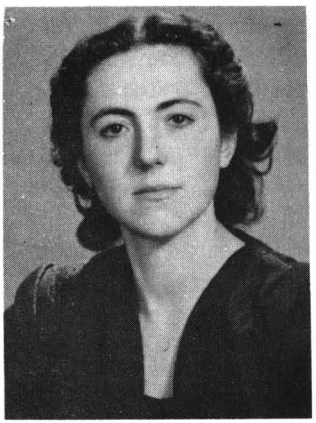
REFERENCES

1. ABNEY, W. de W. and FESTING, E. R. Colour Photometry, Part III, *Philos. Trans. roy. Soc.* A, 1892, **183**, 531-565.
2. PURDY, D. McL. On the Saturation and Chromatic Thresholds of the Spectral Colours, *Brit. J. Psychol.*, 1931, **21**, 283-313.
3. SHEARD, C. Dark adaptation: some Physical, Physiological, Clinical and Aeromedical Considerations. *J. opt. Soc. Amer.*, 1944, **34**, 464.
4. OTERO, J. M., PLAZA, L. and CASERO, L. El intervalo acromatico y las sensaciones fundamentales en la zona media del espectro, *An. Soc. esp. Fis. Quim*, 1948, **44A**, 16.

PAPER 16

SPACE VERSUS TIME DISTRIBUTIONS OF CHROMATIC STIMULI

By ADRIANA FIORENTINI and LUCIA RONCHI



Lucia Ronchi took her degree in Physics at the University of Florence in 1948 and received her Doctor's degree (Libera Docenza) in Physiological Optics in 1956. Since 1949 she has been a research scientist at the Istituto Nazionale di Ottica of Florence. Her scientific activity consists of researches on vision from the electrophysiological, psychophysical and psychological stand-points.

Adriana Fiorentini took her degree in Physics at the University of Florence in 1948 and received her Doctor's degree (Libera Docenza) in Physiological Optics in 1956. Since 1949 she has been Assistant Professor at the Istituto Nazionale di Ottica of Florence. Her scientific activity consists of researches concerning vision, testing of optical systems, photography, theory and practice of spectacles.

16. SPACE VERSUS TIME DISTRIBUTIONS OF CHROMATIC STIMULI *

By ADRIANA FIORENTINI and LUCIA RONCHI

INTRODUCTION

DURING the last years some researches have been carried out at the Istituto Nazionale di Ottica of Florence on the visual response to a more or less rapid variation of the stimulus intensity either in space or in time *(refs. 1,2,3,4)*. As is well known, a *time* variation of retinal illumination may have as a consequence an enhancement of brightness sensation. A variation of illumination from point to point on the retina produces a contrast effect, and in some cases also an enhancement of apparent brightness. It is possible that a correlation may exist between the two phenomena *(ref. 5)*. If eye movements are taken into account, it is clear that a non-uniform illumination on the retina makes the stimulation at a given receptor vary in time.

Previous work has been carried out with white light.

The research has now been extended to coloured stimuli. The effect of a time variation of the stimulus intensity has been investigated both by the electroretinographic method and by a psychophysical experiment with flickering light. The simultaneous contrast effect produced by a space gradient of luminance which presents a sharp variation has been investigated by psychophysical experiments.

I. ELECTRORETINOGRAPHIC INVESTIGATION

TWO different sets of experiments have been made on the electrical response of the human eye. In the first set, light stimuli of practically unlimited duration have been used. The shape of the stimulus was varied by changing the time of rise of the luminance. In the second set of experiments stimuli of finite duration and different shapes have been used.

The electroretinograms (ERG) have been obtained by means of standard equipment, where the corneal electrode was borne by a contact lens. Three normal observers took part in the experiments. Each subject was dark adapted for 30 minutes before the experiment.

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The responses consist of a scotopic b-wave. A set of 3,000 records has been analyzed and the following three characteristic quantities of the b-wave have been measured for each record: height h (in microvolts), slope s (in microvolts/msec) and latency time t_l (in msec).

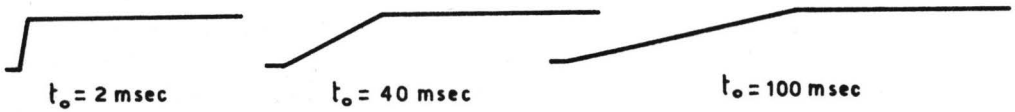


Fig.1 - Stimuli of practically unlimited duration, having the same final level and a different time of rise.

(a) Responses to Stimuli of Practically Unlimited Duration

The stimuli used in the first experiment are represented in *fig. 1*, where retinal illumination is plotted against time. The final luminous level is the same for the three stimuli, while the time of rise t_o is 2 msec, 40 msec and 100 msec, respectively. White, green and blue lights have been used. In the experiment with white light the final level of retinal illumination ranged between 1 and 73 luxes.

Let us call h_{to} and s_{to} the average height and slope of the b-waves obtained with the time of rise t_o, and h_{100}, s_{100} the two corresponding quantities obtained with 100 msec time of rise. In order to compare the responses obtained with stimuli having the three different times of rise and the same final level, two quantities E_h and E_s have been computed according to the formulae:

$$E_h = \frac{h_{t_o} - h_{100}}{\frac{1}{2}(h_{t_o} + h_{100})}; \quad E_s = \frac{s_{t_o} - s_{100}}{\frac{1}{2}(s_{t_o} + s_{100})}$$

In *fig. 2*, E_h and E_s are plotted against t_o. The bottom diagrams represent the latency time t_l as a function of t_o. Each curve of *fig. 2* is characterized by the final retinal illumination.

From *fig. 2* we can see that at low levels of retinal illumination, an increase in the time of rise of the stimulus leaves the height and the slope of the b-wave practically unchanged, while the latency increases. At high levels, the only effect of increasing t_o is to make the b-wave slope decrease, while both height and latency remain practically constant.

In order to discuss these results it has been necessary to check the variation of the b-wave with respect to the illumination level, using stimuli of short time of rise (2 msec). The height, slope and latency of the

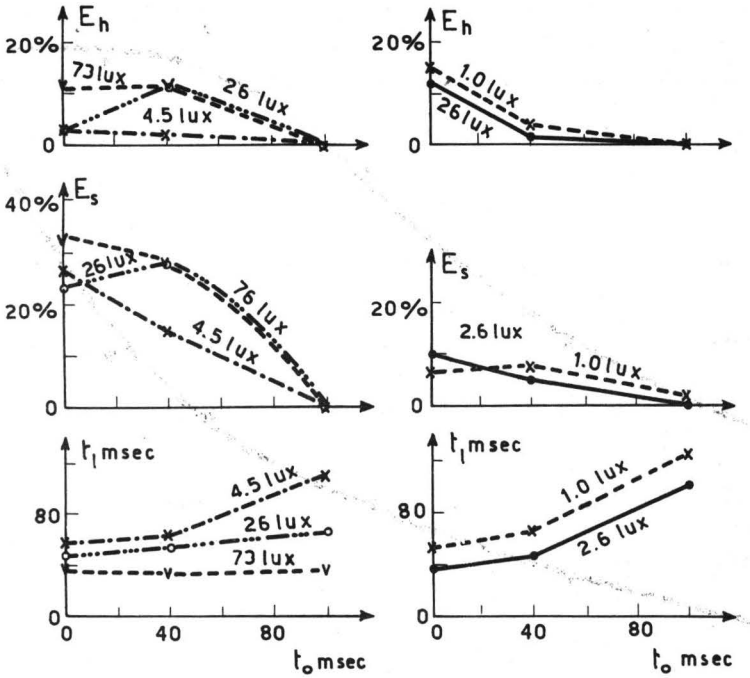


Fig.2 - Variation of the height, rate of rise and latency time of the b-wave as a function of the time of rise of the light stimulus. The luminous level is indicated for each curve. The meaning of symbols such as E_h and E_s is explained in the text. White light.

b-wave are represented in *fig. 3* as functions of log retinal illumination. The height reaches its maximum value at about 40 luxes; no saturation is found for *s* when the illumination is in the range considered.

For a tentative interpretation of our data it is necessary to recall the results of an experiment made with stimuli of finite duration. Johnson and Bartlett *(ref. 6)* found that until a certain critical duration is reached, the amplitude of the submaximal b-wave is determined by the product $IT = C^o$ of intensity and duration of the stimulus. Beyond the critical duration, the amplitude is determined solely by the intensity. If our interpretation of the experimental results of these authors is correct, the latency of the b-wave (which does not depend on stimulus duration, but decreases when intensity is increased) should be of the same order as the critical duration.

This means that when rectangular flashes of different energy are used, the height of the response depends on the energy received by the eye

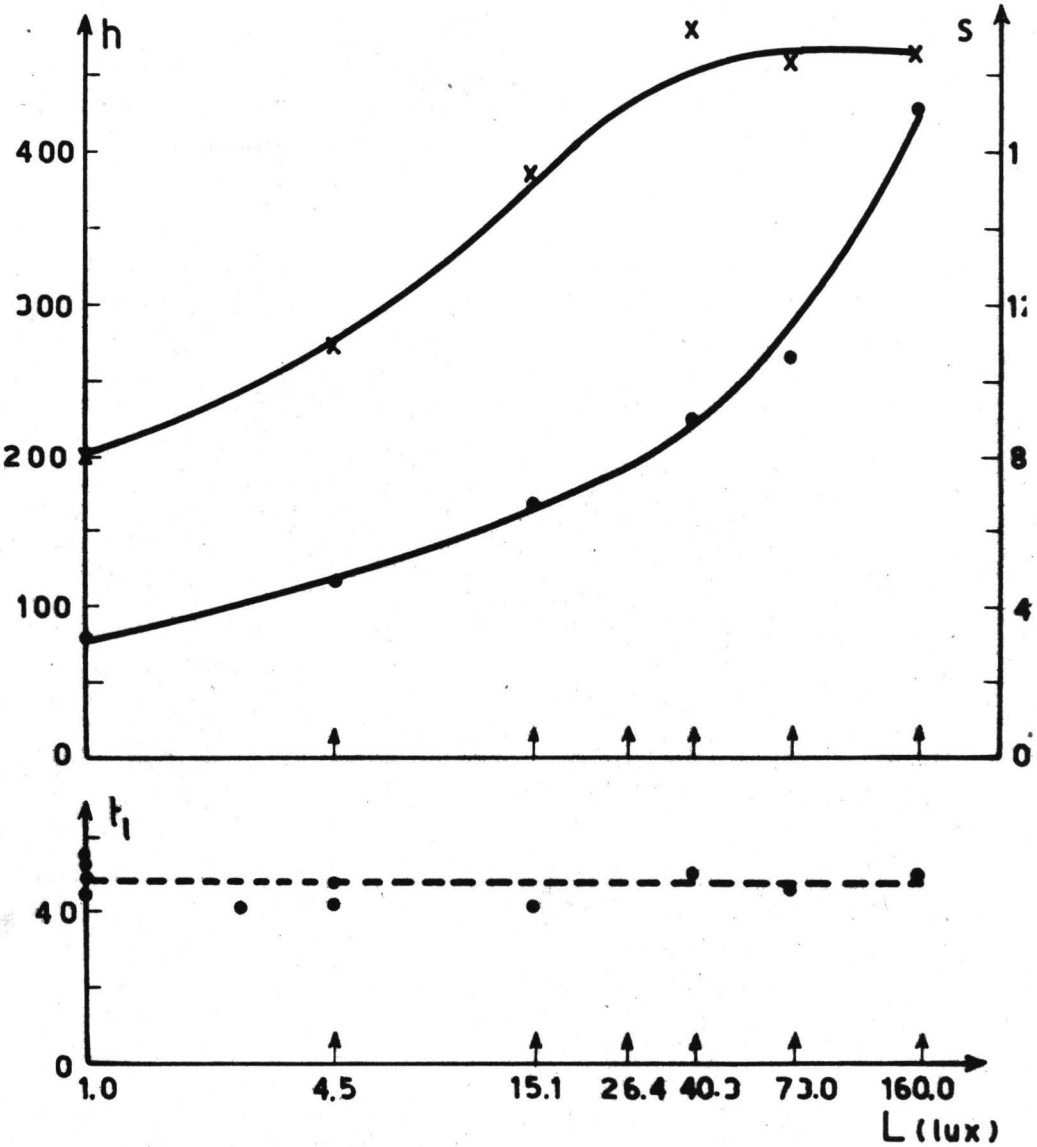


Fig.3 - Variation of the height (crosses), rate of rise (points) and latency time of the b-wave when white stimuli of practically unlimited duration and time of rise t_0 = 2 msec are used, as a function of the logarithm of the final luminous level expressed in lux, and specified as retinal illumination (White light).

during the latency time and is not affected by the energy received after this time.

Looking now at our results, *(fig. 2)*, we find that at *low* levels (below saturation of the b-wave), the 40 msec stimulus should in a sense be regarded as more effective than the 2 msec stimulus, as the energy supplied during the latency time by the first stimulus is about half that supplied by the second stimulus which gives rise to the same response.

The 100 msec stimulus has a latency of about 100 msec. In this case the energy received during the latency time is the same as for the 2 msec stimulus: the two stimuli are equally effective. The only effect of the illumination gradient is to reduce the slope of the b-wave.

At *high* levels, (not far below or above saturation) where the latency is the same for each of the three stimuli, we find the same increase of effectiveness from t_o = 2 to t_o = 4 msec, while from t_o = 40 to t_o = 100 msec, only the slope of the b-wave decreases. It seems likely that for the slowest stimulus (t_o = 100 msec) also the energy received after the latency time contributes to the response.

The same experiment has been performed with green and blue-violet light. Light from a high pressure mercury lamp was filtered either with a narrow band filter with maximal transmission at 5461 A^o or with a $CuSO_4$ solution which cuts off the lines above 4916 A^o.

Only three green and three blue stimuli have been used. The three stimuli of the same colour had the same final intensity, the time of rise being 2 msec, 40 msec and 100 msec respectively. The two quantities E_h and E_s as well as the latency time of the b-wave are reported in *Table I*, both for green and blue lights. These results seem to agree with those obtained with white stimuli of fairly high level, and we may therefore draw the same conclusions about the effect of the illumination gradient.

TABLE I

Green				Blue-Violet			
t_o msec	E_h	E_s	t_l	t_o msec	E_h	E_s	t_l
2	-1%	21%	42	2	6%	28%	44
40	9%	21%	50	40	-5%	26%	48
100	0	0	42	100	0	0	48

(b) Responses to Stimuli of Finite Duration

The results of the experiment with unlimited stimuli cannot be regarded as conclusive about the effectiveness of a slow rise of the stimulus intensity because it is not well known in what way the energy received

after the latency time may contribute to the response. The results of the second set of experiments obtained with two stimuli of finite duration are much more important.

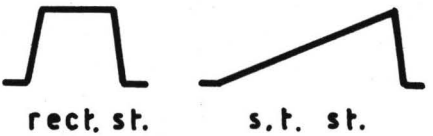


Fig.4a - Stimuli of equal energy but different shape. Left, the rectangular stimulus (rect. st.); right, the saw tooth stimulus (s.t. st.).

Fig.4b - Stimuli of equal energy but different shape.

The two stimuli are shown in *fig. 4a*; the first is a rectangular flash lasting 25 msec, the second is a saw-tooth flash lasting 50 msec. As the final intensity of the two flashes is the same, they supply the same total energy to the eye. The exposure times were chosen greater than 20 msec, in order to avoid some rapid components due to cone reaction appearing in the response *(ref. 7)*, and not exceeding the critical duration in our conditions, which was determined by a preliminary experiment to be 60 msec *(ref. 8)*. In *fig. 5* the mean values of h, s and t_l from records obtained with (a) white, (b) green, and (c) blue-violet lights are plotted against the log luminous level. Solid curves refer to the rectangular flash, broken curves to the saw-tooth flash.

With white and green light, higher and steeper b-waves are obtained with the saw-tooth flash than with the rectangular flash.

With blue-violet light, the b-wave produced by the rectangular stimulus has about the same amplitude and is somewhat steeper that than produced by the saw-tooth stimulus. Moreover, the former has a shorter latency time than the latter.

A third kind of blue stimulus (B in *fig. 4b)* has been used and the response compared with those of the two previous stimuli. This stimulus has the same energy and duration as the saw-tooth stimulus mentioned before (A in *fig. 4b)* while its shape is different. The b-wave obtained has the

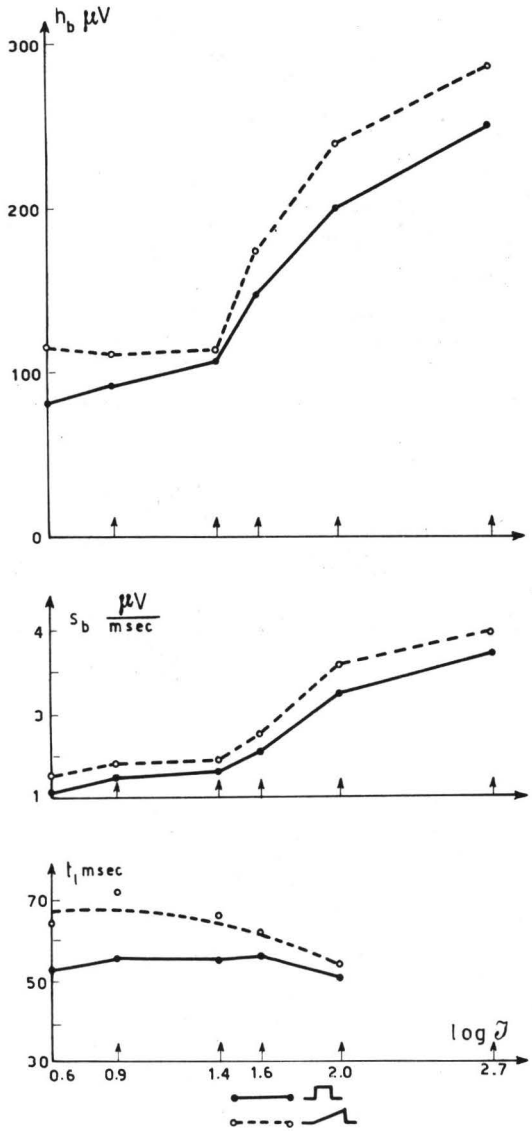


Fig.5a

Fig.5 - Variation of the height, rate of rise and latency time of the b-wave as a function of the logarithm of the peak intensity of the stimulus, expressed in arbitrary units. Results obtained with both rect. and s.t. stimuli, as specified in each figure, are compared: (a) white light; (b) green light; and (c) blue-violet light.

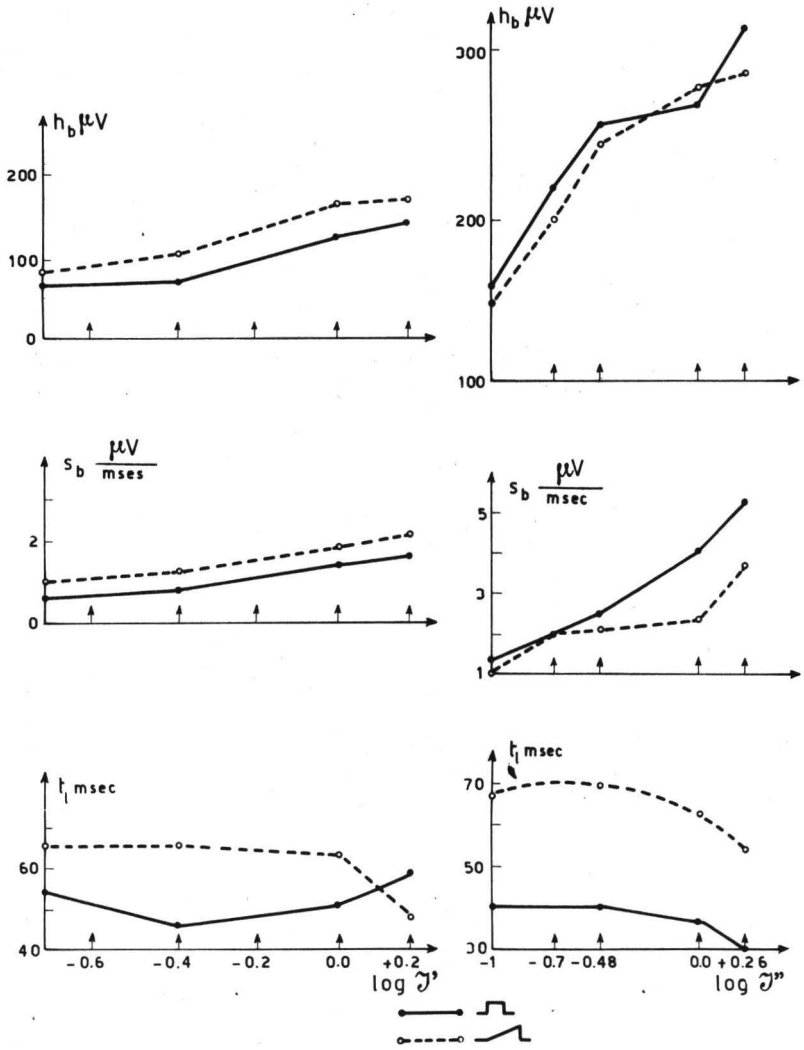

h_b μV
200
100
0
h_b μV
300
200
100
s_b μV/mses
2
0
s_b μV/msec
5
3
1
t_l msec
60
40
-0.6
-0.4
-0.2
0.0
+0.2
log J'
t_l msec
70
50
30
-1
-0.7
-0.48
0.0
+0.26
log J"

Fig. 5b

Fig. 5c

same amplitude as those obtained with the two other stimuli, while its rate of rise has an intermediate value.

From these results it seems possible to conclude that a variation of the intensity during stimulation enhances the activity of the mechanisms which are responsible for white and green scotopic sensitivity. This seems not to be true for the blue mechanism, whose responses tend to be smoothed out and delayed by an increase of the time of rise of the stimulus intensity.

II. PSYCHOPHYSICAL INVESTIGATION

SOME psychophysical experiments have been carried out, with the purpose of investigating vision of time or space gradients of chromatic luminance.

(a) Experiments on the Influence of Pulse Shape Upon Critical Flicker Frequency

The effect of the shape of a single light pulse upon fusion of a flickering light has been investigated by a psychophysical experiment *(ref. 9)*.

Two normal observers took part in the experiment. They were dark-adapted for 30 minutes and then presented with a field subtending 1° at the eye intermittently illuminated with a light-dark ratio equal to unity. Two kinds of pulses ("rectangular" and "saw-tooth" pulses, *fig. 4a*) and four different lights (white, blue-violet, green and red) have been used.

The white light was that emitted by a tungsten filament lamp. The light emitted by this lamp was filtered i) for blue-violet, through a $CuSO_4$ filter which cuts off all the light above 4916 Å; ii) for green through a narrow-band green filter with maximal transmission at 5461 Å; iii) for red, through a filter which cuts off all the radiations below 6100 Å.

The frequency was set at a predetermined value and the luminance varied until fusion was obtained. The measurements were performed foveally as well as at 7°, 10°, and 15° from the fovea.

The results were expressed in terms of the critical luminance, defined as the mean value of the field luminance at critical fusion. In order to facilitate the comparison of the results obtained with the two intermittent lights of different shapes, the following quantity has been computed

$$E = \frac{L_r - L_s}{\frac{1}{2}(L_r + L_s)}$$

where L_r and L_s are the critical fusion luminances for the rectangular and saw-tooth stimuli, respectively. A positive value of E indicates that the saw-tooth stimulus is fused at a lower mean luminance level than a rectangular stimulus of the same frequency.

The results obtained with white and green lights are reported in *Table II* and *Table III* respectively. The first column shows the duration of a single light pulse, the second column the frequency, the third column the angular distance from the centre of the fovea, the fourth column the value of E in percent.

As is seen, E is zero in foveal vision, and assumes increasing positive values when the distance from the fovea increases.

The situation is different in the case of blue or red light, where the critical flicker luminance both in foveal and extrafoveal vision seems to be independent of the shape of light pulses, at least for the frequency considered.

TABLE II

τ msec	f-1 sec	η	E%
30	17	0^0	0
25	20	0^0	0
30	17	7^0 nasal	25%
25	20	7^0 "	26%
30	17	10^0 nasal	72%
25	20	10^0 "	25%
30	17	15^0 nasal	72%
25	20	15^0 "	25%
30	17	15^0 upper	50%
25	20	15^0 "	49%

TABLE III

τ msec	f-1 sec	η	E%
30	17	0^0	0
25	20	0^0	0
30	17	7^0 nasal	25%
25	20	7^0 "	25%
30	17	10^0 nasal	13%
25	20	10^0 "	25%
30	17	10^0 upper	50%

(b) Experiments on the Vision of a Non-Uniform Field with Coloured Light

Two experiments have been carried out in order to investigate the visual response of a spatial gradient of a chromatic stimulus.

The purpose of the first research was to determine whether the contrast effect due to a line of discontinuity of a luminance gradient (Mach band) *(refs. 1,5)* depends on the colour. The observer was presented with a field whose luminance is constant along a given direction and varies perpendicularly according to the diagram of *fig. 6*. The light of a 500W filament lamp *(fig. 7)* was passed through a filter F (Wratten filter No.61 for green, No.25 for red) and produced a diffused illumination of the field D by means of a square opal glass G. Screen S, having a straight edge parallel to one side of G projects its shadow on D, so that the light distribution of *fig. 6* is obtained.

The luminance L_1 of the brighter part of the field is about 3 nits; the luminance L_0 of the darker part does not exceed 10^{-2} nits. These levels were the same for both red and green light. The visibility of the bright Mach band which is seen by the observer along the border A was measured by determining the maximum width of zone AB at which a band is still visible. No appreciable difference has been found between the results obtained with red, green or white light.

The second research had the purpose of investigating whether any contrast effect occurs when the field has uniform luminance and only the colour varies along a given direction. Two fields of different colour (say red and green) were superimposed, as shown in *fig. 8*. The luminance of each field is such as to yield a uniform overall luminance.

The resultant field shows a uniform green zone and a uniform red zone separated by a zone where the colour varies slowly from green to red. The field luminance was about 0.4 nits. The two beams are emitted by two monochromator slits; several different pairs of colours (red-green, green-yellow, blue-red, blue-yellow) have been examined. No colour contrast effect comparable with the luminance contrast has been found.

III. DISCUSSION OF THE RESULTS

THE main result of the ERG experiments seems to be that a white or green stimulus with a low time gradient of luminance is more effective than a rectangular stimulus, while no such effect occurs with blue light.

Very similar results are obtained with intermittent stimulations of different shapes.

The ERG results refer to the scotopic mechanism. The psychophysical results obtained from observations at different retinal locations probably

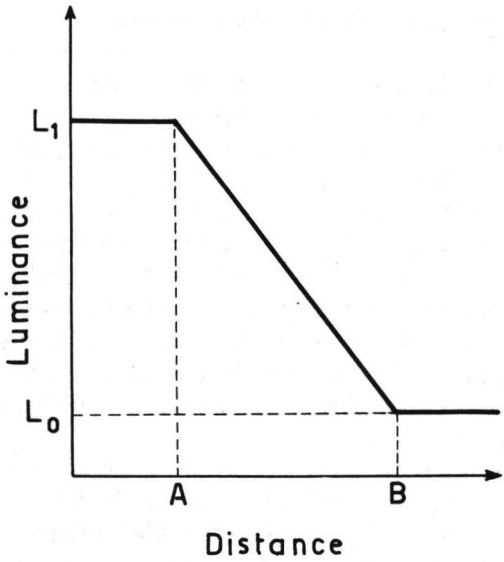


Fig.6 - Luminance distribution of the observed field.

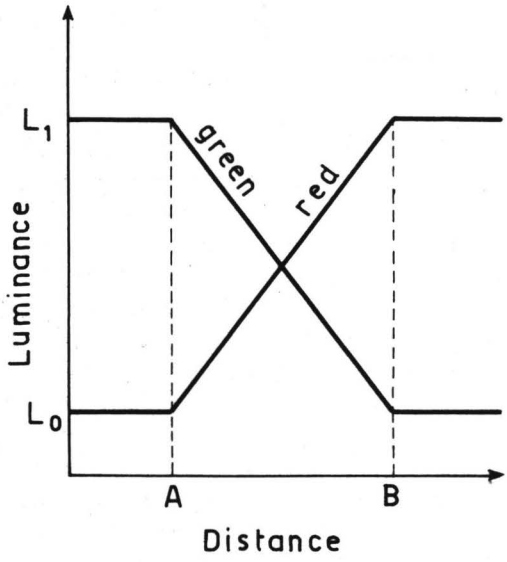


Fig.8 - Colour distribution on the observed field.

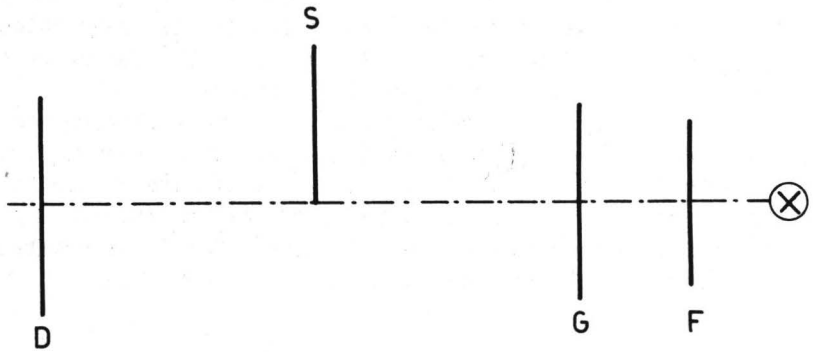


Fig.7 - Sketch of the apparatus.

involve both scotopic and photopic mechanisms. Anyhow, the rods participate in the extrafoveal vision of pulsing lights at fairly high levels, as pointed out by Brooke *(ref. 10)*. If we assume, as suggested by Granit *(ref. 11)* that the rod system is not homogeneous, the hypothesis may be advanced that one kind of rods, the so-called ideal rods, are more sensitive to a slowly rising stimulus, while the rods which are intermediate between ideal rods and cones should be equally sensitive to equal amounts of energy received within a certain time limit, no matter what the energy distribution may be. This hypothesis agrees with Granit's description of the chromatic properties of the intermediate rods, which are supposed to be mainly sensitive to the short wavelengths. The results of the flicker experiment in the fovea with white and green light and also in the periphery with red light, seem to suggest that the cone response is not particularly enhanced by a light gradient. Thus the intermediate rods seem to behave more as cones than as rods from this point of view.

These results seem to contradict the well known difference of response velocity between rods and cones. One would have expected that the classical law of the integration of the energy received within the critical time would be valid rather for the slow rod mechanism than for the faster cones.

The results of the experiments on flickering stimuli of different shapes may be compared also with those on vision of a space gradient of chromatic luminance.

When a field of the kind of *fig. 6* is imaged on the retina, some of the retinal receptors undergo an oscillating stimulation, due to eye movements. Eye movements seem to be one of the main factors in causing the vision of the Mach band, as was pointed out in previous researches *(ref. 5)*. Thus, the two experiments agree in showing that foveal receptors do not present any difference with respect to oscillating stimulations of different colours. Perhaps a different effect would result if the experiment were repeated extrafoveally. But, in this case, quantitative measurements of the brightness distributions would be necessary in order to make a comparison possible. Such measurements have not yet been made.

The experiments on vision of a "linear gradient of colour" and of its discontinuities, show that the mechanism which is responsible for the Mach band is not effective when only the colour of the stimulus varies.

This result seems to agree with the fact revealed by electroretinographic researches that a slow variation of the stimulus wavelength does not produce any electrical response, if the stimulus intensity is constant.

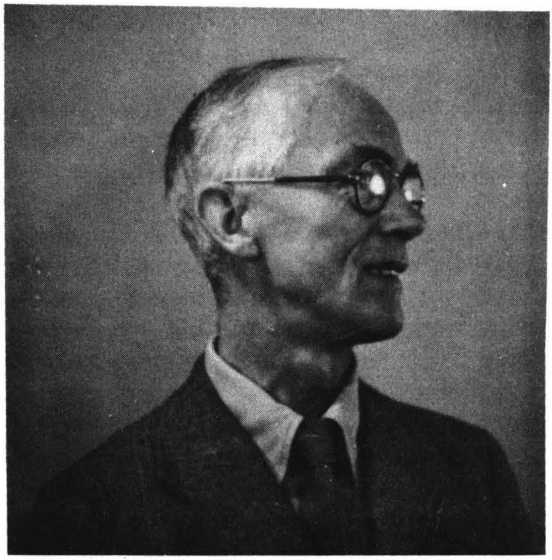
REFERENCES

1. FIORENTINI, A, JEANNE, M. and DI FRANCIA, G. TORALDO., *Atti Fond. G. Ronchi*, 1955, **5**, 371.
2. RONCHI, L. and GRAZI, S., *Optica Acta*, 1956, **3**, 188.
3. RONCHI, L. and MORELAND, J., *Optica Acta*, 1957, **4**, 31.
4. RONCHI, L. and DI FRANCIA, G. TORALDO, *J. opt. Soc. Amer.*, 1957, **47**, 639.
5. FIORENTINI, A. and ERCOLES, A. M., Vision of oscillating non-uniform fields, *Optica Acta*, (in the press).
6. JOHNSON, E. P. and BARTLETT, N. R., *J. opt. Soc. Amer.*, 1956, **46**, 167.
7. WIRTH, A., *Arch. Sci. biol.*, 1956, **40**, 163.
8. RONCHI, L. and STROCCHI, P., *Atti Fond. G. Ronchi*, 1957, **1**, 61.
9. RONCHI, L. and BITTINI, M., *Atti Fond. G. Ronchi*, 1957, **2**, 173.
10. BROOKE, R. T., *J. opt. Soc. Amer.*, 1951, **41**, 1010.
11. GRANIT, R. Sensory mechanisms of the retina, Oxford University Press, 1947.

PAPER 15

EYE-MOVEMENTS IN RELATION TO PERCEPTION OF COLOUR

By R. W. DITCHBURN



Robert William Ditchburn studied Physics at Liverpool University (1919-22) and Cambridge University (1922-28) where he was Senior Scholar of Trinity College and Isaac Newton Student. He was a Fellow of Trinity College and Professor of Experimental Philosophy in Dublin University (1929-46). He worked on visual problems at the Admiralty Research Laboratory (1942-5). He has been Professor of Physics in Reading University since 1946. He is interested in spectroscopy and in the optics of solids as well as in problems of vision. He is author of a textbook on "Light" (Blackie).

15. EYE-MOVEMENTS IN RELATION TO PERCEPTION OF COLOUR

By R. W. DITCHBURN

SUMMARY

SEVERAL investigations have shown that certain involuntary rotations of the eye-ball persist even when the subject fixes his eye as steadily as possible upon a well defined target. Owing to these rotations and also to residual head movements, the image of the target is constantly moving across the retina. By methods previously described, it has been possible to arrange that the eye-movements control the movements of a target so that its image remains on the same part of the retina even when the eye moves. The image so produced is called the stabilised retinal image.

It is found that, with moderately good stabilisation, the perception of form is impaired and that with very good stabilisation the whole field first becomes grey and then goes dark. Normal vision may be restored by introducing controlled movements of the retinal image or by using intermittent illumination. These experiments appear to show that the information by which we distinguish form is conveyed to the brain through on-off signals. These signals may be generated by movement of the edges of a pattern across the retinal receptor mosaic or by intermittent illumination of a stationary image.

It is found that there is an effective desaturation of all hues when the subject views a stabilised image and under certain conditions of imperfect stabilisation all colours are seen as white even when perception of form is still fairly good. It is, however, much easier to produce desaturation of blue and green than of red and there is other evidence that the discrimination of red is based on a process very different from that which is operative for blue and green. An attempt to detect small local clusters of receptors with special properties has given a negative result.

The way in which eye-movements may affect perception of hue is discussed. The possibilities and the difficulties of further investigations are surveyed.

I. INTRODUCTION

IT has long been known *(refs. 1,2,3,4)* that small involuntary rotations of the eyeball persist even when a subject attempts to fix his gaze as steadily as possible on a well defined target. These rotations, and also translations

of the head, cause the image of any object to move across the retina. Though these movements have been ignored in most theories of visual perception, it has been suggested* that the passage of the image of an edge of an object across certain retinal receptors may generate on-and-off signals in the associated nerve fibres and so produce the information required for visual discrimination. In order to see whether eye-movements affect visual discrimination, an apparatus for producing an image which remains on the same part of the retina even when the eye moves was devised. The image which remains always on the same set of retinal receptors is called the *stabilised retinal image*.

The discrimination of shape and of contrast is very much poorer with the stabilised image than in normal vision. We shall see that discrimination of hue and of saturation are also greatly impaired.

In the following discussion, angular movements of the eye are expressed in minutes of arc (abbreviation: min.arc) and distances on the retina are expressed in the same unit, i.e. by equivalent angles in the visual field. The intercone distance in the fovea is of order 0.8 min.arc. The mean *diameter* of the sensitive regions of the cones is probably about 0.4 min. arc.

II. EYE-MOVEMENTS

THE eye-movements which remain when the subject is fixating as accurately as possible include:-

(i) An irregular rapid oscillatory movement called a tremor;

(ii) sharp saccadic movements called 'flicks' (excursus up to 60 min.arc; the movements take about 0.03 sec. and occur at intervals which vary from 0.03 to 5 sec.);

(iii) a slow drift at a rate of a few min.arc/sec. during the interflick period.

Fender *(ref. 9)* has used electronic methods to amplify the tremor which can only just be detected in the drum-camera records. Harmonic analysis of his records, one of which is shown in *fig. 1*, gives a 'spectrum' extending from 20 to 150 cps with a maximum at about 35 cps and a median excursus of 0.2 min.arc.

By analysis of records it is possible to construct a map showing how the image of the point of fixation moves across the retina (see *fig. 2*). The joint effect of flicks and drifts is to keep the image within a region corresponding to 25 minutes of arc in the visual field, i.e. to the central part of the fovea. The tremor is an irregular movement superposed on the

*Hering (1899), quoted by Y. le Grand *(ref.5)*, put forward this idea. It has been independently suggested by several other authors *(refs.6,7,8)*.

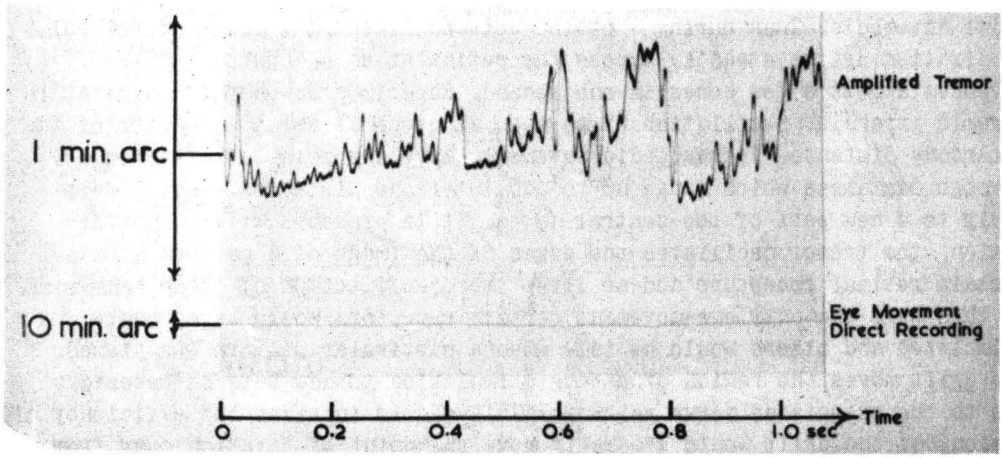


Fig. 1. Records of Tremor. Lower curve shows direct drum camera record and upper curve the electronically amplified tremor.

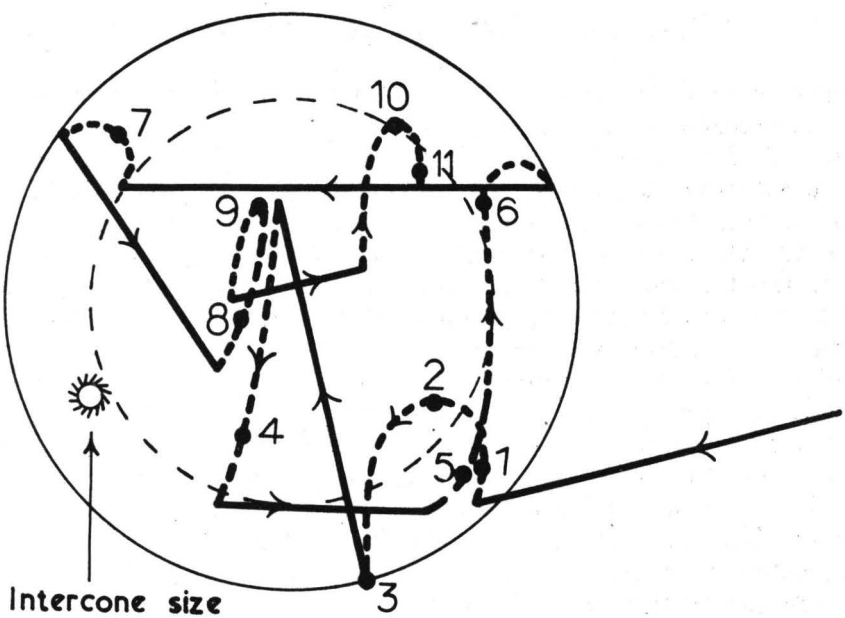


Fig. 2. Movement of image of fixation point across the retina. The diameter of the circle is 10 min. arc. The numbered dots indicate positions at intervals of 0.2 sec. The tremor is not shown. Over this short period the fixation point has remained within 10 min. arc. Over a longer period a somewhat greater "wander" occurs.

drift movements. Thus during a period between flicks the image of the point of fixation drifts steadily across the retina at such a rate that it advances across a few cones in one second. Superimposed on this movement is a rapid irregular oscillation whose mean excursus is about a quarter of the intercone distance. The saccadic movements move the point of fixation through distances which range up to 100 intercone distances, i.e. effectively to a new part of the central fovea. It is probable that in normal vision, the tremor oscillates the edges of the image of a pattern across certain retinal receptors and so fires the on-off action of these receptors. If this were the only eye-movement certain receptors would be strongly stimulated and others would be idle when a particular pattern was viewed. The drift moves the region of strong stimulation to new sets of receptors and to the associated nerve pathways. This should increase the efficiency of vision but the drift would gradually move the point of fixation away from the central fovea. A restoring action is needed and this is provided by the flicks.

III. METHODS OF PRODUCING A STABILIZED IMAGE

IN the experiments to be described three different pieces of apparatus have been used to produce the stabilised image:

Apparatus A. Interference Method (ref. 10)

A contact lens *(ref. 7)* carries a stalk on which is mounted a slice of crystal between two pieces of polaroid *(fig. 3)*. The subject sees a pattern of coloured rings and grey brushes. The central ring is about 4° diameter and the whole field covers about 15°. The choice of pattern is limited. One cannot get sharp patterns or a bipartite field. This apparatus is probably exceedingly good for eliminating slow movements.

*Apparatus B. Reflecting Mirror**

A beam of light is reflected from a mirror attached to a contact lens. When the eye rotates, the beam turns through twice the angle. It passes through an optical system which produces an angular demagnification so that the subject sees an image whose angular movement is the same as that of his eye *(fig. 4)*. Early designs *(refs. 2,3)* of this type gave partial stabilisation in respect of movements in one plane. An advanced design used by Fender *(refs. 4,9)* gives stabilisation better than 99.9% in respect of both horizontal and vertical rotations. It requires severe fixing of the head. A field of up to 2° is used.

Apparatus C

This is similar in principle to apparatus A but gives optical stabilisation for translational movement of the head as well as for rotation of

*See *ref. 9* for a general account of methods of this type.

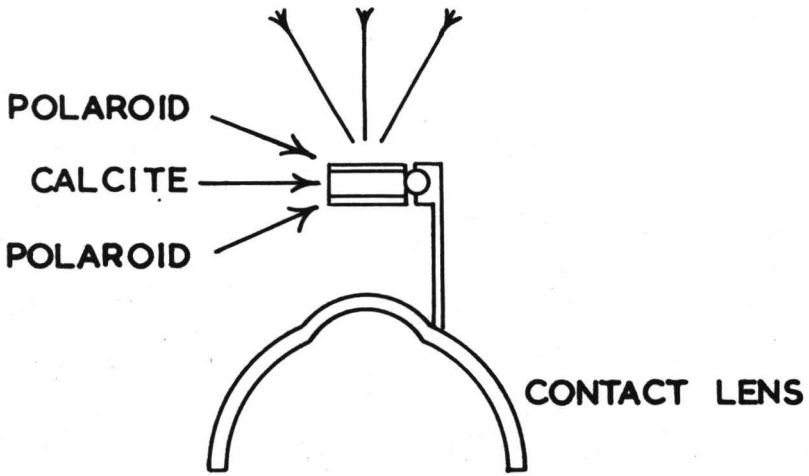


Fig.3. Apparatus for Method A.

the eye. This apparatus is at present fitted with a crude bipartite field colour matching apparatus. A field of 5^{0} is available.

It is intended to use apparatus C for detailed colour work when it is fully developed.

IV. EXPERIMENTAL OBSERVATIONS

IT would appear that the apparatus described should be used for at least two kinds of experiments on colour vision: (i) small scale exploration, (ii) colour matching.

(i) Small Scale Exploration (Method B)

It is possible to explore the fovea with a small spot of light which may be white, blue, green or red. If there exist small regions in which one of the receptors of the simple trichromatic theory (say the green receptor) predominate, we might find local variations of sensitivity and of hue discrimination. It is possible to hold the image of a point source steady on the retina to within about 0.1 of the intercone distance and then to move it slowly across the retina in steps which may be only a few times the intercone distance. A pilot experiment *(ref. 6)* of this type has been carried out using a spot of light which was so small that if the image on the retina were limited only by diffraction, then 70% of the light would sometimes fall on one cone and most of the remainder on about 5 cones. Probably

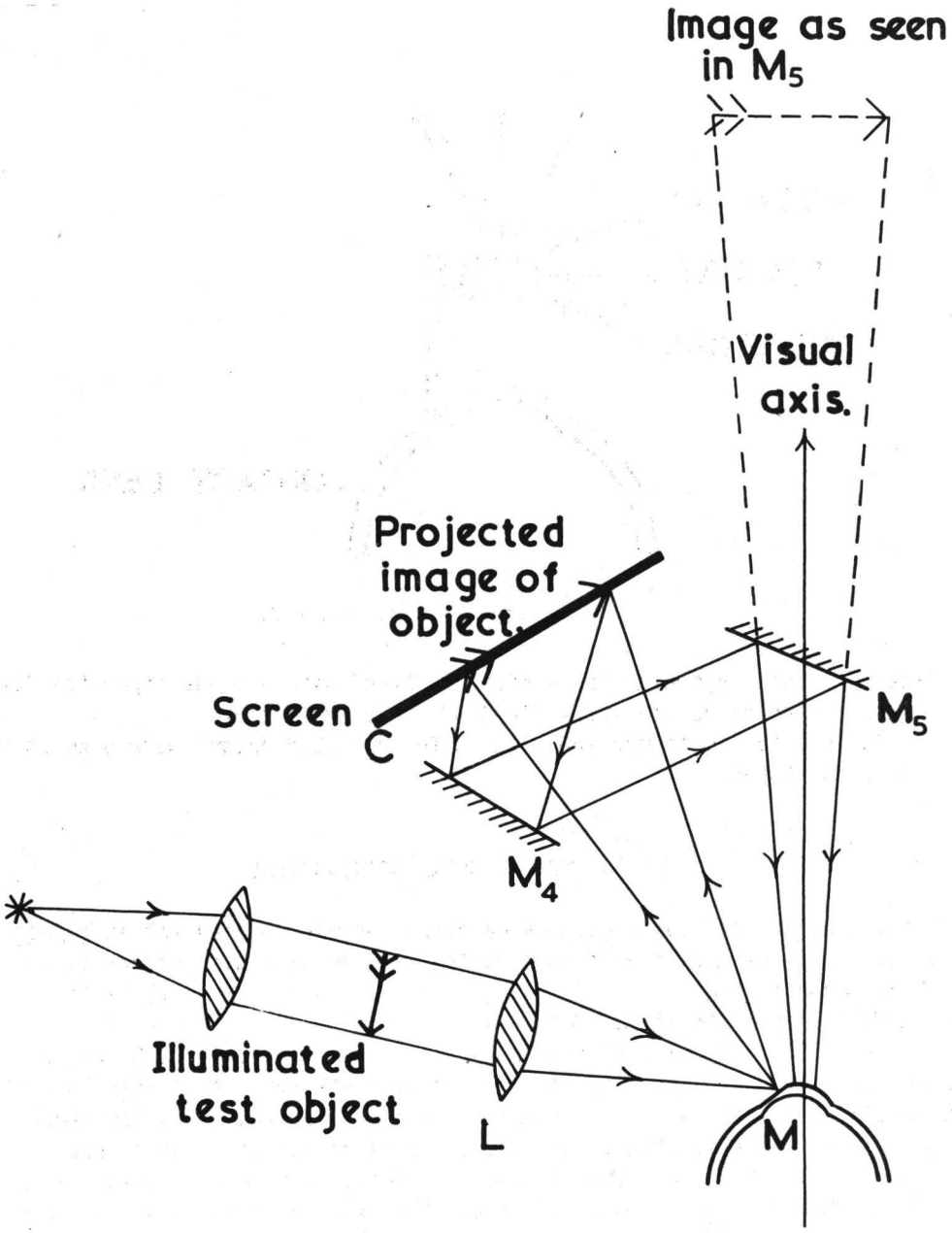


Fig. 4. Apparatus for Method B. The method illustrated is an early design giving stabilisation in one plane only. A more elaborate method is described in *ref.4*.

failure of accommodation, aberrations, the effect of the pulse on the position of the retina and similar effects spread the light so that most of it fell on about 10 cones. About 10 more cones would get a much weaker illumination and there would be a still more feeble illumination of the rest of the retina due to scatter in the optic media. White, blue, green and red spots (Ilford "spectrum" filters) were used in this experiment. Within the fovea no local variations (such as those suggested by Hartridge *(refs. 11,12)*) were observed. These results have been discussed with Professor Hartridge who suggested that the spot might have been so bright that the "spill" of light around the geometric image was sufficiently strong to fire receptors of all kinds. This is a valid point and the experiment ought to be repeated with weaker illumination and with spots of varying size. However, so far, the evidence in regard to small scale local variation of properties is negative.

(ii) Colour discrimination

It is easy to design on paper a series of experiments in which the subject is asked to view stabilised images and to report on his ability to discriminate differences of (a) brightness, (b) hue and (c) saturation. One may design further experiments on colour matching with a stabilised bipartite field. The phenomena observed in experiments on brightness discrimination (i.e. determinations of contrast threshold) in a white field will now be described.

When the subject views a stabilised image he has normal vision for a period of 1 or 2 seconds *(refs. 10,13)*. Then he suffers marked loss of ability to discriminate form for a period of up to 20 seconds. Vision then suddenly improves for a few seconds but soon deteriorates again. The fraction of time for which the subject is able to see moderately well varies with luminance and with many other conditions. With a luminance of order 5 ml. and good stabilisation the fraction may be less than 10%. It can be restored to near 100% either by intermittent illumination at a suitable frequency or by introducing controlled movements of the retinal image *(ref. 13)*.

With moderately good stabilisation (98% of the natural movements annulled), the contrast threshold increases a great deal. In a series of experiments at luminances in the range 5 ml. to 50 ml. using a field of about 1^{0}, the observer could perceive the contrast 50% of the time when one half of the field was twice as bright as the other. In normal vision a one or two per cent difference in luminance would have been observable.

When the stabilisation is still better (99.9% annulment of natural movements), a thick black line (8 min.arc wide on 1^{0} field of brightness 15 ml.) disappears. The whole field goes grey and then black. Using the interference apparatus (A) with the wide field of about 15^{0}, and a luminance of 50 ml. (white light), the fringes disappear after a few

seconds leaving a grey field, which later goes black. After a time which varies up to 20 sec the eye moves sharply and the fringes reappear. At lower luminances of 5 ml. or 0.5 ml. the fade to black is obtained more easily. Partial regeneration of pattern is reported by some subjects without any obvious accompanying eye-movement.

Since, with very good stabilisation, there is a total failure of the light sense there can be no possibility of colour matches. We must begin by making qualitative observations of coloured patches of light seen against darkness or in juxtaposition with other colours. Later, we may be able to do colour matching under conditions where the "black out" is prevented either by introducing small controlled movements or by intermittent illumination.

The results so far obtained with observations of coloured patches are:-

Apparatus B

Using a 1^{0} patch and a luminance of 5 ml. blue and green patches both appear as a faint bluish grey. They are indistinguishable from one another and almost indistinguishable from white. Red patches remain subjectively red so long as they are seen at all. Disappearance of shape is less pronounced with red than with white or blue or green. Normal vision may be restored by using intermittent illumination. White, green and blue have an optimum frequency at about flicker fusion frequency. With red, the effect of flicker is always less and is also much less frequency-dependent.

In these experiments, Ilford narrow cut spectrum gelatine filters red, yellow, green, blue were combined with Chance neutral filters. Transmission was calculated from manufacturers' specifications (including correction for thickness of Chance filters), and C.I.E. photopic visibility factors. Final fine adjustment of luminance was made with polaroids.

Apparatus A

Using the 15^{0} field it was found that at 50 ml.,

(i) with white light, the fringes disappear and the field goes grey-brown and occasionally black;

(ii) with red (Chance's OR_1 or OR_2 or cinemoid 14), the fringes disappear leaving a subjectively red field. The fringes regenerate from time to time;

(iii) with green (cinemoid 19), the fringes fade leaving a green field which goes black after about 2 minutes;

(iv) blue (cinemoid 24) behaves in a similar way to green.

At 5 ml.,

(i) red fades first to a red field and then to a "colour" which the observers refuse to describe - it is not red, it is not a true grey. It cannot be described in terms of any normal colour. After about 2 minutes the field goes black;

(ii) blue, green and white behave as with 50 ml. but the period with black field is longer.

At 0.5 ml.,

all colours fade to black. Intermediate stages are not easily observed.

It is found generally that disappearance of fringes happens less with red than with the other colours. The flicker fusion frequency is normal within experimental error.

Apparatus C

When patches of different hue* are juxtaposed with luminances in ranges 5 to 20 ml. we find:-

(i) discrimination of hue is difficult if photopic brightnesses are nearly equal;

(ii) momentary interruption restores hue discrimination temporarily;

(iii) rapid voluntary movements of the eye generate colour localised at the boundaries of the stimulus patch;

(iv) the after-images are abnormally vivid and of the complementary hue;

(v) sometimes the maximum loss of hue or brightness discrimination occurs at the same time as loss of shape - sometimes these two effects occur separately.

This last effect is related to some observations on brightness discrimination in which two parts of a bipartite field were separated by a thick dark line. The luminances in the two parts were roughly in ratio 2:1. Sometimes the black line disappeared while the difference of brightness remained clear. At other times the two parts of the field appeared to be of equal brightness but the black line was seen clearly. A similar effect occurs when two coloured patches are separated by a black line. Disappearance of the line occurs, disappearance of the hue difference also occurs but not necessarily at the same time. When the hue difference disappears, one hue may appear to spread across the whole field, for example a bright green and a bright yellow placed side by side may appear all yellow. There is a general tendency for the patch with higher luminance and area to "dominate" when these differences are large.

Dark Adaptation Curves (Apparatus B)

A number of dark adaptation curves were obtained for foveal vision using the 1^0 patch. The sensitivity of the eye fluctuates widely. The low sensitivity end of the fluctuation cannot be obtained - even a bright field goes black. The high sensitivity end with very good stabilisation is 40 times less sensitive than normal vision, i.e. the threshold is 40 times higher than the normal photopic threshold. Measuring on the maxima of sensitivity and using about 99.9% stabilisation, dark adaptation curves for red and blue

*Produced by inserting Chance's coloured glasses (OR_2, OG_1, OB_8, OY_4 and OY_1).

were obtained. The form of the curves was the same as that obtained for normal photopic adaptation and the ratio of sensitivity for red to that of blue after 10 minutes adaptation was the normal photopic ratio. Thus, in respect of dark adaptation, foveal vision with the stabilised image has some of the features of normal photopic vision.

DISCUSSION

FROM the results reported two points should be emphasised:-

(i) The negative result of the attempt to find local variations in the fovea.

(ii) The difference between the observations with red on the one hand and with white, blue, green on the other.

The latter result may be related to the work of Rushton *(ref. 14)*. It appears that in stabilised vision with the fovea the subject perceives "red" when only one of the two pigments found by Rushton is bleached and perceives a faintly bluish grey when both pigments are being bleached. It appears that the discrimination of blue, green and white from each other depends on eye-movements in a different way from the discrimination of red. Also the discrimination of form in a white, green or blue field is more affected by partial stabilisation than it is in a red field. When the colours are viewed in a wide field of 15^{0} (with the smallest ring in the pattern of diameter 4^{0}) there is still a difference between red on the one hand and blue, green, white on the other but not the same difference.

The sensitivity of the eye when the subject views a moderately well stabilised image is much less than normal but the loss of discrimination of form, brightness and colour is not explicable in terms of a loss of sensitivity. Vision with the stabilised image is not the same as normal vision with a dark filter or a diffusing glass interposed.

We have shown that the natural eye-movements have a signification function in relation to discrimination of brightness, hue and saturation. We are very far from having the data on which to form a theory of how eye-movements affect these functions.

Our original programme was to measure visual performance (including colour matching) using the best possible conditions of stabilisation. Since we have found that, under the best condition the field goes black, we must modify this programme by deciding to "spoil" the stabilisation in some way. We may either:-

(a) adjust the apparatus to leave a certain percentage (say 2%) of natural movements

or

(b) introduce movements of the retinal image which are controlled. These can be fast or slow and undirectional or oscillatory

or

(c) use intermittent illumination.

Some experiments on the effect of (b) and (c) on perception of form in a white field have been carried out *(ref. 9)*. It is hoped to extend these to colour matching.

ACKNOWLEDGEMENTS

THIS paper describes part of a co-operative research programme in which Dr. D. H. Fender, Dr. Stella Mayne, Mr. M. B. Clowes and Mr. R. M. Pritchard are taking part. The last of these is supported by a grant from the Medical Research Council. This investigation is also supported (in part) by a research grant (B-1233) from the National Institute of Neurological Diseases and Blindness, Public Health Service, U.S.A.

REFERENCES

1. LORD, M. P. and WRIGHT, W. D. *Rep. Progr. Phys.*, 1950, **13**, 1.
2. DITCHBURN, R. W. and GINSBORG, B. L. *J. Physiol.*, 1953, **119**, 1.
3. RATLIFF, F. and RIGGS, L. A. *J. exp. Psychol.*, 1950, **40**, 687.
4. DITCHBURN, R. W. and FENDER, D. H. *Optica Acta*, 1955, **3**, 128.
5. LE GRAND, Y. *Scientia*, 1955, **49**, 1.
6. AVERILL, H. L. and WEYMOUTH, F. W. *J. comp. Psychol.*, 1925, **5**, 47.
7. JONES, L. A. and HIGGINS, G. C. *J. opt. Soc. Amer.*, 1948, **38**, 398.
8. MARSHALL, W. H. and TALBOT, S. A. *Biol. Symp.*, 1942, **7**, 117.
9. FENDER, D. H. Ph.D. Thesis (Reading), 1956.
10. DITCHBURN, R. W. and PRITCHARD, R. M. *Nature, Lond.*, 1955, **177**, 434.
11. HARTRIDGE, H. *Philos. Trans. roy. Soc. B.*, 1947, **232**, 519.
12. HARTRIDGE, H. and THOMSON, L. C. *Brit. J. Ophthal.*, 1948, **32**, 581.
13. DITCHBURN, R. W. *Research*, 1956, **9**, 466.
14. RUSHTON, W. A. H. Paper 1 of this Symposium.

PAPER 26

A TEMPORAL FACTOR IN COLOUR DISCRIMINATION

By D. FARNSWORTH

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SUMMARY

THE C.I.E. colour mixture diagram has been converted to the uniform chromaticity data reported in three major studies to facilitate comparison and scientific and commercial applications.

Analysis of the three studies of colour spacing shows that they are not incompatible and that their differences may depend upon the duration of observation used in obtaining each.

Evidence has been presented to show that the ability to discriminate in the blue dimension of colour space reaches a maximum in a fraction of a second and is subsequently less effective relative to red-green discrimination.

It was not found that a non-Euclidean space was necessary for the description of colour differences in the chromaticity plane.

It appears that studies in colour scaling and redetermination of systems of chromaticity differences should be made under controlled durations of visual fixations and that systems intended to describe colour tolerances should be related to the conditions of observation obtaining in the intended scientific, aesthetic, industrial or commercial application.

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THE standard C.I.E. Mixture Diagram was not intended to be a uniform chromaticity scale diagram, that is, one in which equal space differences represented equal sense differences. Shortly after its publication, various attempts were made to find linear transformations which would represent equal chromaticity differences per unit of space. On the whole, they failed so completely it became evident that no rectilinear solution could be expected. Among the best known of these simple "perspective" type conversions are Judd's RUCS and Adam's chromatic space. Each has to make sacrifices in parts of the diagram in order to be approximately useful in others.

Assuming that the C.I.E. Mixture Diagram was even approximately accurate, it appeared that the colour *mixture* processes could not be directly or simply related to chromaticity discrimination of the "mixes", and therefore

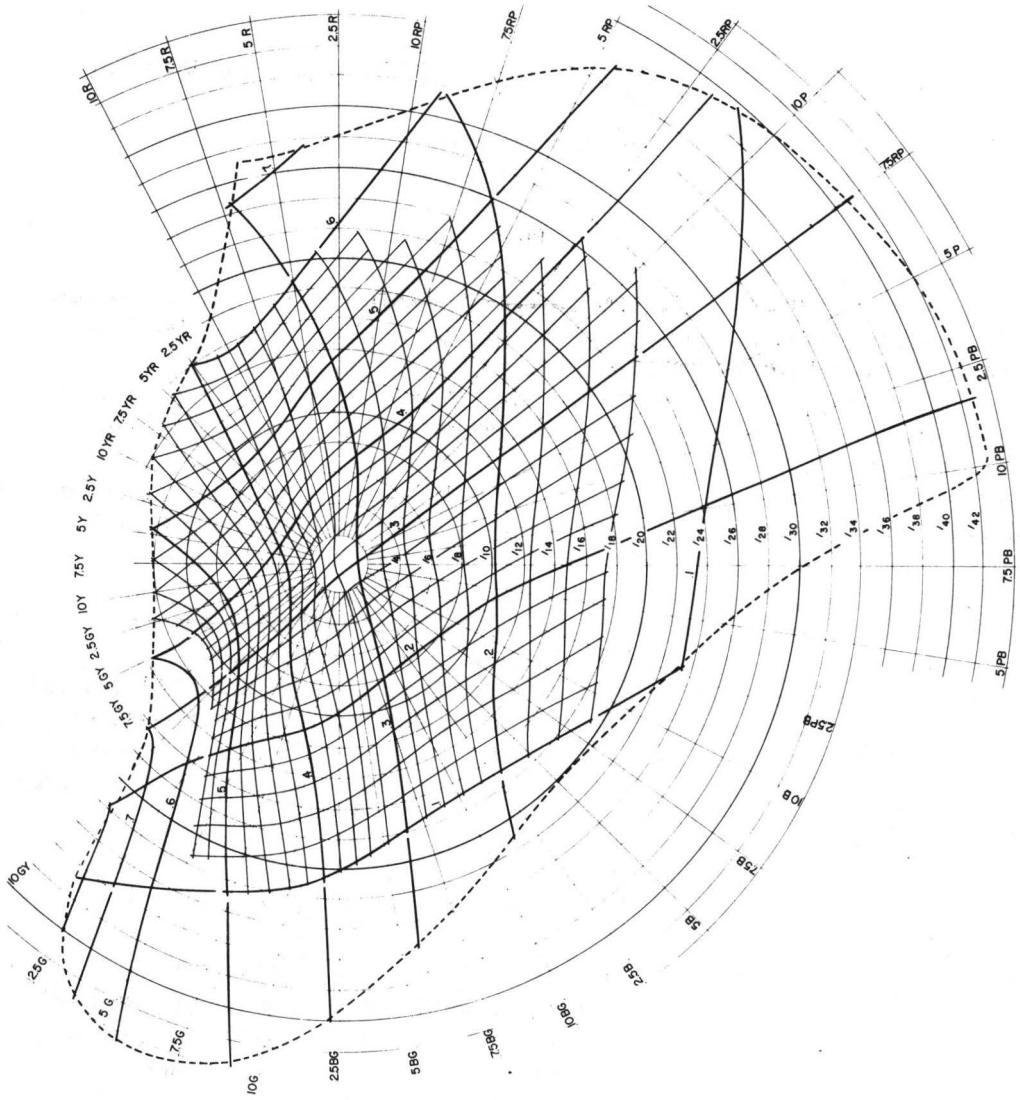


Fig.1. C.I.E. values fitted to Munsell radial spacing. The 0.02 grid covers approximately the area reported by the O.S.A. Committee; peripheral areas are extrapolations.

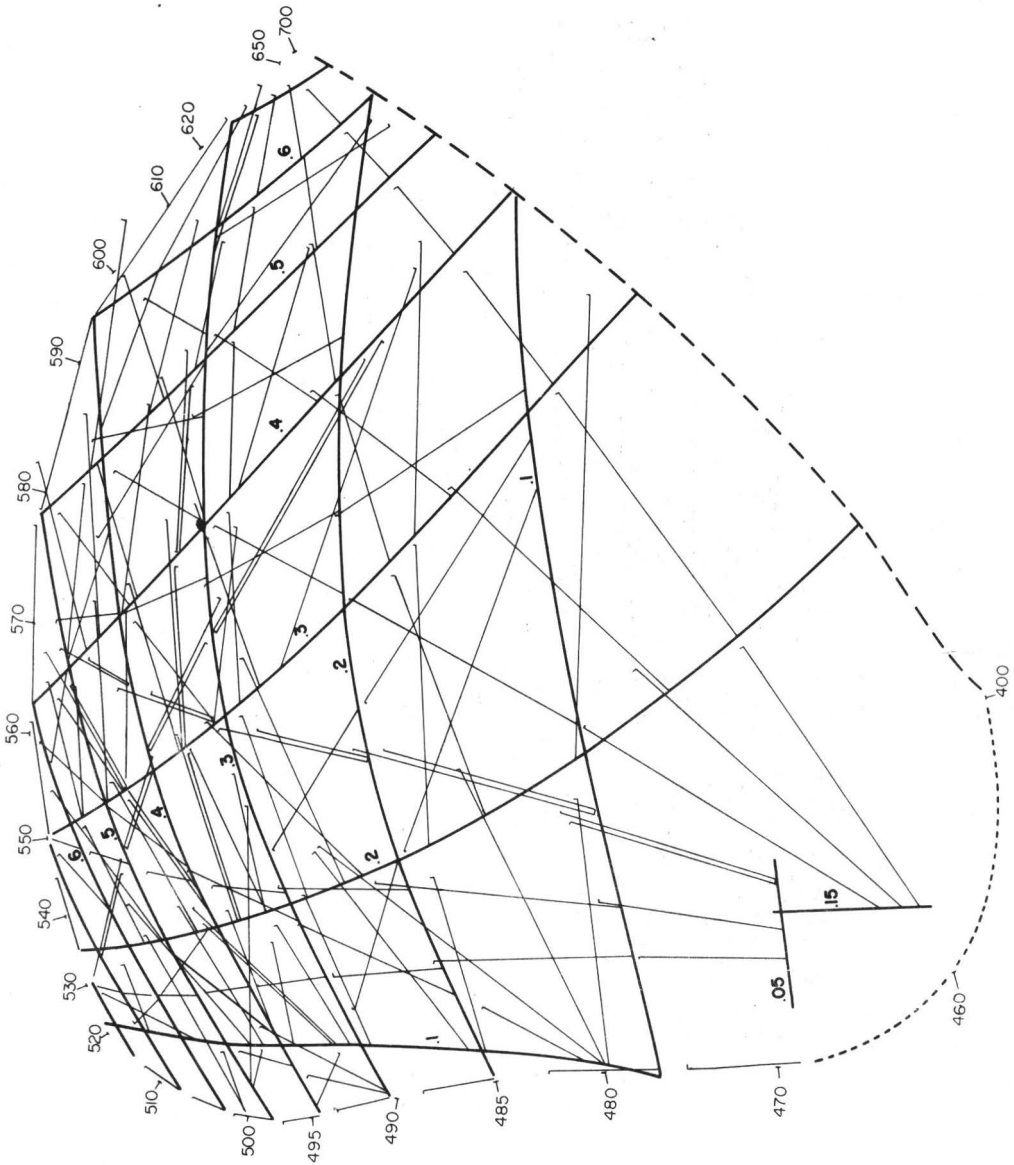


Fig.2. A curvilinear conversion of the C.I.E. Diagram best fitted to Wright's chromaticity discrimination data. A few lines have been omitted for clarity. Parellel lines are those for Obs. W.D.W. and for the average of his other observers.

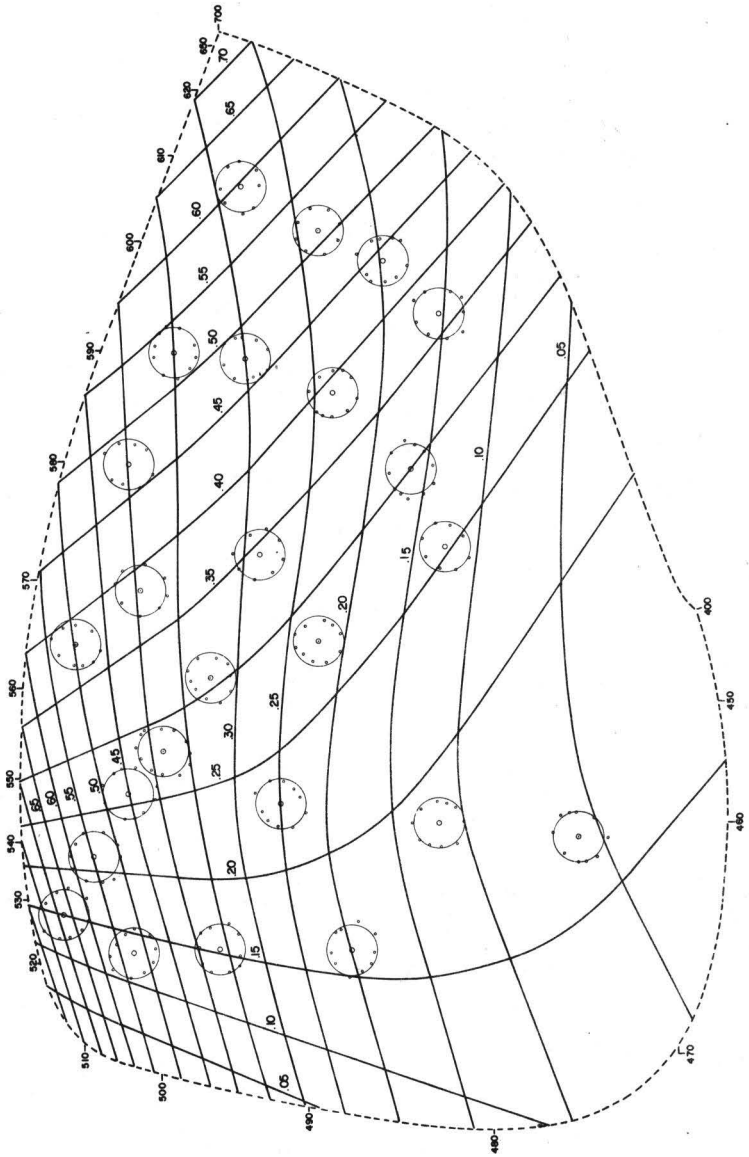


Fig.3. A curvilinear conversion of the C.I.E. Diagram on which MacAdam's ellipses plot approximately as circles of the same size. Small central circles are the size of the mean standard deviation of the matches. Large circles are ten times the standard deviation. Small circles bordering the large circles are ten times the O values shown by MacAdam in his figures 23-47 *(ref.3)*.

it would be necessary to accumulate independent data on equal sense differences of stimuli which would then be specified point-by-point in the C.I.E. System. Three large scale studies appeared in 1941-1943.

The Munsell Color System represented the first comprehensive attempt to set up a psychological system of equispacing. Irregularities in the original spacing were improved by the work of the Optical Society of America Subcommittee which reported in 1943 *(ref.1)*. W. D. Wright had published in 1941 *(ref.2)*. MacAdam's study appeared in 1942 *(ref.3)*, and was followed by similar investigations from the Eastman Kodak Research Laboratories by Brown and MacAdam in 1949 *(ref.4)*, and Brown in 1957 *(ref.5)*.

The three systems of Munsell, Wright and MacAdam were all arrived at by widely different observational techniques and the data was presented in highly diverse fashions. Inspection suggested that the differences were extreme and it became generally accepted that they were irreconcilable.

The questions raised in this paper resulted from an attempt to compare the results of the three studies. For this, the C.I.E. co-ordinate lines were adopted as the common metric; that is, the C.I.E. diagram was distorted to fit each of the three systems. Comparison between the forms of the C.I.E. grids indicated the extent of agreement - or disagreement - between the systems.

Before making the comparisons let us examine the method and the estimated degree of reliability of each of our conversions. *Fig.1* shows the shape of the C.I.E. diagram when the corresponding values are plotted on the Munsell radial network at Value 5. The O.S.A. Committee's report does not specify the shape of the spectral locus which, therefore, had to be approximated by extrapolation. The extrapolations were made by continuance of the progressive change in chroma steps as they were shown in the report. The hue curvatures were simply continued freehand to the spectral limits. Since part of the Committee's report was extrapolated, this further extrapolation must not be taken too rigorously, but it is convenient in order to find the general configuration of the whole region within the spectral locus for visualization. However, the final comparisons will be made only with the region actually studied by the Committee which is the central area of the figure divided into 0.02 co-ordinates. Since the diagram is a point-to-point transformation it is precise within this area.

The problem of how to convert C.I.E. co-ordinates to Wright's data was much more difficult. Wright represented obtained Noticeable Differences by short lines which lay in pathways between spectral loci on the C.I.E. Diagram. Mathematical and geometric analysis proved to be of little help and the following method was finally used. The area within each square formed by 0.1 differences on the x and y axes was treated separately. The average of the length of the discrimination lines for each section of pathways within each 0.1 square was determined. The reciprocal of these values divided by the cosine of the angles of the pathways determined the

approximate shape of the 0.1 squares which were then drawn to scale and assembled. These parallelograms were then adjusted to fit by trial and error seeking the minimum deviations from the data for all the 187 pathway sections. When this point was apparently reached it was found that 171, or over 90% of the sections fitted the C.I.E. grids with deviations of no more than 20%. This construction and proof is shown in *fig.2.*

The MacAdam data was obtained from colour matches made around 25 centres and the standard deviations of the matches were calculated. When plotted on the C.I.E., these points formed a series of ovals. When these dimensions were mathematically converted by Dr. Silberstein to C.I.E. spacing so that the ovals became circles of equal size, and these areas were assembled and pasted up in paper they produced the famous Easter bonnet which was exhibited to the Optical Society of America in 1942. Based upon this artifact, and Silberstein's computations *(ref.6)*, MacAdam repeatedly maintained that his data could not be subsumed on a flat surface: "The impossibility of flattening this surface without rupture or distortion is quite evident and the curvatures computed by Silberstein constitute a rigorous proof of this conclusion" *(ref.7)*.

If we accepted this view it would be difficult to compare the MacAdam data with other systems. Upon inspection, the supposed evidence supporting the need for a three dimensional chromaticity plane did not appear conclusive. It is our belief that a rigid and too elegant mathematical treatment of inherently variable data was responsible for this view. The error was in ignoring the nature of psychological functions. It is too much to suppose that MacAdam's observer was free from observer variability. In fact, subsequent experiments *(refs.4,5)*, supervised in part by the same investigator, using similar techniques, in the same laboratory, resulted in discrepancies from the original data of several *hundred* percent. It is only necessary to permit a latitude of 20% in order to fit the MacAdam data to a construction on a flat plane.

In *fig.3* is shown a conversion of the C.I.E. Diagram upon which the radial diameters of all the MacAdam ellipses plot on circles of the same size with no error of greater than 20%. In fact the majority plot within 10% of the circles. 238 points are shown. Since MacAdam's data has been mishandled in the past, we have presented the calculated points in detail on this diagram in order that the conversion could be given a point-by-point check by unbelievers.

This is *not* evidence that a three dimensional space *is not* required for plotting equal chromatic differences, but it is evidence that within reasonable limits of variability the MacAdam data does *not* prove that a three dimensional space *is* necessary.

The skeletons of the three conversions are shown in *fig.4* for comparison, arbitrarily reduced to a size in which the dimensions from 500 millimicrons to 700 millimicrons are about equal. Inspection certainly indicated that the three studies reported highly different facts.

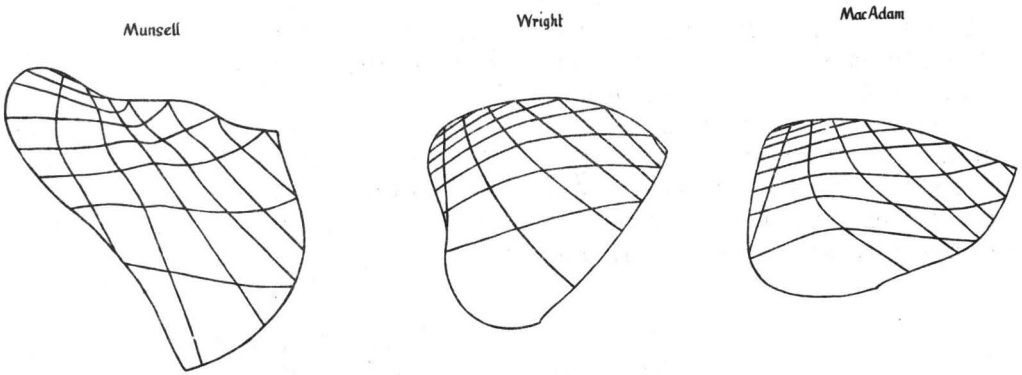


Fig.4. Co-ordinates at 0.1 intervals from *fig.1-3* are shown for comparison.

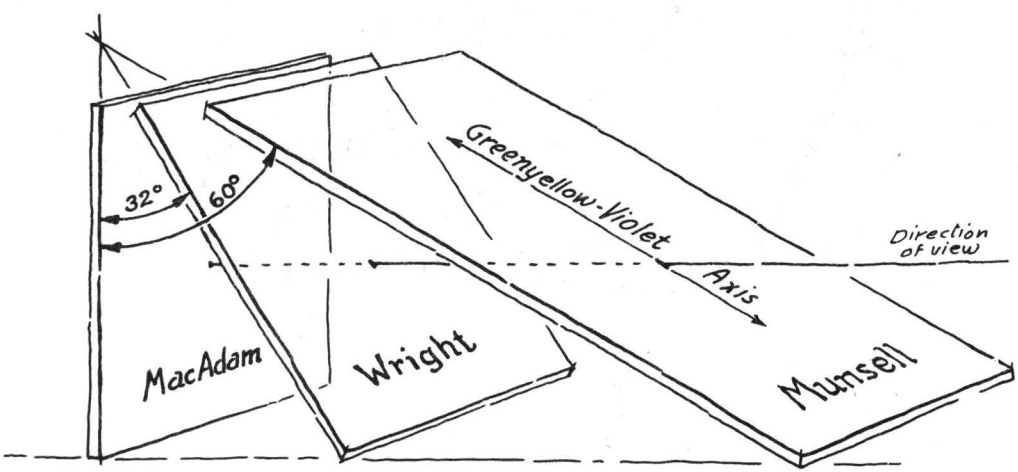


Fig.5. Angles at which the diagrams were tilted to secure best visual coincidence.

Various comparative analyses were attempted without success until the following procedure was used. The diagrams were transferred to sheets of Plexiglas and these were tilted and moved about until the best agreement was obtained by visual sighting. A rather surprising fact then resulted: the best agreement was obtained for all three when all were orientated along the violet-greenyellow axes and tilted so that the latter were reduced in various proportions to the red-bluegreen axes. The sketch in *fig. 5* will make the procedure clearer.

Placing the MacAdam chart in a vertical position the best agreement was obtained with Wright when it was at 32° to the MacAdam and best for the Munsell chart when it was at 60° to the MacAdam. The charts were then photographed in this position with a telephoto lens in order to reduce perspective effects so far as possible.

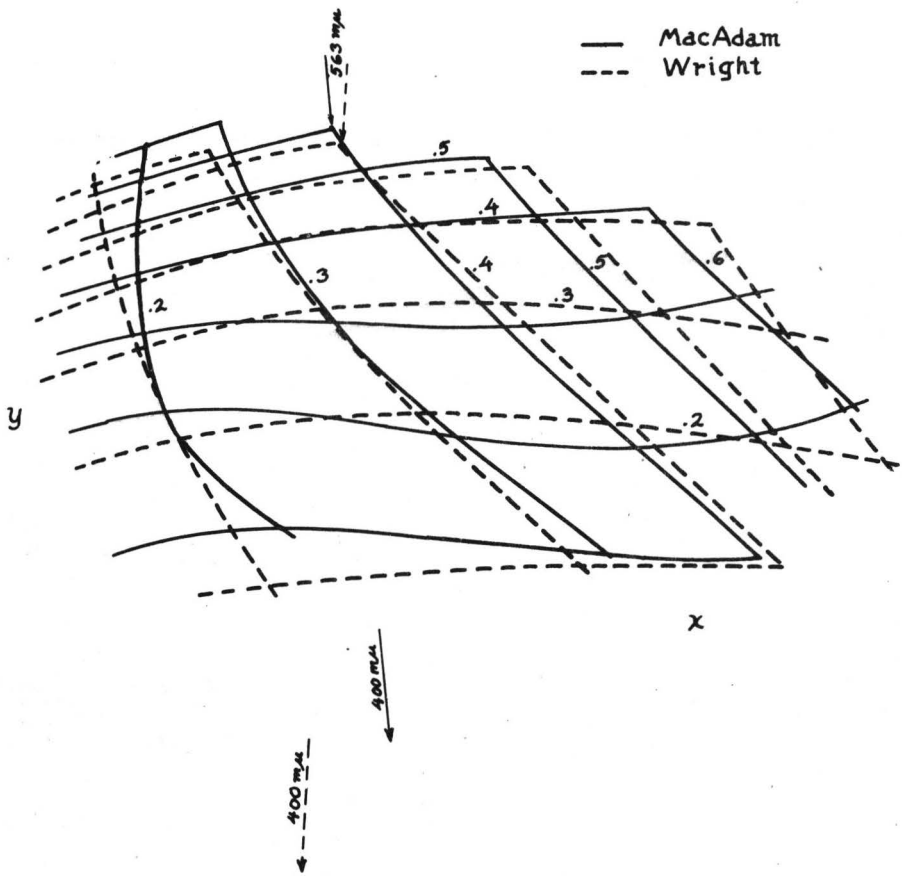


Fig.6. View when Wright diagram is inclined 32° to the MacAdam.

In *fig. 6* are shown those portions of the C.I.E. charts which Wright and MacAdam investigated in common. The Wright diagram stands at a 32° angle to the MacAdam; thus the violet-greenyellow axis of the Wright diagram is reduced to 85%. The coincidence is excellent for this type of data, and remarkable in that only one, uniform treatment was needed to bring about this agreement.

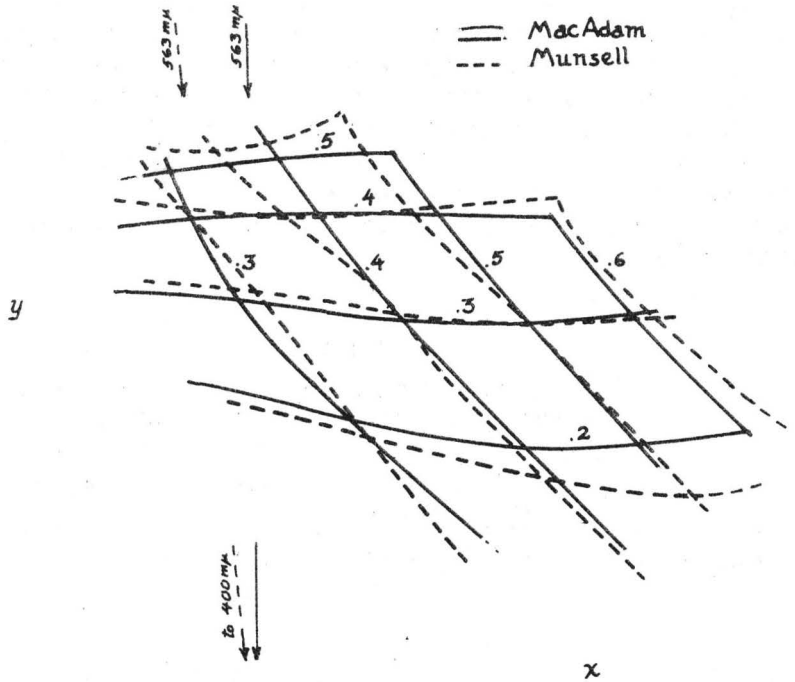


Fig.7. View when Munsell diagram is inclined 60° to the MacAdam.

In *fig. 7* are shown the results of photographing the Munsell slide at an angle of 60° to the MacAdam which reduces the Munsell violet-greenyellow axis to exactly half. Only those parts of the C.I.E. diagram are used which were actually investigated by both. The spatial discriminations are here reduced to a remarkable coincidence except in the upper left hand corner of the diagram. It is evident that both studies are, as psychologists say, measuring the same thing.

These demonstrations indicate that all three studies are compatible except for systematic differences in chromaticity discrimination in the violet-greenyellow dimension of the colour mixture diagram as compared

to the red-bluegreen dimension. Why does this occur and what significance has it in the study of perceptual colour differences and in the standardization of colour tolerances?

The first possibility that comes to mind is a difference in the eyes of the observers. Fifty observers participated in the Munsell renotation; the MacAdam data is based on the eye of one individual; Wright's on only four. However, I was one of the observers in the Munsell experiment, and did not differ significantly from the mean of the other observers; therefore, I took the opportunity to act as observer in the other two situations. Through the courtesy of Dr. W. D. Wright, the late Dr. L. C. Thomson ran me on three of the principle lines of the Wright experiment at the Imperial College, and the results were in substantial accord with their four observers. The MacAdam apparatus was not in a state of readiness at that time, but an equivalent set-up at the Medical Research Laboratory did not give radically different results for my eye at matches around one point in the diagram. We therefore concluded that the major differences were not due to extremes between the observing population for each.

TABLE I

Physical conditions of observation and size of chromatic interval in the three studies

	Test field		Surround	Pupil	Size of interval
	Size	Brightness			
MacAdam	2^0	15 ml	42^0 7.5 ml Ill.C	Artif. 2.6 mm	^{0} of match
Wright	2^0	75 - 125 photons	dark	artif.	Noticeable Difference
Munsell	2^0 - 3^0	20 - 50 foot-candles	white, gray, black,	natural	large, and various

Tabulation of the psychophysical conditions in each study in *Table I* indicates that most of the physical stimuli were similar. The stimulus patches were about the same size in each study and the luminance levels were similar. The surrounds were various, but are not believed to affect chromaticity discrimination importantly; variation of surround brightness produced no significant change in the magnitude of the Difference Limen in chromaticity in four psychophysical methods studied by Sperling *(ref. 8)*. There were extreme differences in the size of the intervals upon which the three

studies were based - very small scalar steps, slightly supra-liminal differences and large psychological intervals - but the work of Halsey *(ref. 9)* does not show evidence of incompatibility of liminal and supra-liminal scales. It is true that both of the above references are suggestive rather than conclusive, but we are without any evidence for the contrary and less likely hypothesis, - that psychophysical methods are differentially selective in different chromatic regions, or that small intervals are proportional to large intervals in one chromatic direction but are not in another.

The only major difference which remains between the three studies is the times of observation. In the Munsell study each of over 2,000 colour patches was observed in relation to a surrounding array. 3,000,000 judgments were made by 40 observers. Obviously considerable rapidity of eye movements were necessary in order to get the job done within a lifetime. We may safely assume that the eyes rested for a duration of only one or two fixations on each colour since the problem involved the relationship of the test colour to the surrounding array. Also, since the colours were mounted on white or grey or black backgrounds, the eyes passed over a change of colour with each saccadic movement. A normal fixation is from a twentieth of a second to not more than a fifth.

In the Wright study the observer made settings on noticeable differences between the colour patches in a bi-partite field. As Wright points out, attempts to make judgments on *just* noticeable difference introduces "something akin to a sporting instinct" and takes more time. Therefore the duration of each Wright observation was probably of the order of a second or two.

At the other extreme in the MacAdam experiment the object was to repeatedly make a complete match to the same colour. The eye stared at the same test colour for indefinite periods of time, possibly 10 to 15 minutes, with momentary change in one-half of the field as the match was upset between settings.

Now, these times of observation correspond to the rank order of the yellow-blue dimension in the charts which have been presented. Was length of exposure the responsible factor for the major differences? Are the differences related to the times of rise and decay of colour sensation? This is an old field in psychology. Bills *(ref. 10)* has reviewed and added to the work of scores of earlier investigators. The phenomena are apparently related to subjective colours, flicker and desaturation with time of exposure. Much of the data appears contradictory. No application appears to have been made to conditions of colour discrimination.

The most clear-cut experiment relating to our inquiry is found in a study by Ferree and Rand *(ref. 11)* from which *fig. 8* is reproduced. It is selected as most applicable since their criteria was by the method of just noticeable difference. Under the conditions of their experiment, blue light

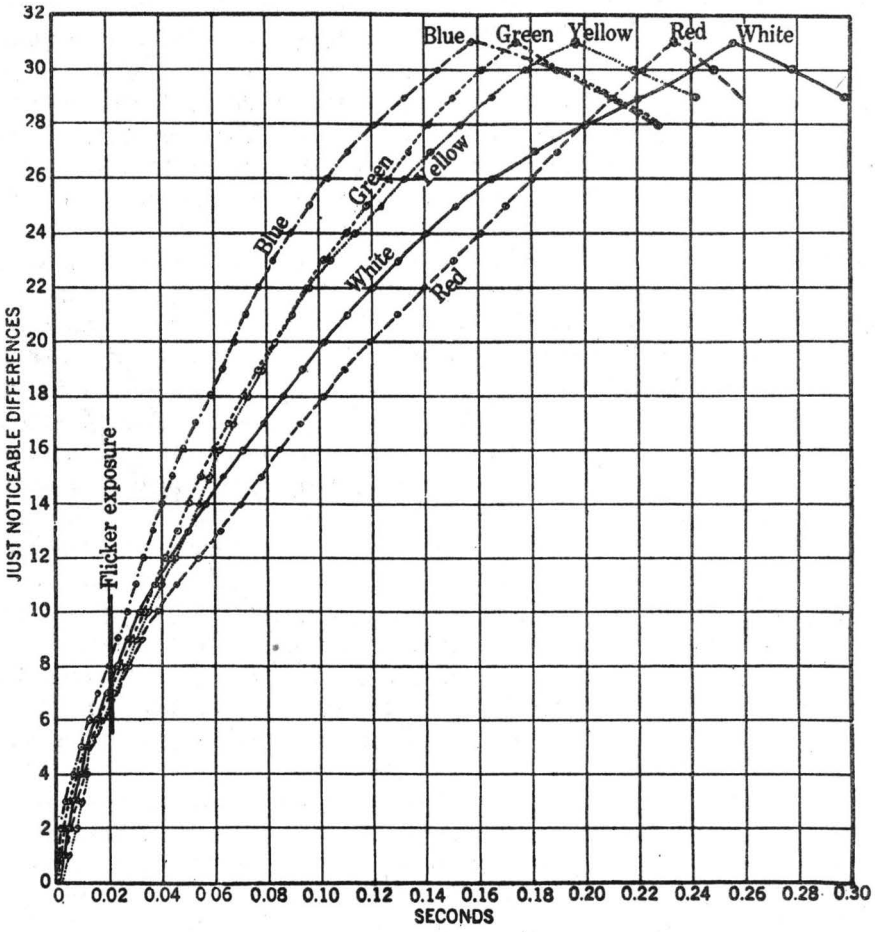


Fig.8. Curves showing the rise of sensation to the maximum for white, red, yellow, green and blue at 12.5 metre-candles (from *ref.11*).

showed the most rapid rise and dominated during brief presentations of stimuli. In fact, for the period of exposure of up to 1/6 of a second the blue predominated over all the other hues. It is noteworthy that upon further exposure there was a rapid decline in the effectiveness of blue and domination by red.

This confirmatory evidence suggested that a specific test should be made. I am indebted to Prof. Jane Torrey of Connecticut College, working under an Office of Naval Research contract, for the following results from an experiment designed to check the hypothesis directly. A white light was produced

in a bi-partite field by a mixture of red and bluish green lights and by a mixture of bluish violet and greenish yellow. Four observers participated, using the method of constant stimuli. Judgments of just noticeable differences were made in the red-green dimension and in the blueviolet-yellow dimension, with exposures of 1/5 second and of 2 seconds. The results are summarized in *Table II*.

TABLE II

Thresholds of discrimination of change in a white light varied between red and bluish green and between bluish violet and greenish yellow with 2 durations of exposure. Average of 4 observers. Data in arbitrary scale units.

1/5 sec.			2 sec.			Ratio 1/5 to 2 sec.
red-green	violet-yellow	Ratio	red-green	violet-yellow	Ratio	
1.72	1.97		.54	.80		
		1.14			1.48	1.30

The data are in arbitrary scale units. Thresholds of discriminations, of course, are higher for all 1/5 second exposures, but the significant result is that the thresholds for violet-yellow differences are *relatively* higher than the red-green differences for the longer durations by 30%. This ratio of 1:1.3 is between the MacAdam-Wright ratio of 1:1.18 and the MacAdam-Munsell ratio of 1:2.00 and is in the same direction.

One is tempted to discuss the possibilities at length, but there is space for only a few comments.

The uniqueness of the violet or blue sensation is evident in several ways. The manner of inheritance of tritanopia is different from that of deuteranomaly or protanomaly. The male-to-female ratio is distinct. Effects similar to tritanomaly are reportedly associated with diseases of the retina, especially those connected with "macular degeneration", and separation of layers of the retina.

The author has previously discussed the tritanomalous effect in the area x intensity relationship *(ref. 12)* in which minimal stimuli in either factor arouses the blue sensation relatively less than the red + green sensation. It would ordinarily follow that minimal time factors would arouse the blue sensation less than the red + green, but we have seen that the opposite phenomenon holds at least over certain temporal ranges. This apparent anomaly may be better visualized if we consider the retina and associated mechanisms

as a computor system with a three-channel input, each of which has a different speed of assimilation, different thresholds and different relative weightings per energy level.

Finally, for those who hopefully strive to reconcile colour mixture with colour discrimination in one simple diagram, there is but one possibility - the present C.I.E. system may be considerably inaccurate. But even in that event a complete resolution of the two systems will require that the data for both be taken under the same psychophysical conditions.

REFERENCES

1. NEWHALL, S. M., NICKERSON, DOROTHY and JUDD, D. B., Final report of the O.S.A. Subcommittee on the spacing of the Munsell colors, *J.opt.Soc. Amer.*, 1943, **33**, 385.
2. WRIGHT, W. D., Sensitivity of the eye to small colour differences, *Proc. Phys. Soc.*, 1941, **53**, 93.
3. MACADAM, D. L., Visual sensitivities to color differences in daylight, *J.opt.Soc.Amer.*, 1942, **32**, 247.
4. BROWN, W. R. J. and MACADAM, D. L., Visual sensitivities of combined chromaticity and luminance differences, *J.opt.Soc.Amer.*, 1949, **39**, 808.
5. BROWN, W. R. J., Color discrimination of twelve observers, *J.opt.Soc. Amer.*, 1957, **47**, 137.
6. SILBERSTEIN, L., Investigations of the intrinsic properties of the color domain, II, *J.opt.Soc.Amer.*, 1943, **33**, 1.
7. MACADAM, D. L., On the geometry of color space, *J.Franklin Institute*, 1944, **238**, 195.
8. SPERLING, H. G., The discrimination of color, I. An experimental evaluation of four methods for measuring the difference limen of chromaticity, Med.Res.Lab. Report No.151, 1950. 54.
9. HALSEY, Rita M., A comparison of three methods of color scaling, *J.opt.Soc.Amer.*, 1954, **44**, 199.
10. BILLS, Marion A., The log of visual sensation in its relation to wavelengths and intensity of light, *Psych.Monographs*, 1920, **28**, Whole No.127.
11. FERREE, C. E. and RAND, Gertrude, Flicker photometry, I and II, *Ill. Engr.Soc.*, 1923, **18**, 151-207.
12. FARNSWORTH, D., Tritanomalous vision as a threshold function, *Die Farbe*, 1955, **4**, 185.

PAPER 17

THE EFFECT OF TEST SIZE AND ADAPTING LUMINANCE ON FOVEAL CRITICAL FUSION FREQUENCIES

By R. A. WEALE

Dr. R. A. Weale is a member of the Visual Research Division of the Medical Research Council's Ophthalmological Research Unit. Between 1948 and 1951 he studied peripheral colour vision and some visual characteristics of cone-monochromats. Since then he has worked on the physical and photo-chemical properties of living eyes, and on measurements of human visual functions with very small test fields. He has been Honorary Secretary of the Physical Society Colour Group since 1955.

17. THE EFFECT OF TEST SIZE AND ADAPTING LUMINANCE ON FOVEAL CRITICAL FUSION FREQUENCIES

By R. A. WEALE, with the technical assistance of MARGARET R. BRIGHT

INTRODUCTION

GRAHAM and Margaria *(ref. 1)* have emphasized the importance of examining human visual functions with small test-fields. This has recently been confirmed in experiments on dark-adaptation (Arden and Weale, *(refs. 2, 3))* when it was found that the absolute thresholds (for white light) of small numbers of rods and cones respectively were of the same order (cf. Stiles and Crawford, *(ref. 4)*; Craik and Vernon, *(ref. 5)*; Baumgardt, *(ref. 6)*; Riezler, Esper, and Meurers, *(ref. 7)*; Weale, *(ref. 8)*, but see Barlow, *(ref. 9)*).

An interest in the areal variation of the critical fusion frequency naturally stems from these experiments, and as it has engaged also Hecht's attention (Hecht and Smith, *(ref. 10)*, it may be appropriate to report on some related studies on this occasion.

This problem has received repeated consideration (cf. Lloyd, *(ref. 11)* . The earliest systematic study appears to be due to Granit and Harper *(ref. 12)*, who used field sizes (A) ranging in diameter from 21' to 6°. They examined both the fovea and the perifovea at 10°. The relation between the critical fusion frequencies n and $\log A$ was linear ($n = c \log A + d$) over a portion of the range examined. Since, for a constant field size, n and the stimulus luminance I are related by the expression $n = a \log I + b$ (the Ferry-Porter equation), Granit and Harper suggested that the general relation between n, A and I was given by

$$n = \alpha \log I . \log A + \beta . \log I + \gamma . \log A + \delta \qquad (1)$$

where α, β, γ, and δ are constants.

Piéron *(ref. 26)* concentrated his attention on the fovea; he used test-fields of angular diameter ranging from 0.5 to 30' at three luminance levels, and observed that the slope $dn/d(\log A)$ increased with field-size A. Hecht and Smith *(ref. 10)* state: "Under the circumstances of possessing the same surround, a nine-fold increase in area of the test-field hardly changes the relation of critical frequency to intensity so far as cone function is concerned." More recently, the effect of A on n was examined in great detail by Lloyd *(ref. 11)* and Kugelmass and Landis *(ref. 13)*. The former measured n as a function of I with 1° and 2° fields in the fovea and at 20° above the fixation area. The periphery was examined also with 6° and 14° fields. The effect of A on the n-$\log I$ curves was consistent in that larger areas always gave higher n-values, I being constant. A similar finding

was made by Kugelmass and Landis who were particularly concerned in correlating discontinuities in the n-log$A$ curves with receptor population.

THE PROBLEM

FROM the above papers it may be concluded that, for a given value of I, an increase in A is accompanied by one in n. But there is a difficulty in the interpretation of this result. While it is true to say that n and log$A$ values were compared for constant values of I, no attention was paid to the integrative faculty of the retina. This is important especially where small areas are concerned (cf. Graham and Margaria, *(ref. 1)*. Thus, if a test-field of size A and luminance I produces a threshold sensation, an increase in A will give rise to a supra-liminal sensation. In general, the two quantities are linked, for a threshold sensation, by the expression

$$I \times A^{p} = \text{constant} \qquad (2)$$

where p may be regarded as a measure of retinal integration, the latter being perfect when $p = 1$, and non-existent when $p = 0$.

This raises the question of whether, due allowance being made for its limitations, the Ferry-Porter law does not represent a special case of a more general relation, namely

$$n = k.\log Q + k' \qquad (3)$$

where Q, measured in threshold units, is the effective quantity of light, given by the expression

$$Q = I.A^{p}.t^{r} \qquad (4)$$

I and A have their previous meanings, t represents the time of exposure, and p and r are the indices of spatial and temporal integration respectively. k and k' are constants. Keeping t constant, (3) can be written

$$n = k.\log I + kp.\log A + k' \qquad (5)$$

which, it is suggested, replaces (1).

Two predictions can be made from (3) and (5). First if the quantity of light Q is kept constant, the critical fusion frequency n should be independent of A. Secondly, a comparison of $dn/d(\log I)$ with $dn/d(\log A)$ should yield a measure of the index of spatial integration p. This can also be estimated from threshold measurements and hence provides an independent check for the validity of (5).

Kugelmass and Landis *(ref. 13)* have published data which show that, within limits, $dn/d(\log A) = 7$, and $dn/d(\log I) = 11$. Thus p, the index of spatial integration, is approximately 0.64. Over the range of validity of (4), therefore, it should be possible to plot loci of constant numbers of threshold units Q: these should be horizontal in *fig. 4* taken from Kugelmass and Landis' paper, i.e. for Q constant, $\Delta n = 0$. Several such plots *(fig. 1)* show that, within limits, the prediction is fulfilled.

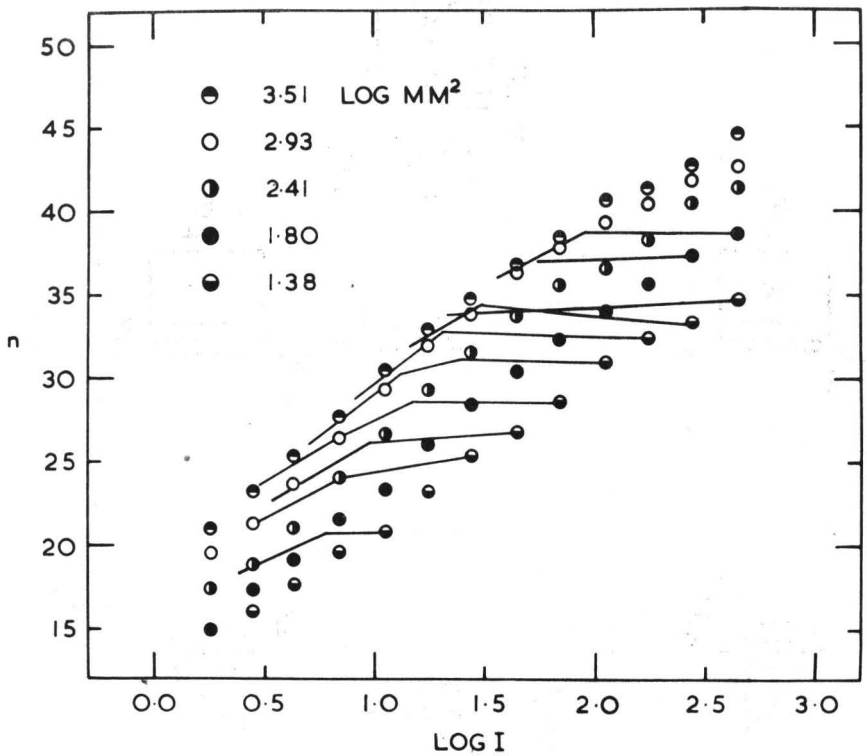


Fig. 1: Critical fusion frequency as a function of log intensity (mL) for test-fields (A) of angular diameter ranging from 1.27^0 to 14.6^0 (after Kugelmass and Landis, *(ref.13))*. The lines represent loci of constant values of the product $I \times A^{0.64}$.

The limits are, indeed, wider than would be expected from the known range of applicability of (2).

It remains to be shown whether the converse experiment, in which the stimulus is measured in threshold units, gives rise to horizontal lines, when n is plotted against A.

PRESENT EXPERIMENTS

(a) Apparatus. The test source *(fig. 2a)* consisted of a neon tube (type: T47MES), N, which was imaged by the lens L_1 on a circular aperture, A_1 (dia. = 0.075 cm). This, in turn, was imaged by the photographic lens L_2 in the plane of the observer's right pupil P_r, the image being 2 mm

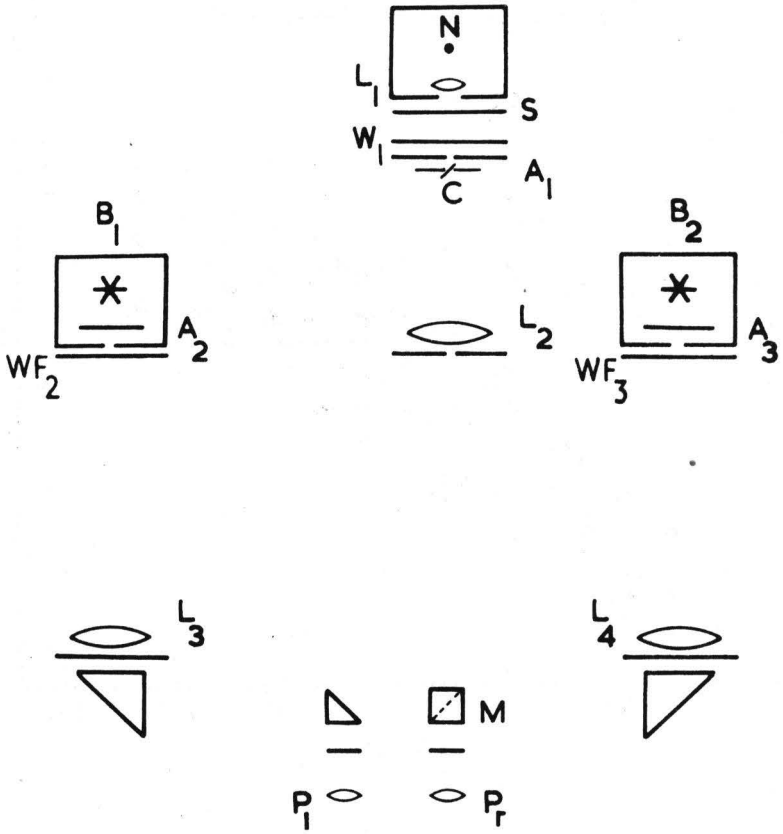


Fig. 2: (a) Apparatus. For details see text.

in diameter. The intensity, I, was controlled by means of a step wedge, S, and a neutral density wedge, W_1, the time of exposure by a Compur shutter, C. L_2 carried a rotatable disk with five circular apertures, fixed eccentrically, so that the centre of any one of them could be made to coincide with the optic axis of the arrangement. The diameters of the apertures subtended at the eye angles of 2.5, 5, 10, 20, and 40' respectively.

The incandescent lamps, B_1 and B_2 (12v 36w) controlled fixation and the level of adaptation. Like N, they were each enclosed in a light-proof box. The small apertures, A_2 and A_3, were each covered with a piece of ground glass, and the photographic lenses $L_{3,4}$ formed images (dia. = 2 mm) of $A_{2,3}$ in the plane of the observer's left and right pupils, $P_{l,r}$,

respectively. In front of each lens, $L_{3,4}$, there was a photographic slide (angular dia. = 5^0) with a black ring: the left slide had a black dot above, the right one below the ring *(fig. 2b)*, the fused image appearing as a single ring (angular dia. = 1.5^0) with a black dot above and below the ring. The test-field appeared at the centre of the ring, the superposition being effected for the right eye with the mixing cube M. The luminance levels of the adapting fields were the same and controlled with neutral density wedges, $W_{2,3}$, and filters, $F_{2,3}$. In front of the observer's eyes there was a carrier, supporting two red filters (Ilford 204) and spectacle lenses, which imaged the test and adapting fields on the retinae. The power of the lenses depended on the adapting luminance. The voltages, supplying both test and adapting sources, were under constant control, B_1 and B_2 being underrun at 9v.

The neon lamp was driven by a relaxation oscillator, designed for relay operation (Attree, cf. Dickinson, *(ref. 14)*), the relay being replaced by the lamp. Resistor-condenser banks were incorporated so as to give a 1:1 light-dark ratio, accurate to 5% or less (cf. Crozier and Wolf, *(ref. 15)*), and enabled one to alter the flicker frequency in steps of approximately 2 c/s in the range of 6.7 - 33.4 c/s. The flicker properties of the stimulus were calibrated with an RCA/931A photomultiplier tube, the output of which was fed into a Cossor oscilloscope. The resulting trace and an a.c. 50 c/s trace were recorded cinematographically *(fig. 2c)*. The shutter C was calibrated in an analogous manner.

The linearity of the wedge W_1 was established, and its slope determined in the usual manner, as were the densities of the neutral density filters and the step-wedge (cf. Weale, *(ref. 16)*). The luminance levels of the test and adapting fields were measured with an S.E.I. photometer.

(b) Procedure. At the outset, differential thresholds for continuous stimuli of different areal subtense had to be established. This was done by determining, for adapting retinal illuminations of 950 trolands (H) and 9.1 trolands (L) in turn, that setting of W_1 and S, which for a given time of exposure t, and field-size A, elicited a "seen" response twice in three consecutive presentations. The times of exposure ranged from 0.004 to 0.895 s. A and t were varied at random. Every threshold determination was repeated on three or four different occasions. The experimental data follow their usual course (cf. Piéron, *(ref. 17)*) in spite of the fact that they represent differential instead of absolute threshold measurements. It was, therefore, thought legitimate to assume that, for exposure times of 1.3 s, as used in the flicker experiments, the variation of $\log\Delta I$ with A would be the same as for t = 0.9 s. A subsidiary experiment showed that the threshold did not depend systematically on the rate of flicker in the range tested, namely 6.7 - 18.1 c/s. It also confirmed that the light output of N did not vary with the frequency of flicker.

It has often been emphasized (cf. Mahneke, *(ref. 18)*) that the thresholds from fusion to flicker and from flicker to fusion respectively do not

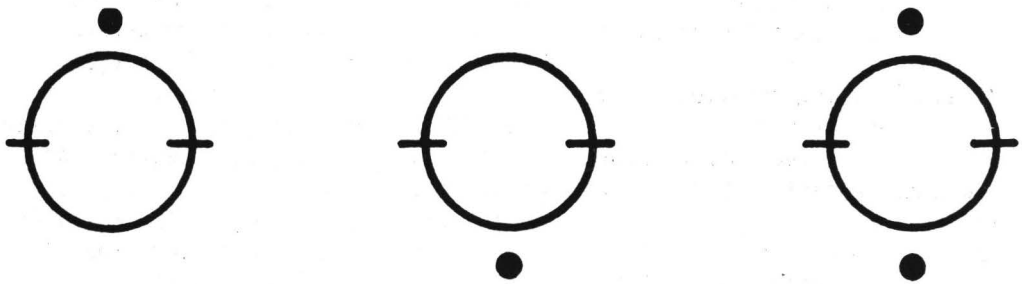


Fig. 2: (b) The adapting fields as seen by each eye separately and fused.

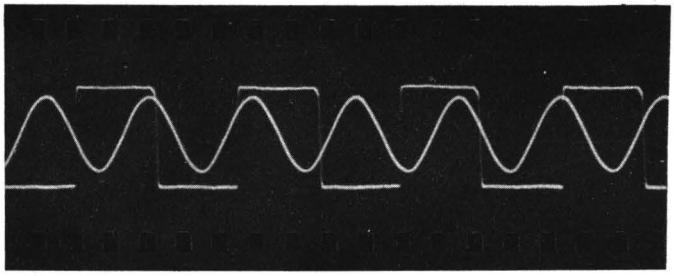


Fig. 2: (c) A sample of the oscillographic calibration record for the neon-lamp.

coincide. There appears to be no merit in preferring one to the other, and, although the average of the two was used in a subsidiary experiment *(vide infra)*, a forced choice method was employed in the main study. The observer was presented with a stimulus and had to decide whether or not it flickered.

Three types of experiment were performed. First, the differential threshold luminances were increased by 0.2 log units. These stimuli, one corresponding to each test-area, were presented at a number of flicker frequencies in turn, so that the region of fusion might be established. This done, four neighbouring frequencies in the relevant range were presented five times per area in each session. Secondly, the luminance was kept fixed at the threshold + 0.2 log units corresponding to the 5' field at level H, and similarly for the 2.5' field at level L. The procedure for determining ranges of fusion and presenting flickering stimuli within them was followed again. Fifteen to twenty presentations were made in all for each frequency, area, and luminance level. The critical fusion frequency, n, was defined as the frequency corresponding to 50% of "fused" responses.

Thirdly, for the test-fields of angular diameter 5, 20, and 40', n-logΔI data were collected at both luminance levels over the luminance range as limited by the threshold on the one hand and the output of neon lamp on the other. In this case, the more orthodox method of "bracketing" was used, i.e. the critical fusion frequency was approached from the extreme ends of the gamut in turn, and the average defined as m. This was done on five different occasions for each level with the 20' field, and on three occasions with the 5 and 40' fields. There is no doubt but that the former method is sounder because the observer does not use his memory. Considering, however, that the change in test-frequency is discontinuous in the present method, and that the change of n with log$I$ is large, the second procedure seems preferable because it saves time.

All the tests were done in a dark-room, after about two minutes' dark-adaptation.

(c) The observer. One observer (R.A.W., 34 years old) was used throughout the study. His small refractive errors were fully corrected. Artificial pupils were not used as the images of the light sources were only 2 mm. in diameter. The observer was carefully placed with respect to the three light beams, and his head supported with a dental impression, attached to the Kee-Klamp scaffolding which carried the optical apparatus.

RESULTS

(a) Differential threshold luminance measurements. These are shown in *fig. 3*, where log ΔI is plotted against log$A$ for the L (⊙) and H (○) levels respectively. The gradient d(logΔI)/d(log$A$) decreases as the adapting

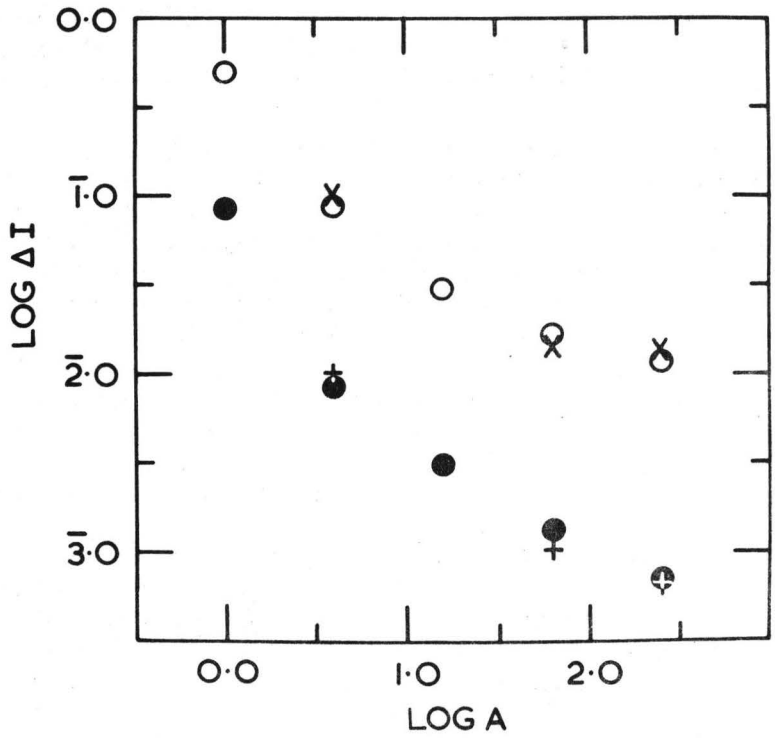


Fig. 3: log threshold luminance as a function of log stimulus area.
log ΔI = 0 is equivalent to retinal illumination of 4420 trolands.
log A = 0 corresponds to an area of angular diameter equal to 2.5'.
(o): data obtained with an adapting retinal illumination of 950 trolands;
(⊖): data obtained with an adapting retinal illumination of 9.1 trolands.
+ and X represent data obtained from *Fig. 5* for n = 14 c/s.

luminance is raised. This may be interpreted as a decrease in p, the spatial integrating power of the fovea, and agrees with other studies (cf. Lythgoe, *(ref. 19)*).

(b) Measurements of n as function of A at constant threshold. These are shown in *fig. 4*. The data for the H level (o) lie on a horizontal line, corresponding to n = 15.6 c/s, those for the L level (⊖) lie on a line of small slope, and correspond to an average n of 11 c/s. The inset shows an example of a frequency-of-fusion curve (level H, area of 20' dia.).

(c) Measurements of n as a function of A at constant luminance. These are also shown in *fig. 4*, L representing the H data, and T the L data. The

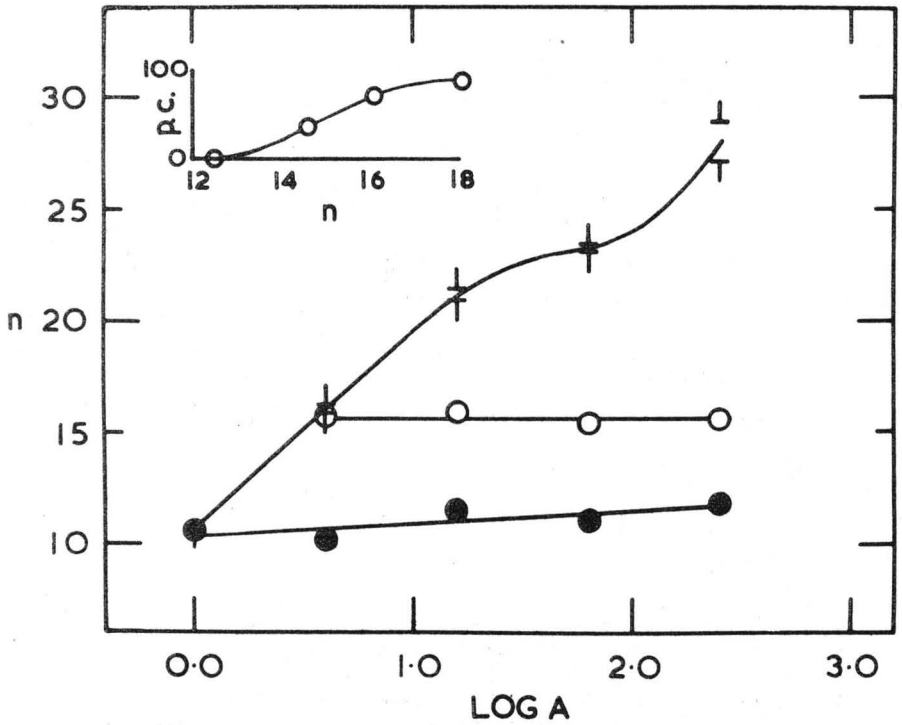


Fig.4: Critical fusion frequency as a function of log area. Log$A$ = 0 corresponds to an area of angular diameter equal to 2.5'. Constant threshold data for an adapting retinal illumination of 950 trolands (o), and of 9.1 trolands (⊖); constant retinal illumination data (700 trolands) for an adapting retinal illumination of 950 trolands (L) and of 9.1 trolands (T). Inset: a typical "frequency-of-fusion" curve, obtained with the 20' field and an adapting retinal illumination of 950 trolands

coincidence of the two sets of data is fortuitous and arises from the fact that the L-threshold of the 2.5' field happens to be equal to the H-threshold of the 5' field (cf. *fig. 3)*. As mentioned above, these luminance levels, increased by 0.2 log units, provided the constant values $I_{H,L}$ respectively.

(d) Measurements of n as a function of logΔI for constant A. The data for this experiment are reproduced in *fig. 5* with the usual symbols. It is noteworthy that Student's t-test reveals a statistically significant difference (s) between the two sets of data (20') in the logΔI range from 2.3 to 1.0. The difference between the general trends of the two curves

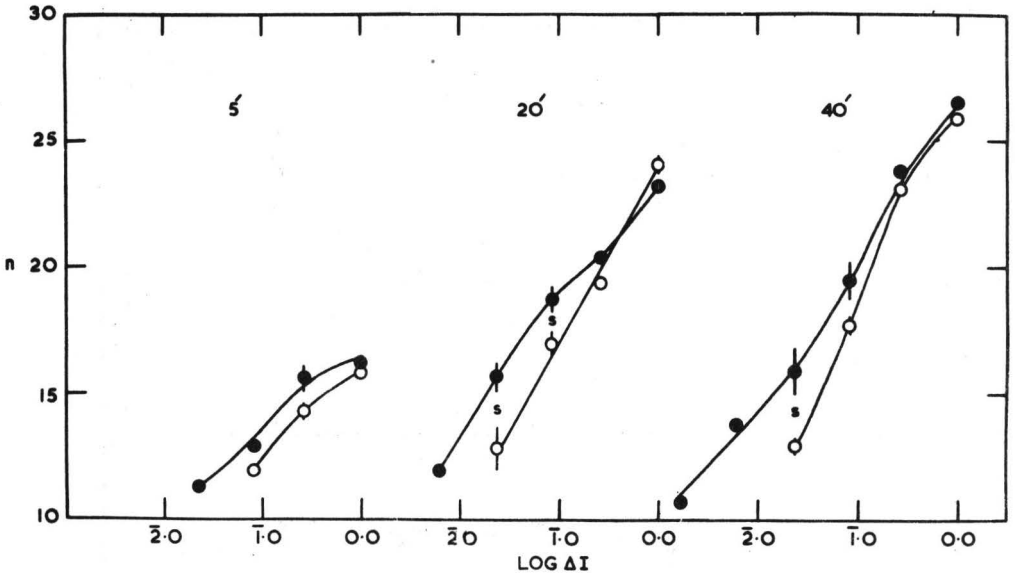


Fig. 5: Critical fusion frequency as a function of luminance.
Log ΔI = 0 represents a retinal illumination of 4420 trolands.
(o): data for an adapting retinal illumination of 9.1 trolands.
(o): data for an adapting retinal illumination of 950 trolands.
The angular diameters of the test-fields are indicated. Samples of the standard error of the mean are shown; a statistically significant difference being indicated by *s*. Each point represents the mean of three observations for the 5' and 40' field, and of five observations for the 20' field.

confirms a previous finding (Lythgoe and Tansley, *(ref. 20)*). (This agreement may be partly fortuitous because their test-patch was larger, and not superimposed on, but surrounded by, the adapting field.) The agreement between the n-values for the threshold region as given in this figure and *fig. 4* respectively is good for the L-level, but poor for the H-level. The difference in the methods of determining n may perhaps account for this.

DISCUSSION

THE linear part of the data obtained by Kugelmass and Landis *(ref. 13)* shows a slope of $dn/d(\log I) \doteq 11$. This is nearly independent of the size of the test-field, which ranged from 1.27° to 14.60°. $dn/d(\log A)$ is approximately 7, in general agreement with the trend of the data, obtained by some of the authors quoted in the Introduction. It follows from (5) that the index of spatial integration p equals 0.64. Baumgardt *(ref. 21)* derived a

theoretical value of 0.63, which was closely approached in his measurements of the absolute threshold as a function of A. The theoretical value was assumed to apply to the whole of the dark-adapted rod-free part of the fovea. Therefore the remarkable agreement between Baumgardt's result and that derived from Kugelmass and Landis' data should be treated with reserve.

The present data do not lend themselves to an estimate of slopes because neither n-logΔI nor n-log$A$ are linear over sufficient portions of the ranges examined. They can, nonetheless, be used in testing the validity of (5). Clearly, when n is constant, Q must be. It is thus possible to select from each of the n-logΔI data *(fig. 5)* a value of logΔI, which corresponds to a fixed value of n. When this is done for each of the three test-areas for which n-logΔI data were obtained, logΔI can be plotted against log$A$. As the critical fusion frequency selected (n = 14 c/s) is low, this plot should be comparable in shape with the data shown in *fig. 3.* The points so derived for the L and H levels (+ and x) are seen to agree with the original differential threshold values. This implies that the retina integrates similarly in the two cases.

Kugelmass and Landis and other authors have tentatively ascribed discontinuities in n-log$A$ curves to regional changes in the receptor population, probably because such correlations are generally made in analogous curves involving other visual functions. The range here examined is too limited to throw much light on the nature of these discontinuities, but the inflexion observed for the 20' field is noteworthy. Kugelmass and Landis state that some kind of break might be expected in this region because the central foveal bouquet of slim, elongated cones covers just such an area (in one or two histological preparations). Indeed, Allen's *(ref. 22)* and one of Piéron's *(ref. 26)* sets of data show some discontinuity for test-fields of this angular size. It is not clear why such breaks should be due to transitions from one variety of cone to another (cf. Hecht and Verrijp, *(ref. 23);* other factors may be operative. Autrum *(ref. 24)* has shown that, in the eyes of the dragon-fly Aeschna and its larva, n is a function of the distance between the photo-receptor and its bipolar cell, being high when the distance is short and vice versa. It is, therefore, conceivable that the increase in n for areas larger than 20' in angular diameter may be partly due to the fact that the test-field covers cones with much shorter cone-bipolar distances than those of the central cones. An analogous hypothesis offers a simple explanation also for the observation that, at high luminance levels, peripheral cones give rise to higher values of n than do foveal ones (Lythgoe and Tansley, *(ref. 20);* Lloyd, *(ref. 11).* Cone size may also matter *(vide infra).*

While a consideration of the effective quantity of light rather than its intensity has gone some way towards harmonizing sets of flicker data which, at first sight, appear to be unconnected, it does not provide a complete explanation. This becomes obvious when one examines the n-log$Q$

ranges on each side of the rectilinear portion. It is conceivable, for example, that when A is kept constant, the factor governing n for small values of I is the rate at which a visual sensation is built up. But, at large stimulus intensities, the decisive factor may be the rate at which the sensation falls off. Entirely different effects operate when A is varied. When the test-field is virtually a point image at or near threshold level, the observations are impeded by Troxler's phenomenon (cf. Clemmeson, *(ref. 25)*). This may be due to physical or physiological causes, or both; but the fact that even a physically constant source appears to fluctuate in luminance continuously and at a relatively rapid rate tends to set a lower limit to the frequency at which the light pulses of a minute flickering source can be fused. The result will be that $dn/d(\log A)$ approaches zero as A approaches zero. For large values of A, another effect has to be considered, namely the discontinuity of the receptor system. If a uniform field of light is imaged in the retinal periphery, e.g. in measurements of the absolute threshold of rods, about 30% of the light flux is wasted because it falls on cones or interstitial areas. Such wastage must, of course, be allowed for. Similarly, if the eye is adapted to a high luminance level in the course of flicker experiments and the test-field, fixated centrally, is increased well beyond the foveal boundary, the number of receptors stimulated will in no way increase in proportion. Hence $dn/d(\log A)$ would be expected to approach 0 also for large values of A. The fact that the rectilinear relationship between n and $\log A$ persists for larger values of A than would be expected on the basis of this crude picture may well be due to the retinal periphery being more sensitive to flicker than is the centre; a possible reason for this has already been advanced. Other factors, such as regional and areal variations of the latent and refractory periods, differential sensitivity, and persistence of vision also enter the problem, but cannot be considered with profit at present.

In conclusion, however, one or two comments may be made on the difference between the trends of the n–$\log\Delta I$ data for the H and L levels respectively *(fig. 5)*. The fact that the H data lie below the L data is explained most easily by assuming n to be a function not of Q but of ΔQ. An intense source of light may appear to flicker when superimposed on a background of low luminance, whereas the eye may be unable to follow the alterations in luminance when the background luminance is high. Then fusion will prevail. Such an effect is illustrated in *fig. 5*. When I is large as compared with the adapting luminance, n is high. Lythgoe and Tansley's *(ref. 20)* foveal data show a progressive increase in $dn/d(\log I)$ with the luminance level of the surround. This suggests that the differential of (5), namely

$$\Delta n = f(\Delta Q/Q) \qquad (6)$$

is a more general description of flicker data. Whether or not (6) can be

integrated to give (3) depends on the conditions of the experiment. It would not follow from such a step that "the Ferry-Porter equation and the Granit-Harper equation are special cases of the Weber-Fechner equation" (Kugelmass and Landis, *(ref. 13)*) because n cannot be identified with a sensation. In actual fact, there is an increase in value of $dn/d(\log\Delta I)$ with the luminance level of the adapting surround in a luminance range where, in the absence of a surround, $dn/d(\log I)$ is constant. This suggests that Δn is not necessarily additive and supports the view that the similarity between (6) and the Weber-Fechner equation is merely formal.

REFERENCES

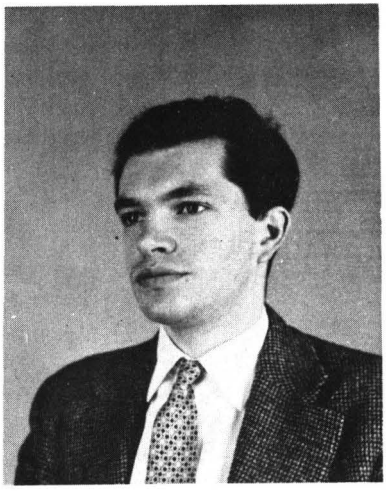
1. GRAHAM, C. H. and MARGARIA, R. *Amer.J.Physiol.*, 1935, **113**, 299.
2. ARDEN, G. B. and WEALE, R. A. *J.Physiol.*, 1953, **123**, 12P.
3. ARDEN, G. B. and WEALE, R. A. *J.Physiol.*, 1954, **125**, 417.
4. STILES, W. S. and CRAWFORD, B. H. *Proc.roy.Soc.* B., 1937, **122**, 255.
5. CRAIK, K. J. and VERNON, M. D. *Brit.J.Psychol.*, 1941, **32**, 62.
6. BAUMGARDT, E. *C.R.Soc.Biol.*, 1949, **143**, 786.
7. RIEZLER, W., ESPER, F. and MEURERS, H. *Ztschr. Physik*, 1954, **137**, 238.
8. WEALE, R. A. *J.Physiol.*, 1955, **127**, 587.
9. BARLOW, H. *Nature*, 1957, **179**, 255.
10. HECHT, S. and SMITH, E. L. *J.gen.Physiol.*, 1935, **19**, 979.
11. LLOYD, V. V. *Amer.J.Psychol.*, 1951, **65**, 346.
12. GRANIT, R. and HARPER, P. *Amer.J.Physiol.*, 1930, **95**, 211.
13. KUGELMASS, S. and LANDIS, C. *Amer.J.Psychol.*, 1955, **68**, 1.
14. DICKINSON, C. J. Electrophysiological Technique, Publ. by Electronic Engineering, 1950, *Fig. 41*.
15. CROZIER, W. J. and WOLF, E. *J.gen.Physiol.*, 1943, **27**, 119.
16. WEALE, R. A. *J.Physiol.*, 1951, **114**, 435.
17. PIÉRON, H. *C.R.Soc.Biol.*, 1920, **83**, 1072.
18. MAHNEKE, A. *Acta Ophthalm. Kbh.*, 1956, **34**, 113.
19. LYTHGOE, R. J. *Brit.J.Ophthalm.*, 1940, **24**, 21.
20. LYTHGOE, R. J. and TANSLEY, K. *Proc.roy.Soc.* B., 1929, **105**, 60.
21. BAUMGARDT, E., *Rev.Opt.*, 1949, **28**, 661.
22. ALLEN, F. *Canad.J.Res.*, 1945, **23A**, 21 (quoted by Kugelmass and Landis).
23. HECHT, S. and VERRIJP, C. D. *J.gen.Physiol.*, 1933, **17**, 269.
24. AUTRUM, H. *Die Naturwissenschaften*, 1952, **39**, 290.
25. CLEMMESON, V. *Acta Physiol.*, 1944, **9**, Suppl.27.
26. PIÉRON, H. *C.R.Soc.Biol.*, 1935, **118**, 25.

PAPER 12

A STUDY OF NORMAL AND DEFECTIVE COLOUR VISION

By M. A. BOUMAN and P. L. WALRAVEN

Maarten A. Bouman, born in 1919 in Utrecht, Holland, obtained his degree in physics in 1942 from the State University of Utrecht and his Ph.D. for work in physiological optics in 1949. From 1942 to 1949 he was a member of the scientific staff of the physical laboratory of this university. In 1949 he was engaged for work on perception in the National Council for Applied Scientific Research T.N.O.
For these studies an "Institute for Perception RVO-TNO" was founded in 1956 under his directorship, where work is done on vision, hearing and other sensory functions as well as on human engineering and related medical problems. Originally Dr. Bouman started this work in 1949 in the "Research Unit for observations N.D.R.C.".



P. L. Walraven, 26 years old, was born in Rotterdam. He obtained his degree of physical engineer in 1953 at the Technical University in Delft. Since that time he has been scientific collaborator in the Institute for Perception N.D.R.C. His work includes studies on colour recognition, in particular at the threshold of vision, and the colour discrimination of normal and colour defective subjects.

12. A STUDY OF NORMAL AND DEFECTIVE COLOUR VISION

By M. A. BOUMAN and P. L. WALRAVEN

SUMMARY

MEASUREMENTS were made of saturation discrimination of normal and colour defective subjects with illuminant *A* as reference colour.

The colorimeter used in the experiments was of a special design developed for easy use by untrained persons.

The results for normals are not quite in agreement with the data of MacAdam. Different experimental conditions are probably responsible for the differences.

In the results for the colour defective subjects there is a tendency for protans to have a decreased ability for detecting saturation differences in a part of the spectrum to the short-wave side of the places in the spectrum where deutans are seriously handicapped. The confusion directions in the C.I.E. diagram for dichromats seem not to have much meaning for the corresponding anomalies.

The overall impression from the results so far obtained is of a more or less random distribution of peaks in the saturation discrimination curves of colour-defectives, in the red-green region of the spectrum.

Two deuteranomalous observers whose mothers were sisters had a peak at the same wavelength.

The achromatic zone in colour-naming experiments in the dark-adapted eye for a normal and a deuteranomalous observer exhibits a dependence on wavelength corresponding to that shown in the measurements of saturation discrimination.

INTRODUCTION

THERE is an urgent need for information on the colour discrimination of people with defective colour vision in order to evaluate their potentialities for special jobs. Such evaluation can only be made effective in the development of selection procedures when the corresponding data for normal people are also available. In consequence of these needs, and highly stimulated by our interest in colour vision theories and by the recommendations made by important investigators in this field on several occasions, we started some research in this subject. For these studies a special trichromatic colorimeter was developed by us. The instrument had to be easy to handle for untrained subjects in order to obtain in a short time sufficient data with acceptable accuracy.

EXPERIMENTAL ARRANGEMENT

THE measurement of ability to discriminate colour is made by comparison of stimuli presented simultaneously in adjacent parts of the visual field with unaided and unrestricted binocular vision from four to five metres distance.

In the instrument a test plate painted matt white has its central part perforated by a great number of holes of equal area. The centres of these holes are so close to each other that, when observed from beyond about four metres, the holes cannot be distinguished separately, *(fig. 1)*.

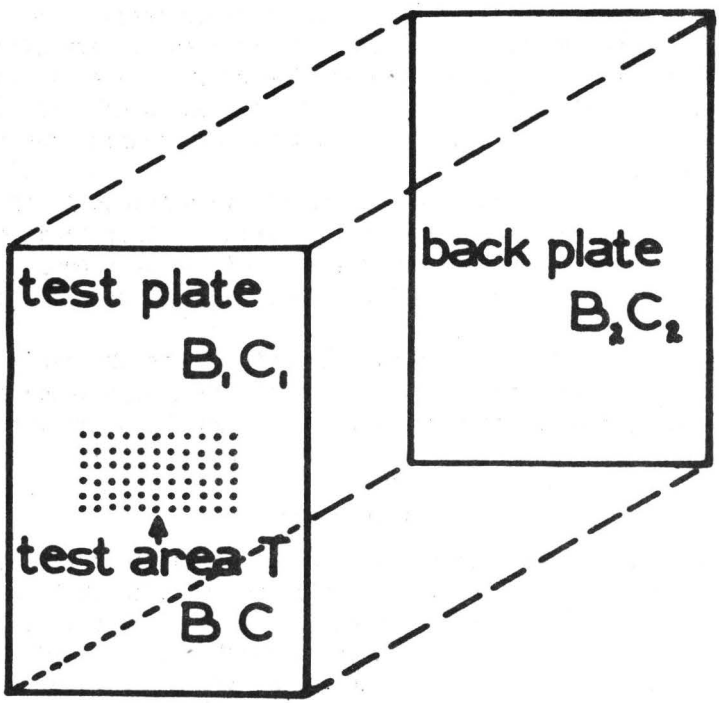


Fig. 1. Schematical representation of the experimental arrangement.

The front of the plate is illuminated by light of adjustable colour C_1 and brightness B_1. Through the holes, light from a second painted white plate behind the first one is incident on the eye. The second illumination is also adjustable (C_2 and B_2). If α is the fraction of the central area covered with holes, the resulting brightness in this area is $B = (1-\alpha)B_1 + \alpha B_2$ and, in colour space, the resulting colour is determined by

$$\alpha B_2 : (1-\alpha)B_1 = CC_1 : CC_2 \text{ and, if } B_1 = B_2, \text{ by}$$

$$\alpha : 1-\alpha = CC_1 : CC_2.$$

Uniform illumination of the two plates was obtained by making them part of the walls of two integrating spheres. The front plate was perforated in several strips with various α-values. Through a window in the front of the front sphere three strips at a time were presented to the observer. We were able to present 12 combinations of strips by changing the position of the plate *(fig. 2)*. Each α-value was presented several times, the value $\alpha = 0$ being included. The subject's answers seen and not-seen were recorded automatically. The registration apparatus calculated the chance for detection for each α-value separately. The apparatus is operated by the subject pressing buttons for strips seen.

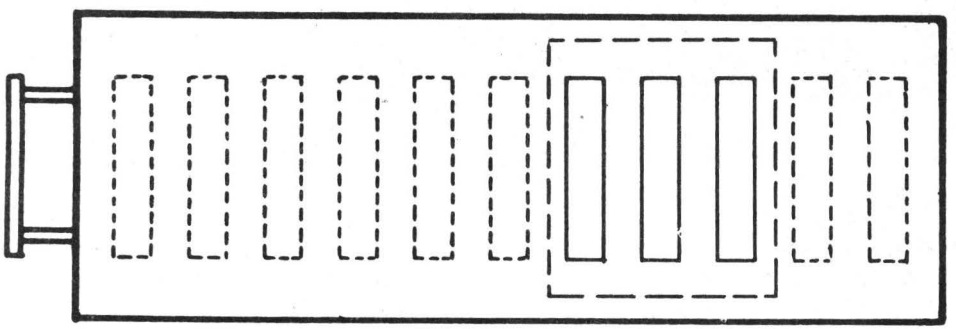


Fig.2. The front plate. By changing the position of the plate, three other strips can be shown.

In the spheres, white light and spectral lights are mixed. The white light is produced by headlight bulbs with colour temperature of about 2848° K. The spectral lights were obtained with the aid of a special projector containing a lamp of 750 Watts, a special mirror, and interchangeable interference filters which had to be effectively cooled with a water cell. For $\lambda = 650$ mμ we could reach a brightness of 30 cd/m^2, for $\lambda = 440$ mμ about 5 cd/m^2. With this projector the brightness of the unfiltered (white) light was 6000 cd/m^2 in the 40 cm diameter spheres! An illustration of the apparatus is shown as *fig. 3*.

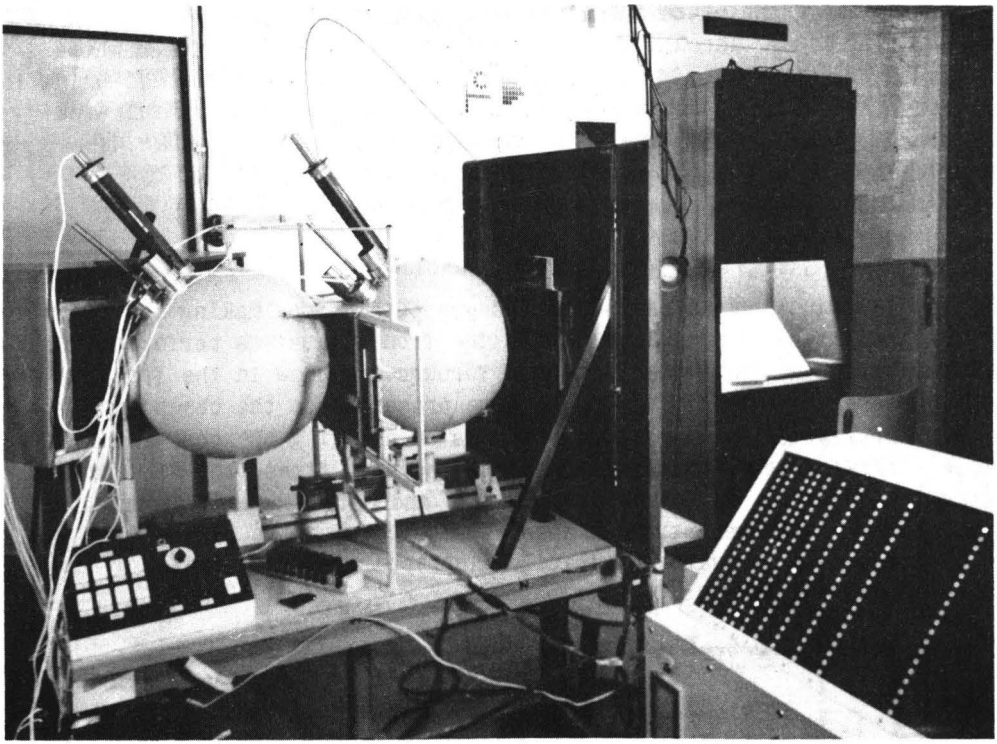


Fig. 3. The apparatus. One can see the plate with the strips between the spheres. The observer views from the right side. In the registration apparatus a frequency of seeing curve is recorded.

The window in the front sphere is surrounded by a large white screen 1 x 1 metres. This screen can be illuminated with white or even coloured light for the elimination or inducement of adaptation effects from the surroundings. The window itself is closed by a blind shutter which is made part of the large white screen just mentioned. For the test observations this shutter is opened for about a second for each judgement . The strips were 6 x 1.2 cm (viewing angle 48' x 8'), the square window being 1^{o} in diameter.

PROCEDURE

TWO different procedures are used. The choice between them in an actual experiment is guided by the relation between brightness - and colour discrimination for the particular subject. If the just noticeable colour step in terms of variation of the colour component is at least three times the just visible brightness step the simpler method can be used:

1. Both spheres are first made white of equal brightness, the subject checking that the strips are invisible. Next the brightness of the

second sphere is decreased. The strips with sizeable α-values are visible. Now the subject has to regulate the brightness of a spectral light in the second sphere such that a strip with a certain α is invisible again. The brightnesses in both spheres are then equal again and other α-values can be shown.

2. In this case instead of the brightness of the spectral light in the second sphere that of the white is varied until a strip with a special α-value is invisible. The brightnesses in both spheres are now equal and the sensitivity for the spectral light in relation to white is known from the difference in brightness of the white of the front- and back plates.

The second procedure is not as convenient as the first one. The variation of brightness by current regulation of a lamp as is done in case 1 for the spectral colour is easier than the variation with the aid of a diaphragm. The latter is necessary for the white variation in method 2. When colour discrimination is as good as or better than brightness-discrimination, as in the blue and red end of the spectrum for normal people, the second procedure has to be used. For less good colour discrimination the first procedure is sufficiently accurate. After all, the actual setting - whether by regulation of the white or the spectral light - must be determined by a brightness match and not by a subjective compromise in colour- and brightness difference in order to obtain minimum overall difference in appearance between the strip and the front plate.

The ratio of the contributions of spectral light and white in the second sphere has to be such that the α-value, for which the chance for detection is approximately 50%, is in the middle of the region of α-values covered by the test plate. The chance for a yes-response increases with increasing α-value from 0 - 100%. For the brightness used in the experiments in this paper, 30 cd/m^2, the frequency of seeing curve is approximately independent of the subject and of the colours. The 10% level is reached at a colour step about 0.7 times the step for 50%; the 90% at about 1.3 times the step for 50%. When the frequency of seeing curve does not extend over a suitable region of α-values in the test plate the experiments are repeated with another ratio between colour and white in the second sphere. Otherwise the accuracy is not as good as possible.

Reproduceability and accuracy are poorest when brightness- and colour steps are of approximately the same size, but deviations between repeated experiments are still on the average below 15 to 20% in the colour discrimination step. Determination of the sensitivity by flicker is not preferable. Firstly, this must be done with another apparatus, and that can introduce errors. Secondly, when white and spectral light are flickered against each other one is not sure that the resulting sensitivity for the spectral colour is the same as when it is mixed with a considerable amount of white.

SATURATION discrimination curves around the 2848° K white for two normal subjects were first determined. The results are given in *fig.4*. For comparison MacAdam's data are also represented. He did not measure around 2848° K and his ellipse is obtained by interpolation between neighbouring ellipses. The axes of our ellipse and his are not quite the same and our ratio of the short and long axes is greater. The difference in size of test area in our experimental set-up and his could be the cause for this effect. In our arrangement, the test area is smaller and some small-field tritanomaly could be introduced in these results.

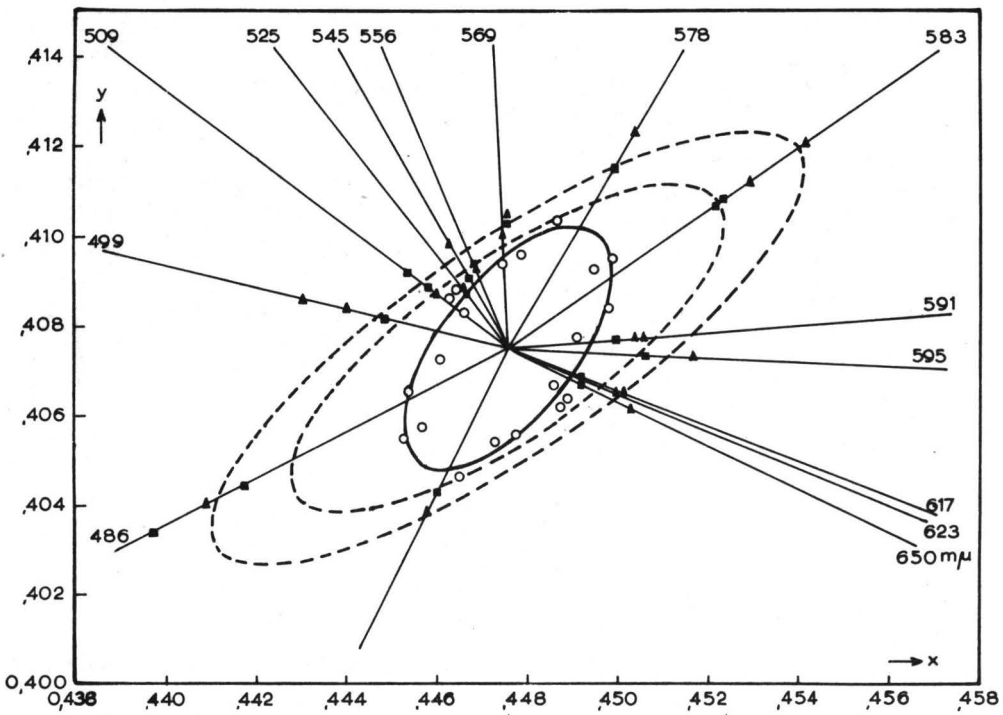


Fig.4. Saturation discrimination ability around the 2848° K-point for two normal observers plotted in the C.1.E.-diagram, together with MacAdam's data.

In a preliminary study we measured the saturation discrimination curves as a function of λ for 12 colour defective subjects for a restricted number of λ's. These results are shown in *fig.5*.

Points with arrows indicate that the percentage spectral light had to be greater than could be obtained. The classification of the colour defectives is based on the combined use of pseudo-isochromatic plates and the anomaloscope. The accuracy of these results is not as good as in the previous figure.

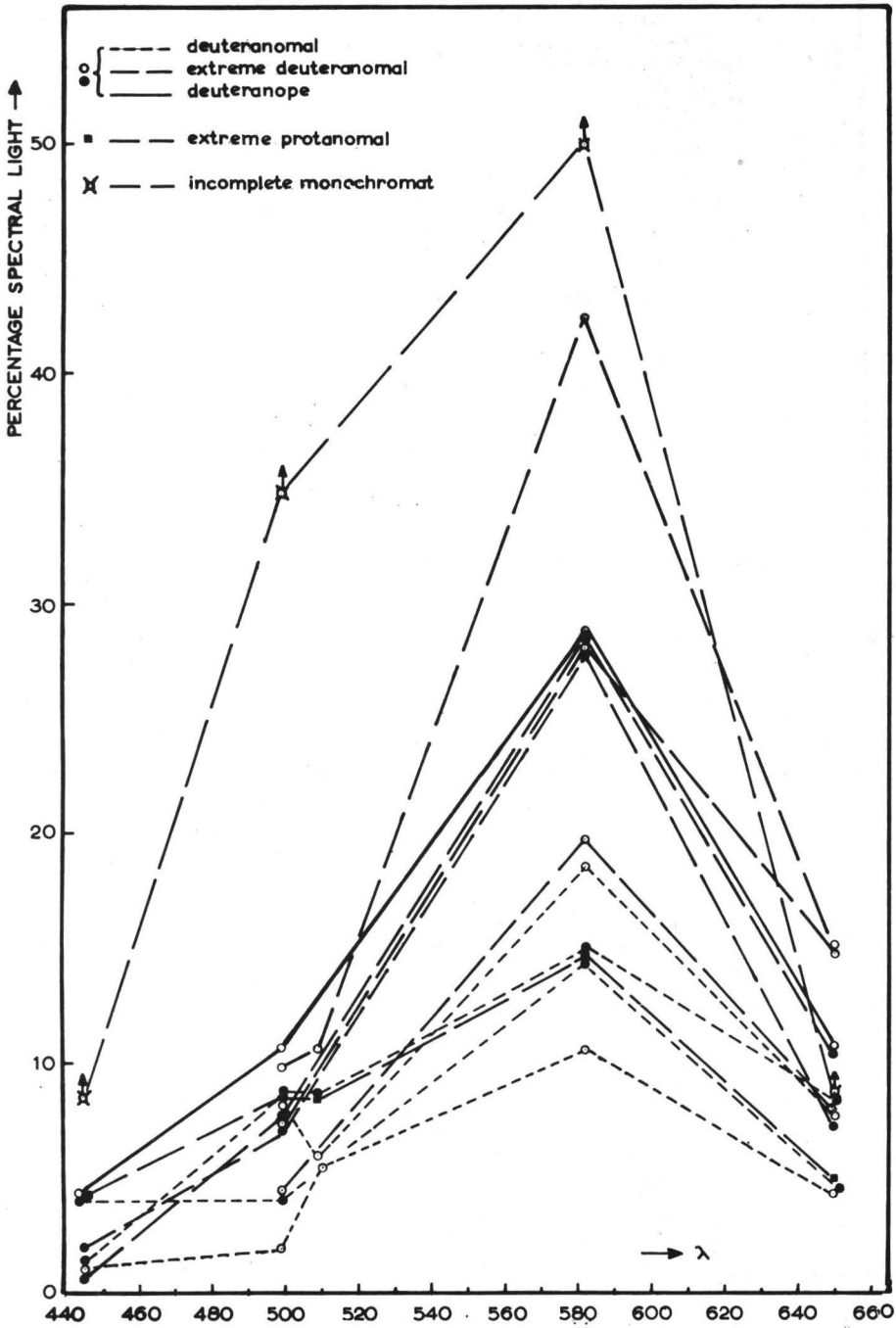


Fig. 5. Saturation discrimination curves for some colour defective subjects for a restricted number of wavelengths.

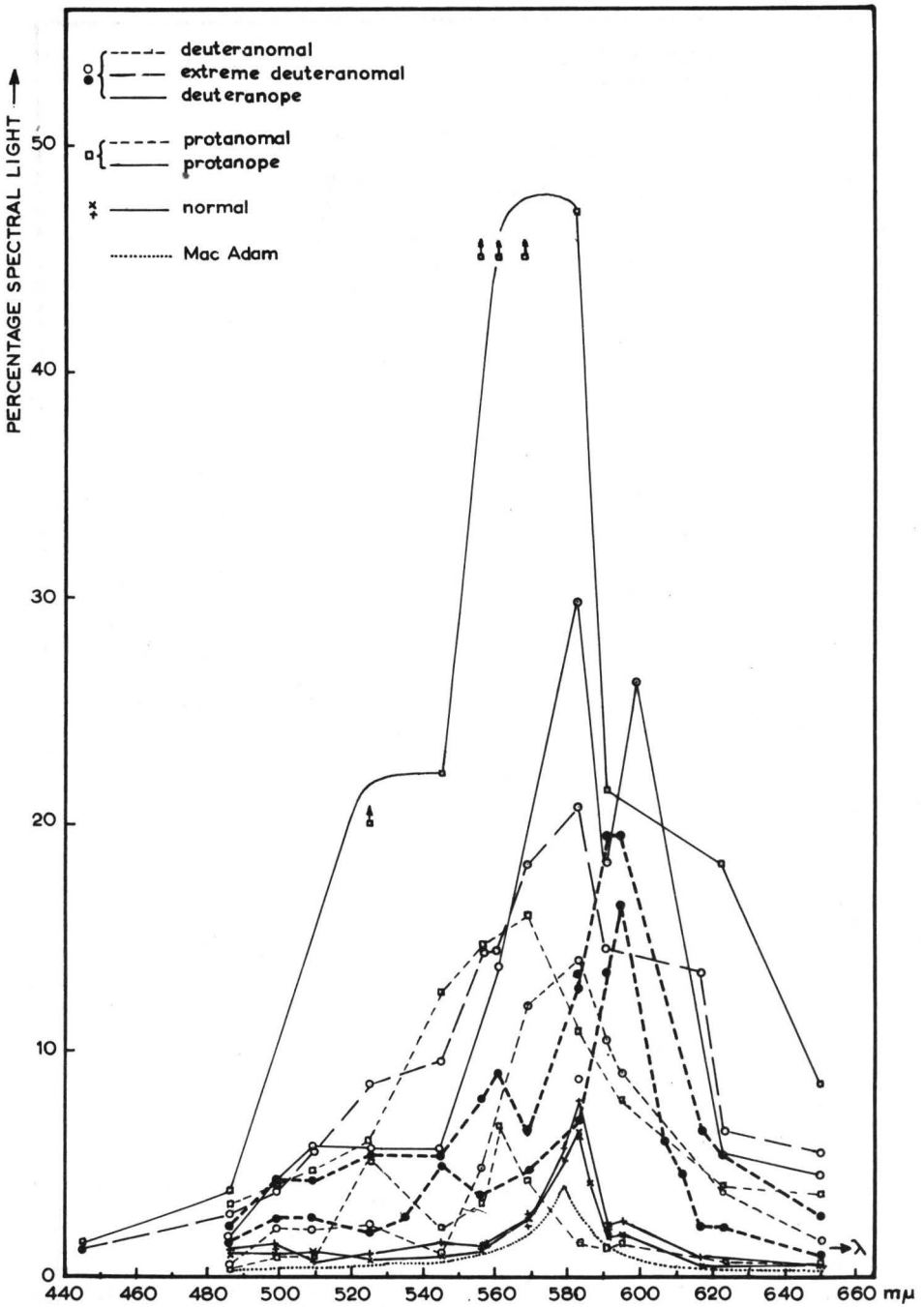


Fig.6. Saturation discrimination curves for two normal and some colour defective subjects.

The decrease in discriminating ability is not mainly restricted to special hues. We expected that colour defectives should be especially handicapped in accordance with the confusion lines for deuteranopes, protanopes and tritanopes.

In a subsequent study for seven colour defectives, the saturation discrimination curve was obtained by more extensive measurements. For comparison the ellipses of *fig. 4* are represented together with these data in *fig. 6*. The sharp peak at 595 mμ for two weakly deuteranomalous observers whose deficiency could hardly be detected with the plates is striking, as is the double peak of the protanomalous observer. The two deuteranomalous subjects are cousins, both on their mothers' side. For one of the deuteranomalous observers and for one of the normals, determinations of the size of the achromatic zone for monochromatic lights with small and large fields are available *(fig. 7)*.

The achromatic zone is that region of intensities where a light gives only a colourless sensation. *Fig. 7* shows, as a function of λ, the ratio of the intensity at which the chance of getting a coloured sensation is 60% (colour threshold) to the intensity at which the chance of getting any sensation at all is 60% (absolute threshold).

These results make it evident that the remarkable peak at 595 mμ is not an artifact in the measurements of saturation discrimination for the deuteranomalous observer. The achromatic zones are determined with colour-naming experiments in the dark-adapted eye, without reference colours in the background.

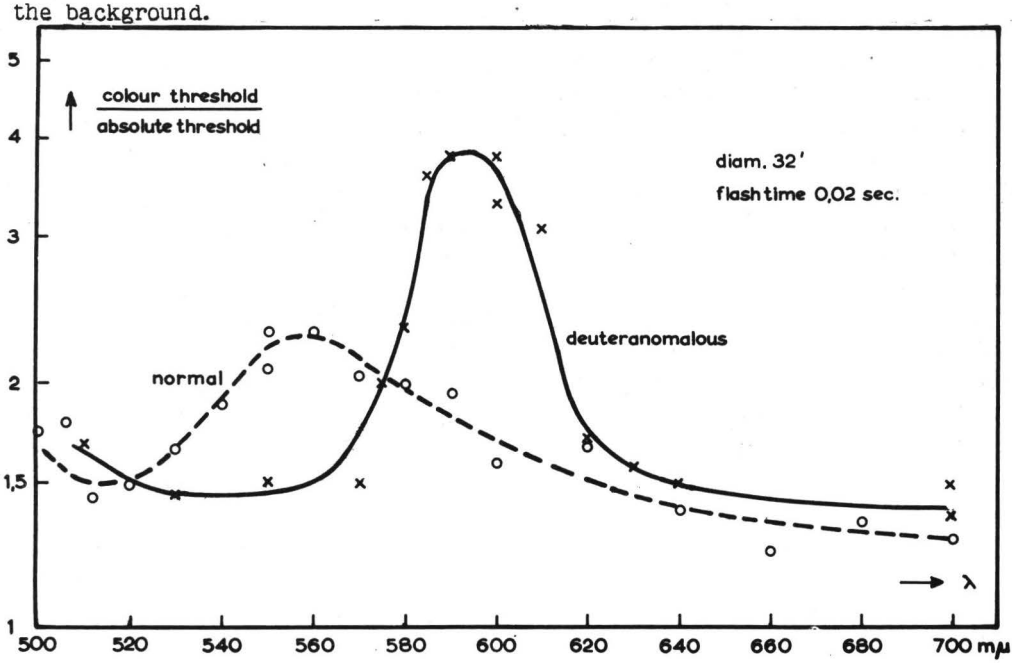


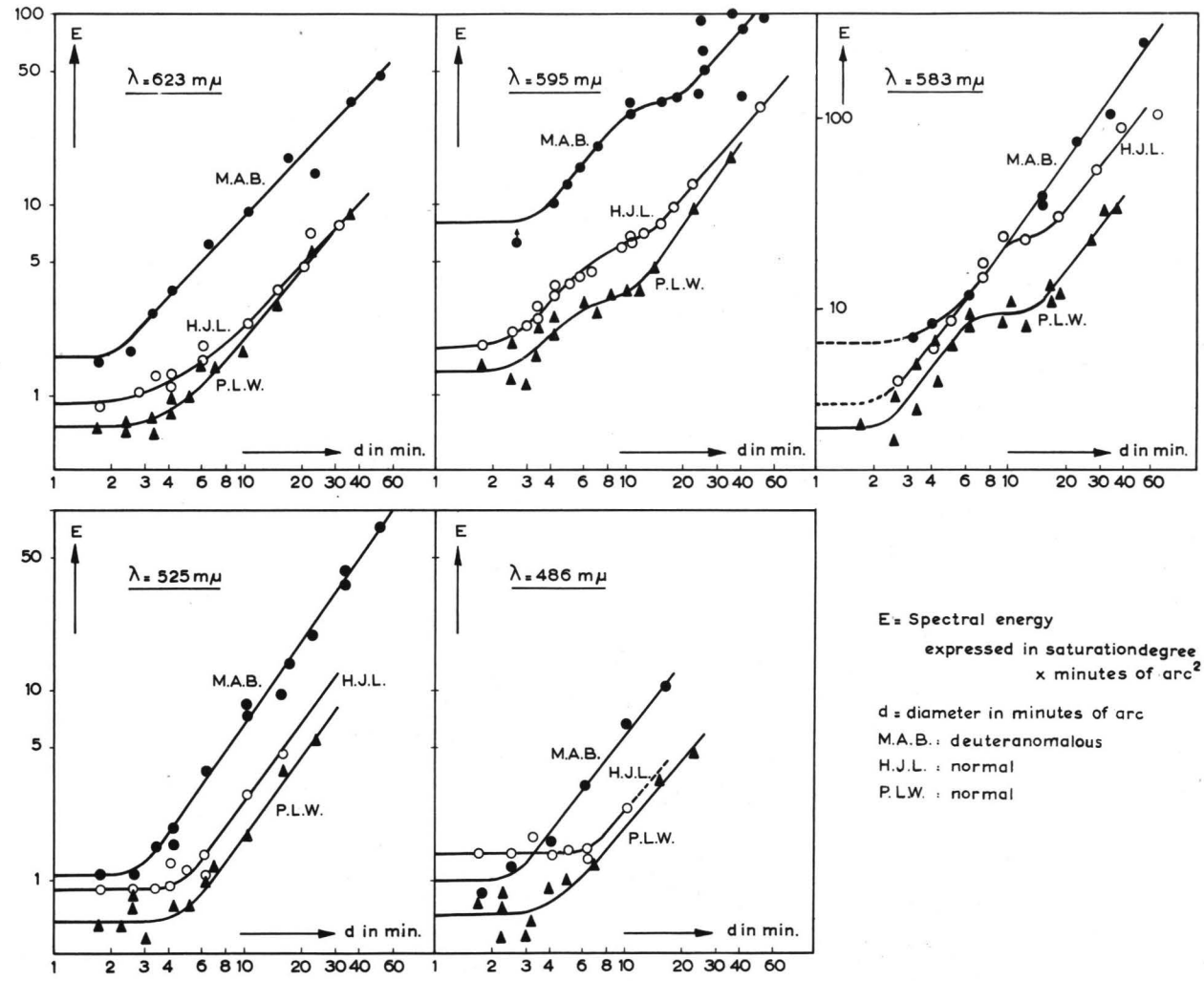
Fig. 7. The ratio of colour threshold and absolute threshold as a function of wavelength for a normal and a deuteranomalous observer.

ADDENDUM

TO check the idea of small-field tritanomaly being the cause for the difference in size of our ellipses and that of MacAdam, we measured the saturation discrimination ability as a function of diameter. Instead of strips we used round test-patches of diameters ranging from 1 to 60 min. of arc. The results are represented in *fig. 8*. The total spectral energy is plotted against the diameter, instead of the saturation-degree. The total spectral energy is the saturation-degree times area, this last expressed here in units of (min. of arc)^2. In this manner the occurrence of a Ricco-region is shown in a convenient way: the visibility of the test-patch up to about 3' is determined only by the total spectral energy, for the two normal observers H.J.L. and P.L.W., as well as for the deuteranomalous observer M.A.B. Also here, of course, the energy is chosen according to the luminosity curve of the particular subject.

For yellow and orange the relationship is not represented by a straight line for the larger diameters, as is the case for red, green and blue. For example, for the observer P.L.W. in a region of 6 to 15 min. of arc. for λ = 583 mμ, there is scarcely an increase in energy for an increase in diameter, showing very clearly the tritanomalous effect for small diameter. For the deuteranomalous observer M.A.B. such a region is missing for λ = 583 mμ, but it is clearly seen at 595 mμ, notwithstanding the low accuracy of the measurements for large diameters. So the remarkable peak at 595 mμ of the lowest of the thick-dashed curves of deuteranomalous observers (M.A.B.) in *fig. 6* can be caused by small-field tritanomaly, the neutral point in the spectrum being shifted to longer wavelength.

A second remarkable point is the variation of the slope of the curves as a function of wavelength. It is not so easy to speak about a slope for the yellow and orange, but for red and green it is clear that the average slopes are very different, the averages of the three observers being 1.07 and 1.40 respectively. This seems to be of great importance, because it indicates so clearly the dependence on stimulus diameter of the MacAdam ellipses in the colour diagram. Hence it seems that extensive studies on transformations to equicontrast colorimetric systems are fruitless, without a good understanding, as Farnsworth has already indicated, of the effects of the diameter and perhaps of brightness.



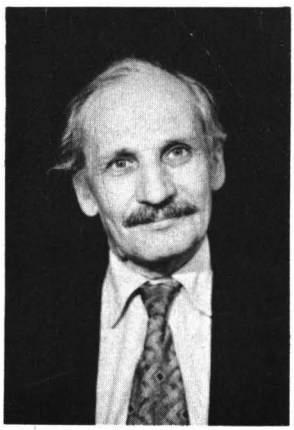
E = Spectral energy
expressed in saturationdegree
x minutes of arc^2

d = diameter in minutes of arc
M.A.B. : deuteranomalous
H.J.L. : normal
P.L.W. : normal

PAPER 32

RESEARCHES ON DICHROMATIC VISION AND THE SPECTRAL SENSITIVITY OF THE RECEPTORS OF TRICHROMATS

By N. D. NUBERG and E. N. YUSTOVA



E. N. Yustova, born in 1910, graduated from the Faculty of Physics of Leningrad University in 1932, and is at present working at the State Optical Institute. Master of Sciences. She is mainly concerned with colorimetry and physiological optics and studies the effect on the eye of colour adaptation in connexion with the problems of colorimetry.

N. D. Nuberg, Doctor of Physics and Mathematics, was born in 1898. Having graduated from the Physical Mathematical Faculty of Moscow University in 1925, he worked in the fields of colorimetry and physiological optics, devoting himself chiefly to a study of the theory of colour-rendering in polygraphy and colour films. He is the author of several books on colorimetry and colour-rendering theory. He is at present head of the Biophysics of Vision Laboratory at the Biophysical Institute of the Academy of Sciences of the U.S.S.R.

32. RESEARCHES ON DICHROMATIC VISION AND THE SPECTRAL SENSITIVITY OF THE RECEPTORS OF TRICHROMATS

By N. D. NUBERG and E. N. YUSTOVA

SUMMARY

THE method of investigating dichromatic vision by the use of all the three colour co-ordinates is described. Emphasis is placed on the essential advantages of this method in comparison with the use of only two colour locus co-ordinates in the chromaticity diagram. "Deficient" colours of protanopes and deuteranopes are determined and the simple procedure of direct experimental test of the correctness of these determinations is explained. Spectral receptor sensitivity curves are calculated both for the case of the correctness of the "fall-out" hypothesis for all the three types of dichromasy, and for the case when the "fusion" hypothesis for deuteranopia is adopted. It is pointed out that there are no reasons for the adoption of the latter hypothesis.

1. GENERAL

DICHROMATIC vision complies with the following:

(a) Any match made by a normal trichromat is also acceptable to a dichromat;

(b) Grassman's additivity law holds true for dichromats; it reads: "If any two radiations $e_1(\lambda)$ and $e_2(\lambda)$ are visually indiscriminable, the radiations $e_1^1(\lambda) = e_1(\lambda) + e_3(\lambda)$ and $e_2^1(\lambda) = e_2(\lambda) + e_3(\lambda)$ will also be visually indiscriminable, whatever the nature of the radiation $e_3(\lambda)$ added to the two radiations." *

It is therefore possible to maintain, that if $\mathbf{A}_1$ and $\mathbf{A}_2$ are some two colours different to a trichromat, but indiscriminable by a dichromat, then a dichromat will always accept the following colour equalities:

$$\mathbf{B} \overset{d}{=} \mathbf{B} + k(\mathbf{A}_1 - \mathbf{A}_2) = \mathbf{B} + k\mathbf{D} \qquad (1)$$

where $\mathbf{B}$ is an arbitrary colour, and k is an arbitrary number.

* This is just the most strict formulation of this law, and the verification of its correctness should indispensably precede the introduction of any system of numerical colour characteristics. There is no evidence of deviation from this law, as it is here formulated, which indicates that all numerical deviations from the rule of additivity represent nothing but experimental error.

Here and later we regard colours as vector quantities of three dimensions and designate them by bold type, as used for vectors in mathematics. Scalar quantities are printed in ordinary type. Colour equations should always be understood to be ordinary vectorial equalities, but by no means to be "unit equations", as introduced by some authors in colorimetry. The letter d above the sign of equality indicates that the corresponding equality refers only to a dichromat.

The vectorial equality (1), in which **B** and k are variable parameters, is the well-known vectorial equation of a beam of parallel lines in space. Therefore it can be stated, that colours which are located in colour space on parallel lines of a certain direction are indiscriminable by a dichromat. All the other colours are discriminable by him, otherwise he would not be a dichromat, but a monochromat. The direction of the above-mentioned lines is determined by the direction of the vector **D**, which is the vector-difference of any two colours indiscriminable by the given dichromat.

In a central projection of the colour space on a plane, i.e. in a colour triangle (chromaticity diagram), the lines parallel in space will form, generally speaking, a beam of straight lines intersecting at one point (a perspective view), namely, at that point where the extension of the vector **D** intersects the plane of projection. If, by chance, the plane of projection is parallel to the vector **D**, the point of intersection may be at infinity. In this particular case the lines parallel to the vector **D** in space will be parallel also in the projection plane.

The question as to whether the lines in the colour triangle intersect at one or another finite or infinitely distant point (parallel lines) is, in fact, of no physiological significance and depends entirely on the method of projection of the colour space onto the plane. In a central projection the points at infinity in the plane of projection do not differ in the least from the finite points. The parallelism of the lines has nothing to do with the colours which are assumed to be "the primary physiological colours", as the orientation of the plane of projection has no relation to the physiological interpretation of experimental data.

Some authors *(refs. 1, 2)*, referring to Helmholtz *(ref. 3)*, attach a physiological significance to the parallelism of lines in the colour triangle, which is a sheer misunderstanding, for in the corresponding place *(ref. 3* VII pp.123-125*)* there is nothing but a mathematical demonstration absolutely similar to our deduction of the formula (1).

For brevity we shall further call the lines in colour space, or in the colour triangle, on which lie the colours indiscriminable to a certain dichromat - "the lines of this dichromat". Vector **D**, corresponding to the direction of these lines in space, will be called "the deficient" colour of the dichromat.

As shown, all the differences between normal and dichromatic colour equations are determined entirely by the direction of vector **D** in colour

space, which is given in the equality:

$$k\,\mathbf{D} = \mathbf{A}_1 - \mathbf{A}_2 \qquad (2)$$

where $\mathbf{A}_1$ and $\mathbf{A}_2$ are two colour vectors, corresponding to any two colours, indiscriminable to the given dichromat.

This formula (2) directly indicates the simplest method of dichromatic vision research. It is the same method by which Maxwell determined the deficient colour of one protanope *(ref. 4)*. The same method has also been adopted as the basis of the present experimental investigation.

2. EXPERIMENTAL METHOD

A colour sample (coloured glass) was mounted in a trichromatic colorimeter* in the visual field of the test subject. A normal trichromat matched the sample colour **F** to a mixture of the three primary colours of the instrument $\mathbf{A}_r$, $\mathbf{A}_g$, $\mathbf{A}_b$:

$$\mathbf{F} = f_r\,\mathbf{A}_r + f_g\,\mathbf{A}_g + f_b\,\mathbf{A}_b \qquad (3)$$

where f_r, f_g, f_b are the readings of the three scales of the instrument.

This equality was acceptable to a dichromat.

Having recorded the readings we sharply changed one of them (the red – f_r – in a protanope test, or the green – f_g – for a deuteranope). This resulted in a definite match breakdown for the normal trichromat. It was a breakdown also for the dichromat, as the primary colours of the instrument cannot coincide with the deficient colours of dichromats. Therefore the dichromat was asked to re-establish the match, without altering the reading previously changed by the experimenter. The dichromat was always able to do this only by changing the other two mixed primary colours. The match obtained by the dichromat will never be a match to the normal observer. Designating the new readings as $f^1{}_r$, $f^1{}_g$, $f^1{}_b$, the differences $d_r = f_r - f^1{}_r$, $d_g = f_g - f^1{}_g$ and $d_b = f_b - f^1{}_b$ will obviously be the components of the difference vector of the two colours indiscriminable to the dichromat, i.e. the components of the deficient colour **D**, in the primary colour system of the instrument. If the colorimeter is calibrated, it is easy to compute the co-ordinates of the colour **D** in any other system, for instance, the **X Y Z** system. Then the location of the point D in the colour triangle may be found.

Since it is possible in the experiment to change the corresponding reading arbitrarily, the numbers d_r, d_g and d_b can always be obtained sufficiently large, so that the direction of vector **D** is determined with a fair degree of accuracy. Furthermore, if without changing the initial test field colour **F**, a dichromat (a deuteranope, for instance) is asked to establish a field match for several different values $f^1{}_g$, $f^{11}{}_g$, $f^{111}{}_g$, etc., a number of points of the same straight line in the colour space will be obtained,

* Most of the tests have been performed on a Donaldson colorimeter.

and by employing the least square method, the direction of the line and consequently that of the deficient colour vector, will be determined with greater precision.

A number of independent determinations of the vector **D** directions was made for each dichromat, taking for **F** different colours, i.e. in the colour space a whole range of parallel lines was found. Each line was usually drawn through several points (from 5 to 12 points). Tests were conducted on 10 protanopes and 12 deuteranopes.

Figs. 1 and *2* illustrate the data for one protanope and one deuteranope. These figures represent, instead of a central projection of the colour space (colour triangle), the parallel projections on the plane (A_r, A_g) of the primary colours of the instrument. Such projections are quite common in descriptive geometry and mechanical drawing for representation of spatial objects. A complete picture of spatial correlations is provided by two projections of this kind, of which we made use when the case required.

In parallel projection of space upon a plane, the parallelism is preserved so that it is easy to judge the degree of possible error in determining the direction of the deficient colour vector, by the presented charts. The drawing of such projections is exceedingly simple, as it only requires the plotting on the axes of co-ordinates of the instrument scale readings obtained in the experiment.

This method of determining the deficient colours of dichromats which we used following Maxwell, presents great advantages in comparison with the method of determining the intersection point of the dichromatic lines in the colour triangle employed by Pitt *(ref.1)*. In our experiments, for one independent colour trial only one dichromat match is required, that is, half the number required to determine the intersection point even of only two lines. Besides that, the precision of our determinations is much greater, especially in tests with deuteranopes, for a small discrepancy in determining the direction of two lines may be a source of considerable error in determining the point of their intersection. We attribute these advantages to the fact that the problem is regarded as a spatial one, and all the *three* colour co-ordinates are made use of, instead of two, as is the case when solving the problem on a plane.

According to our data the deficient colours; **R** for protanopes and **G** for deuteranopes, have in the colour space the following component characteristics in the **XYZ** system:

$$\bar{x}_r = 0.75, \qquad \bar{y}_r = 0.25, \qquad \bar{z}_r = 0.0;$$

$$\bar{x}_g = -1.70, \qquad \bar{y}_g = 0.70; \qquad \bar{z}_g = 0.0;$$

The loci of the corresponding points in the colour triangle will be:

$$x_r = 0.75, \qquad y_r = 0.25, \qquad q_r = +1.0,$$

$$x_g = 1.70, \qquad y_g = -0.70, \qquad q_g = -1.0,$$

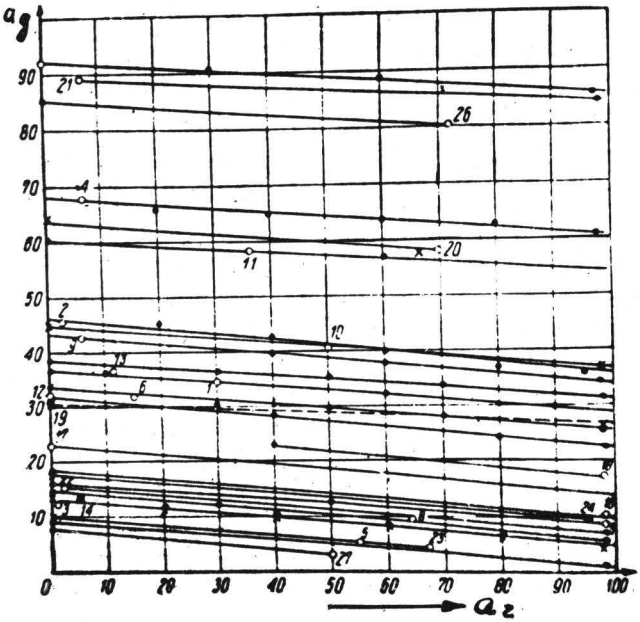


Fig. 1. The projection of the lines of protanopes upon plane $A_r A_g$.

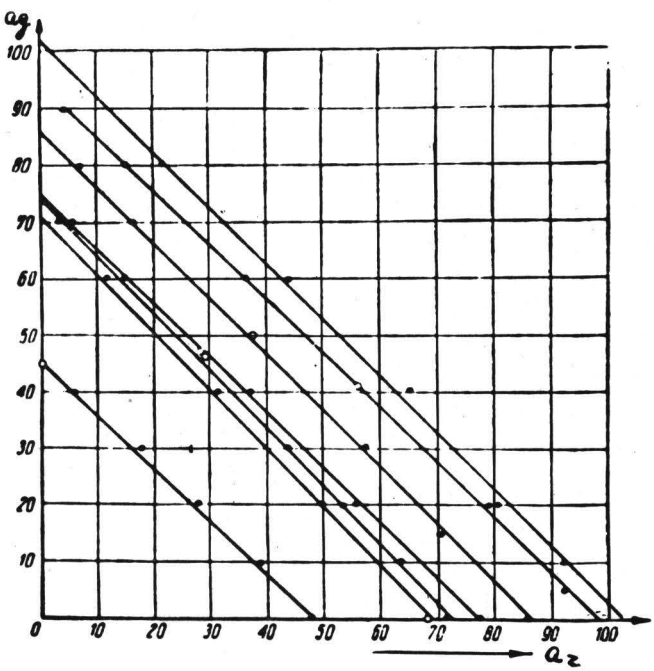


Fig. 2. The projection of the lines of deuteranopes upon plane $A_r A_g$.

where $q = \bar{x} + \bar{y} + \bar{z}$ is the third co-ordinate of the baricentric system, which, unfortunately, is usually neglected by modern authors.

The signs of the spatial and planar co-ordinates for **G** are inverse, because the *positive* direction of vector **G** does not intersect the plane of the triangle X Y Z, and the point G in the triangle X Y Z is the trace from the intersection of its plane by the extension of vector **G** made in the inverse (negative) direction. This is indicated by the sign of the third baricentric co-ordinate

$$(q_g = -1.0 < 0).$$

The use of all the three co-ordinates also has the advantage that it facilitates a very simple test of the correctness of the dichromatic deficient colour determination, and of the similarity of this colour for all the dichromats of a given type.

For this purpose, it is most convenient to use the components d_r, d_g, d_b of the supposed deficient colour **D** in the primary colour system of the instrument. Having invited the dichromat observer to establish a colour match acceptable to him, some quantities proportional to d_r, d_g, d_b should be added to the readings set by the dichromat on the instrument scales (the "addition" here is algebraic as one, and often, two of the components d_r, d_g, d_b are negative). If the deficient colour is determined correctly, then such alteration of the instrument scale readings should never cause a breakdown of the dichromat's colour-match.

As the values of **R** and **G** cited above were obtained by averaging the data of different observers, we tested each of them. The results were positive. In the same way we examined Judd's assumption *(ref. 5)*, according to which:

$$\bar{x}_g = 0.0, \qquad \bar{y}_g = 1.0, \qquad \bar{z}_g = 0.0.$$

All deuteranopes tested, without exception, definitely rejected the equalities which they should have accepted if Judd's assumption had been correct. Hence it follows, in particular, that the visibility curve for all the deuteranopes available to us differs essentially from the standard visibility curve for normal trichromats.

The checking procedure cited is exceedingly simple and can be performed in any laboratory equipped with a calibrated trichromatic colorimeter. It is greatly desired that verifications of our data, as well as of other experimental data, should be carried out by different experimenters.

3. DETERMINATION OF SPECTRAL SENSITIVITY OF RECEPTORS OF NORMAL TRICHROMATS

As has long ago been pointed out by Helmholtz, it inevitably follows from the theses 1.(a) and (b) that the spectral sensitivity curves for the receptors of dichromats in the most general case can only be linear combinations of spectral sensitivity curves for receptors of normal trichromats:

$$s^d(\lambda) = a_1 s^t{}_1(\lambda) + a_2 s^t{}_2(\lambda) + a_3 s^t{}_3(\lambda) \qquad (4)*$$

where $s^d(\lambda)$ is the spectral sensitivity curve for any one of the dichromat's receptors, $s^t{}_1(\lambda)$, $s^t{}_2(\lambda)$, $s^t{}_3(\lambda)$ are the three curves for a trichromat, and a_1, a_2, a_3 are numerical factors. The simplest particular case of formula (4) occurs when both receptors of a dichromat just coincide with two of the trichromat's receptors, while the third normal receptor of the dichromat for some reason is not functioning ("falls out"). This kind of dichromatism can evidently be of only three types, and, in fact, there are only three types of dichromat.

If it is assumed that the "falling out" of a receptor is the cause of dichromatism of all the three types, then the knowledge of the deficient colours for all the three types of dichromatism *R*, *G*, *B* will suffice to determine the spectral sensitivity of the receptors, which in this case are the same in dichromats and in trichromats. For this purpose three deficient colours R, G, B should be taken in terms of which the equal-energy spectrum

TABLE I

λ	$\bar{r}(\lambda)$	$\bar{g}(\lambda)$	$\bar{b}(\lambda)$	λ	$\bar{r}(\lambda)$	$\bar{g}(\lambda)$	$\bar{b}(\lambda)$
380	0.0000	0.0000	0.0065	570	0.9540	0.9462	0.0021
390	0.0001	0.0001	0.0201	580	0.9394	0.7672	0.0017
400	0.0004	0.0003	0.0679	590	0.8984	0.5641	0.0011
410	0.0011	0.0012	0.2074	600	0.8056	0.3761	0.0008
420	0.0034	0.0044	0.6456	610	0.6893	0.2280	0.0003
430	0.0071	0.0156	1.3856	620	0.5515	0.1300	0.0002
440	0.0136	0.0358	1.7471	630	0.3990	0.0697	0.0000
450	0.0191	0.0639	1.7721	640	0.2710	0.0345	0.0000
460	0.0255	0.1046	1.6692	650	0.1685	0.0171	0.0000
470	0.0469	0.1548	1.2876	660	0.0971	0.0080	0.0000
480	0.0824	0.2212	0.8130	670	0.0512	0.0038	0.0000
490	0.1369	0.3116	0.4652	680	0.0273	0.0019	0.0000
500	0.2271	0.4621	0.2720	690	0.0132	0.0009	0.0000
510	0.3717	0.6945	0.1582	700	0.0066	0.0004	0.0000
520	0.5196	0.9436	0.0782	710	0.0034	0.0003	0.0000
530	0.6986	1.1010	0.0422	720	0.0017	0.0001	0.0000
540	0.8089	1.1651	0.0203	730	0.0008	0.0001	0.0000
550	0.8837	1.1568	0.0087	740	0.0004	0.0001	0.0000
560	0.9340	1.0836	0.0039	750	0.0001	0.0000	0.0000

* In this respect see also *ref.6*.

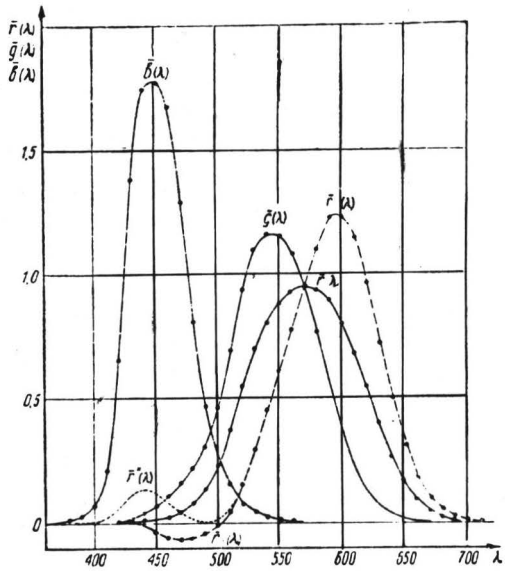


Fig.3. Spectral sensitivity curves for normal trichromat's receptors.

---o--o--- $\bar{r}(\lambda)$, $\bar{g}(\lambda)$, $\bar{b}(\lambda)$ - in case of correctness of the "fall-out" hypothesis.

— o — o — $r^1(\lambda)$, $r^{11}(\lambda)$ - spectral sensitivity of the "red" receptor in case of assuming the "fusion" hypothesis for explaining deuteranopia.

colours for different values of λ should be expressed. In vector form we have:

$$S = \bar{r}(\lambda)R + \bar{g}(\lambda)\ G + \bar{b}(\lambda)\ B \qquad (5)$$

$\bar{r}(\lambda)$, $\bar{g}(\lambda)$, $\bar{b}(\lambda)$ are coefficients of the vectorial colour equation (5), which when regarded as functions of wavelength will be the desired spectral sensitivity curves for the receptors.

As we had no tritanopes at our disposal, we have determined only **R** and **G**. As far as **B** is concerned, we made use of the data of other investigators, and some general considerations forming a consistent whole. Thus we have assumed:

$$\bar{x}_b = 0.17,\ \bar{y}_b = 0.0,\ \bar{z}_b = 0.83.$$

The calculated spectral receptor sensitivity curves are seen in *Table 1* and in *fig. 3*. If the assumed vector **B** components proved to be incorrect, we would have to add to or subtract from the functions $\bar{r}(\lambda)$ or $\bar{g}(\lambda)$ the function $\bar{b}(\lambda)$ multiplied by a certain coefficient. But in this case curves would be obtained either with two maxima, or with negative ordinate values for some wavelengths. Therefore it is most likely that the vector **B** components adopted here are close to the truth.

The calculation of spectral receptor sensitivity curves is also possible if it is assumed that these curves for the dichromat's receptors are combinations of normal curves. It is merely necessary to know the corresponding coefficients of formula (4).

Some authors *(refs. 1,2)*, adopting the "fall-out" hypothesis for the explanation of protanopia and tritanopia, hold that in deuteranopes one of the receptors is a fusion of the normal "red" and "green" ones. Though these authors do not indicate clearly enough the coefficients of the formula (4), these can be calculated from the components of the "white" radiation, which is of great importance for this hypothesis. But it is necessary to indicate exactly which radiation is considered as "white" ("equally-stimulating" all the three normal receptors).

The authors mentioned computed the spectral sensitivity curves, taking different radiations as the "white" one. In all cases the adoption of the "fusion" hypothesis leads to the red receptor having negative ordinates. *Fig. 3* shows such curves adopting as "white" the source *C* (giving the least negative values). To eliminate negative ordinates it would be necessary to take as "white" a radiation much more "greenish" than the source *C*.

Even apart from these calculations the above mentioned version of the "fusion" hypothesis seems to have little validity. It does not explain the existence of only three types of dichromatism and presumes for one of the three types, which from a general standpoint are quite analogous to each other, an absolutely different physiological cause than for the other two, though there is no necessity for it.

The arguments for advancing this hypothesis seem from our point of view to be certainly erroneous. The "parallelism" of the lines of dichromats, as has been seen, cannot fundamentally be related to the physiological causes of dichromatism, and in Helmholtz's work, to which reference is usually made, there is no proof of the reverse.

The coincidence of the deuteranopic "visibility curve" with the normal one, suggested by Judd, is refuted by experiment, as we have already mentioned; but even if such coincidence had taken place (if point G should lie on the alychne), it would mean that the "primary green" has zero brightness and its "falling out" is not contrary to the invariability of the visibility curve for deuteranopes. Though at the present time, after the recognition of the non-additivity of heterochromatic brightness, the question of the linear connection of the visibility curve with spectral receptor sensitivities no longer arises.

In addition we should like to refer to the following experiment which was carried out for testing the "fusion" hypothesis. If the "green" receptor does not "fall out", but is only "fused" with the "red" one, then adaptation to a green or red stimulus, suppressing either one or the other of the fused receptors, should alter their resultant spectral sensitivity curve. In particular, adaptation to green light should convert a deuteranope into a protanope, or bring him closer to the latter.

In any case deuteranopic matches unacceptable to the trichromat after green or red stimuli adaptation should also be unacceptable to the deuteranope. Experiment shows that this is not the case. Deuteranope colour matches are not altered by adaptation.

We think there is no sufficient reason to consider the physiological cause of deuteranopia essentially differing from that of the other two types of dichromasy. Experimental data contradict, rather than confirm, such a hypothesis.

For a more detailed account of our experimental data see *ref. 7*.

REFERENCES

1. PITT, F. H. G. - Characteristics of dichromatic vision *Spec. Rep, Ser. Med. Res. Coun., Lond.*, 200, 1935.
2. WRIGHT, W. D. Researches on normal and defective colour vision. London, 1946.
3. VON HELMHOLTZ, H. Handbuch der Physiologischen Optik, 2 Aufl. Leipzig 1911.
4. MAXWELL, J. C. On the theory of compound colours. *Phil. Trans.*, 1860, **150**, 57.
5. JUDD, D. B. Standard response function for protanopic and deuteranopic vision. *J. opt. Soc. Amer.*, 1945, **35**, No. 3, 199-221.
6. NUBERG, N. D.: *Problemi Fiziologicheskoi Optiki* 1950, **9**, 61.
7. NUBERG, N. D., and YUSTOVA, E. N.: *Trudy Gos. Opticheskogo Instituta* Vol. 24.

PAPER 34

A NEW ANOMALOSCOPE AND THE CLASSIFICATION OF COLOUR VISION FORMS

By G. N. RAUTIAN

G. N. Rautian, born in 1889, graduated from the Faculty of Physics of St. Petersburg University in 1912. Since 1921, he has worked at the State Optical Institute, except for an interval from 1936 to 1944, when he worked in industry. In 1938, he became a Doctor of Technical Sciences. He has been the head of the Colorimetry Group since 1945.

34. A NEW ANOMALOSCOPE AND THE CLASSIFICATION OF COLOUR VISION FORMS

By G. N. RAUTIAN

SUMMARY

A description of an anomaloscope is given which makes it possible to determine four quantitative indices, three of which assess the acuity of discrimination characterising each of the three systems of foveal receptors, while the fourth indicates the normality or abnormality of the spectral sensitivities of these receptors, after Rayleigh. The investigation of several thousands of persons with such an anomaloscope showed new peculiar forms of colour vision. A new scheme of classification that embraces all the variety of phenomena observed is proposed.

A NEW ANOMALOSCOPE AND THE CLASSIFICATION OF COLOUR VISION FORMS

THE new anomaloscope, developed in recent years, was constructed according to the idea of the presence in the fovea of three systems of lightsensitive cellular receptors, differing in their spectral sensitivity $\rho(\lambda)$, $\gamma(\lambda)$, $\beta(\lambda)$. The concrete values, used by us, of these important magnitudes of the science of colour had been obtained by E. N. Yustova *(ref. 1)* in her work, carried out according to the scheme proposed by N. D. Nuberg *(ref. 2)*. We may note that her values received in our apparatus a complete practical approbation, while our early attempts to use the Judd curves *(ref. 3)*, showed the latter to be groundless *(ref. 4)* *.

It is possible to make four (or five)** tests by means of the anomaloscope. Three of them are concerned with colour discrimination. By means of these tests the problem of the separate trial of each of the three systems of retinal receptors is solved. This is an original feature in which our apparatus differs from all other anomaloscopes.

During the first test we have an estimation of discrimination acuity, controlled by the system of receptors, the spectral sensitivity of which

* Although Walls' and Heath's *(ref. 5)* recent work was made under unfavourable experimental conditions it gave the results that confirmed Yustova's data for deuteranopes, and for protanopes data which differ by 1 mμ.

** According to whether or not a test on tritanomaly is introduced.

we designated as $\rho(\lambda)$ and which is impaired in protanopes. In the second and third tests the discriminative acuity evaluated is that connected with each of the other two systems which are characterized by $\gamma(\lambda)$ and $\beta(\lambda)$ and which do not operate in deuteranopes and tritanopes.

The idea of these tests is as follows. Let us take some colour C_1 with the co-ordinates ρ_1, γ_1, β_1, of the basic physiological co-ordinate system, and another colour C_2 with co-ordinates ρ_2, γ_1, β_1, that is which lies together with C_1 on a line parallel to the corresponding co-ordinate axis, which is always possible. When proceeding from C_1 to C_2 across the intermediate colours the action of radiation upon the first system of receptors will change ($\rho_1 \neq \rho_2$), while the action on the two others remains constant ($\gamma_1 = \gamma_2$, $\beta_1 = \beta_2$). In spite of the great difference between C_1 (blue-green) and C_2 (red-purple), it comes about that we distinguish these two colours only because of the objective difference of signals from the first system $\rho(\lambda)$. If these receptors do not operate, as in the case of protanopia, the observer will fail to perceive the whole difference between C_1 and C_2 ($\gamma_1 = \gamma_2$, $\beta_1 = \beta_2$).

If, in general, we determine what change ($\Delta\rho$) of the action on the first system takes place at the threshold of our perception, we get a measure of acuity of colour discrimination connected with, and characteristic of, the first system. We may accomplish the same for two other systems and so analyse the quality of functioning of each of them separately.

The scheme of the apparatus is shown in *fig. 1*, and its outward appearance is shown in the photograph (*fig. 2*). The lamp L is in the white enclosure, a portion of the back wall of which, in fact, serves as a light source. The twin objectives O-O project S on the white screens e-e and give on them coloured light-spots, because between O-O lightfilters F-F are inserted which always fill the square aperture of diaphragms D-D, which are also put between O-O. The light-spots on e-e fill with light the reflecting-surfaces of the prisms P-P, that face the field lens O^1 and are observed through the ocular tube. The filters between O-O are situated on rotatable disks. The change of filters is carried out by the drums B_1 and B_2 (*fig. 2*). The disk to the right can be put, apart from rotation, in translational movement by means of a divided drum B_0. Owing to this movement a transition from the colour C_1 to the colour C_2 is realized in the right part of the field of vision, while the left part of it keeps its own colour C_1 constant (the colour of the spot at the left screen).

The person tested must give a signal as soon as he perceives the beginning of the change of colour at the right half-field while the controller rotates the measuring drum B_0 smoothly and slowly, moving by this means the right disk between O-O and gradually substituting the filter F' by F" in the aperture of the diaphragm D. The test, repeated 3 or 5 times, allows one to obtain a reliable average value (m_i) of the threshold expressed in divisions of the drum B_0.

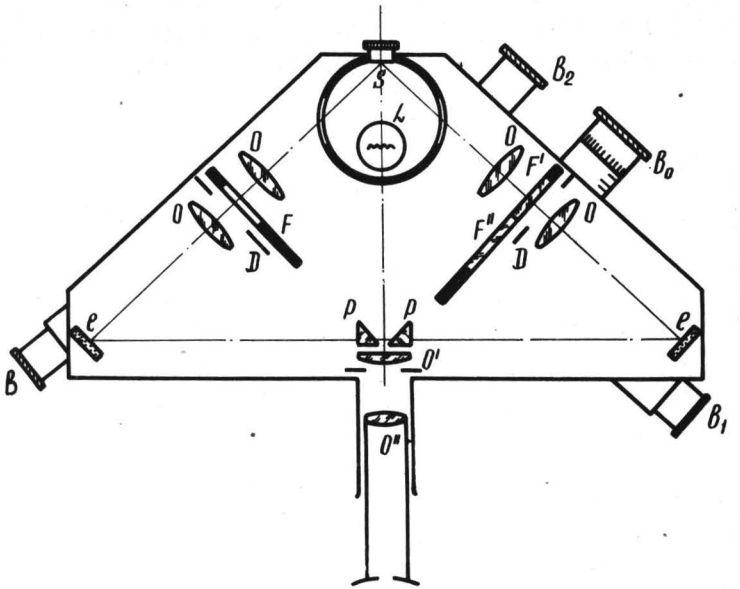


Fig. 1

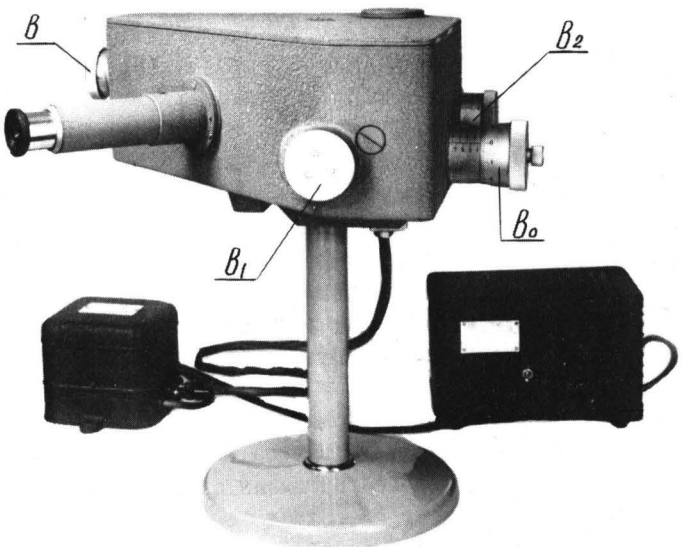


Fig. 2

The graduation of the intervals (C_1-C_2) in thresholds made step by step on a specially constructed instrument (paired anomaloscope) allows one to evaluate the acuity of colour discrimination by the index $n_i = 1/N_i$,

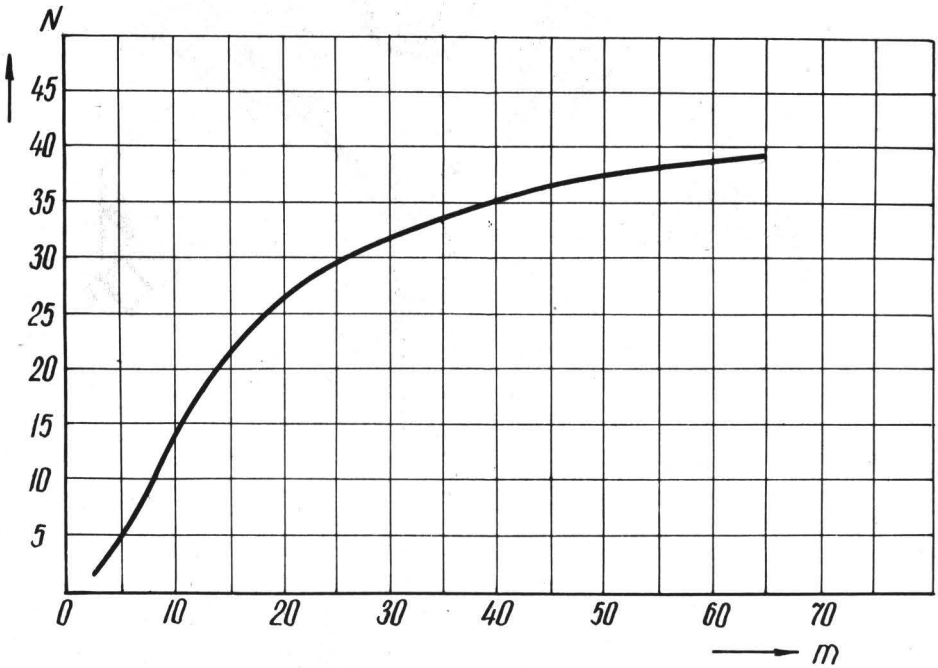


Fig. 3

where N_i is the number of normal thresholds *(fig. 3)* lying within the interval (m_i) of the scale divisions which correspond to the threshold obtained. For the complete dichromats in corresponding tests $(i = 1,2,3)$, the limit of the scale is reached without their perceiving any difference in the colour of the half-fields. Thus, our instrument operates in its three first tests according to a specifically threshold method, that is by statements of inequality.

The fourth test coincides in the main with Rayleigh's as the colour of a yellow monochromatic lightfilter is equalized with a mixture of two colours - red and green - obtained by means of glass filters. Thus, the fourth test * is a colorimetric one, that is it uses the method of equality and shows whether the spectral sensitivity of receptors is normal, that is, typical for the majority, whether there are some deviations from the normal course of the curves $\rho(\lambda)$ or $\gamma(\lambda)$ *(ref. 7)* in what sense and by how much.

* The same as the fifth.

Thus, this test serves for detection and estimation of anomalies of colour vision. As is known, it may also serve for the detection of dichromasy - on the basis of multiple matchings of any mixtures of red and green with the yellow of suitable lightness (regulated by the drum B).

As a result, we can see that the method of investigation carried out by means of the instrument allows the differentiation in a simple way of the forms of colour vision, characterizing them quantitatively and in diverse ways. It leads to a new, more distinctive classification of these forms and to a corresponding terminology.

At the present time, the number of persons tested by the anomaloscope exceeds 3,000. The data obtained reveal a great variety of colour vision forms *(ref. 8)*, much more extensive than that known before and provided by the usual classification scheme *(ref. 9)*.

A very important regularity can be mentioned: each of the three systems of receptors can vary in its functioning independently of the other two, and within wide limits.

The discrimination acuity of any one system of receptors may be super-acute, two - three times as high as the normal. Simultaneously, for the other system it may be at the normal level or lowered in various degrees down to its complete disappearance, that is down to dichromatism. It happens, and not so seldom, that both systems have a lowered acuity of colour discrimination and to a different extent. There are also cases of lowering (sometimes to a very large extent) of the discrimination acuity of all the three systems.

As to the anomaly, that is the distortion of the course of the functions $\rho(\lambda)$, $\gamma(\lambda)$, $\beta(\lambda)$, we may affirm that varying within vast limits, it is more or less independent of the variations of colour discrimination. Sometimes it happened that all three thresholds were normal or even less than the norm (super-acute colour discrimination), while the fourth test (n_A) showed a clearly expressed anomaly* *(ref. 11)*. On the contrary, sometimes the threshold being very high, the index of anomaly n_A was about 1, that is normal.

It is necessary to point out that such relations were correctly noticed by Rayleigh *(ref. 12)*, at the time he discovered the phenomenon of the anomaly itself. Later on, however, rather confused ideas about the anomaly as an intermediate form between normal vision and dichromasy were formed. According to this point of view, the anomaly suggests a deterioration of colour discrimination and, at least, it leads to dichromatic colour blindness** *(refs. 9,13,14,15)*.

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* In their recent article on anomalous colour vision D. Jameson and L. Hurvich *(ref.24)* reckon me among those who suppose the anomaly to be caused by reduced spectral sensitivity of some kind of receptors. Such a point of view has always been considered by me as completely wrong. Cited by Jameson and Hurvich, my article *(ref.4)* deals exclusively with the thresholds of colour discrimination, and if the facts of the *reduction of colour discrimination* were mentioned there, this is by no means the reduction of the ordinates of the spectral sensitivity curves of the receptors.

** And it is in spite of the fact that common dichromats approve colorimetric equations of normal trichromats.

The truth is, that some authors' statements *(refs. 16,17,18,19)*, which were suggested by experiment, contain elements of disapproval of this point of view, as there are indications of the absence of direct correlation between the anomaly (alteration) and lowering of the colour discrimination (reduction). However, the clear statement that the combined manifestation of both must be considered as an accidental superposition, but not as an obligatory correlation, has not been made exactly by any one. The reason for this we see in the character of the instruments which were at those investigators' disposal and which were designed in the main to detect the anomaly, while the colour discrimination manifested itself only accessorily in the "breadth" of the scatter of the readings.

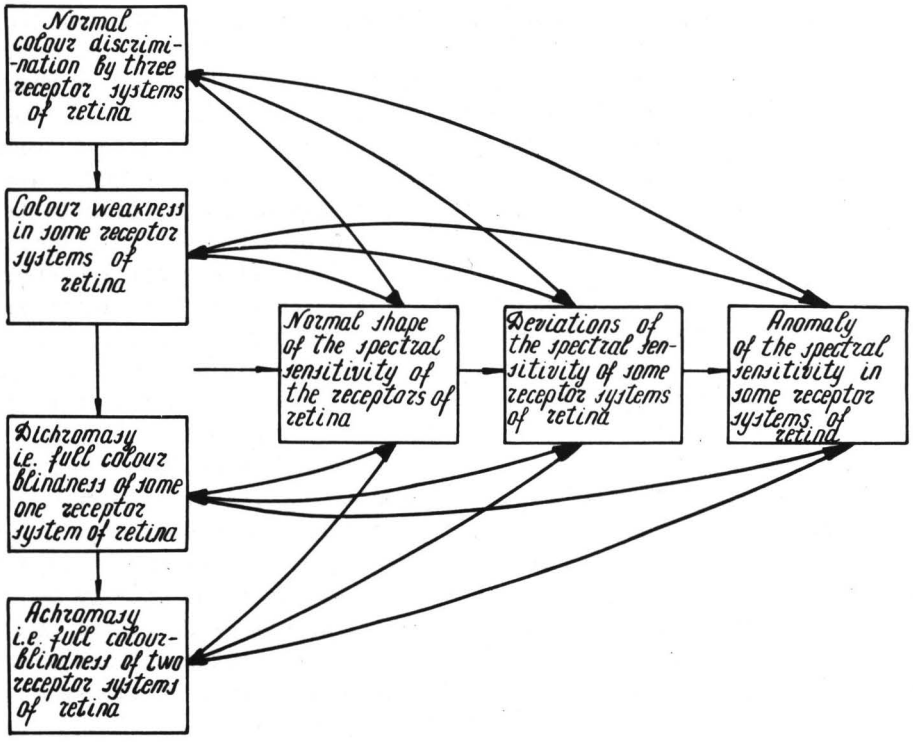


Fig. 4

A new system of classification of colour vision forms *(fig. 4)*, proposed by us, is in accordance with the facts observed. *(ref. 20)*.

It assumes a fundamental possibility of various combinations of different levels of colour discrimination acuity of the several receptor systems with a normal or abnormal course of their spectral sensitivities. The arrows in *fig. 4* show this scheme.

The new classification legalizes the terms "colour weakness" and "colour weak" which are used in the literature *(ref. 21)* and sometimes in the practice of physicians.

The classification based on the new anomaloscope *(ref. 17)* makes possible, for instance, such diagnoses as: "a trichromat with a high discrimination acuity along the axis β", "a protanomalous, colour weak along the axes ρ and γ", "a trichromat, colour weak along all the three axes ρ, γ, β". Finally, there are possible cases of "abnormal dichromasy of this or that kind" and also of "monochromasy" when there is no possibility to determine the indices n_ρ and n_β *(ref. 22)*.

The adoption of such a classification puts, in the first instance, the question about the symptoms of its types and especially to indicate (in quantitative form) the boundaries between normal and defective, suitably adjusted for different professions. Joint efforts of many investigators are necessary for the accomplishment of this task*.

* The first step in this direction is to be seen in A. B. Flekkel's work *(ref. 23)*. He laid down the doubled value of the threshold readings as the limit of the norm for persons showing some deviation.

REFERENCES

1. YUSTOVA, E. N. *Dokl. Akad. Nauk., S.S.S.R.*, 1949, **65**, 5, 661
   Problem. physiol. Opt., 1953, **8**, 112.
   Troudy G.O.I., 1955, **24**, 143, 33.
2. NUBERG, N. D. *Dokl. Akad. Nauk., S.S.S.R.*, 1948, **63**, 4, 379.
3. JUDD, D. B. *J. Res. nat. Bur. Stand.*, 1944, **33**, 6, 407.
4. RAUTIAN, G. N. *Dokl. Akad. Nauk., S.S.S.R.*, 1950, **73**, 1, 99.
5. WALLS, G. & HEATH, G. *J. opt. Soc. Amer.*, 1956, **46**, 8, 640.
6. RAUTIAN, G. N. *Biophysics*, 1957, (in the press)
7. LOBANOVA, N. V. *Dokl. Akad. Nauk., S.S.S.R.*, 1956, **110**, 4, 552.
8. RAUTIAN, G. N. *Dokl. Akad. Nauk., S.S.S.R.*, 1950, **74**, 6, 1073.
9. KRIES, J. von, Normale & anomale Farbensysteme. *Helmholtz; Handbuch physiol. Opt.*, 1911, **2**, 347.
   JUDD, D. B. *J. opt. Soc. Amer.*, 1943, **33**, 294.
10. RAUTIAN, G. N. *Dokl. Akad. Nauk., S.S.S.R.*, 1951, **81**, 5, 815.
11. RAUTIAN, G. N. *Dokl. Akad. Nauk., S.S.S.R.*, 1956, **111**, 1, 92.
12. RAYLEIGH, J. *Nature*, 1881, **25**, 64.
13. KOELLNER, H. Die Abweichungen des Farbensinnes. *Bethe; Handbuch norm. path. Physiol. B.*, **12**, Pt. I, 513.
14. WRIGHT, W. D. Researches on normal and defective colour vision. London, 1946, 298.
15. LE GRAND, Y. Optique physiologique, v. II Lumière et couleurs. Paris, 1949, 328.
16. GÖTHLIN, G. F. Abderhalden; Handbuch biolog. Arbeitsmethoden Section V, 1926, Pt. 6, 908.
17. KOELLNER, H. Die Abweichungen des Farbensinnes. *Bethe; Handbuch norm. path. Physiol. B.* **12**, Pt. I, 515.
18. WRIGHT, W. D. Researches on normal and defective colour vision. London, 1946, 301.
19. JUDD, D. Color in Business, Science and Industry, New York, 1952, 68-69.
20. RAUTIAN, G. N. *Biophysics*, New York, 1956, **1**, 3, 245 (also see *ref. 10*).
    Dokl. Akad. Nauk., S.S.S.R., 1950, **76**, 6, 1073.
21. KOELLNER, H. Die Abweichungen des Farbensinnes. *Bethe; Handbuch norm. path. Physiol. B.*, **12**, 511-515.
22. WEALE, R. *J. Physiol.*, 1953, **121**.
23. FLEKKEL, A. B. *Dokl. Akad. Nauk., S.S.S.R.*, 1955, **100**, 1, 57.
24. JAMESON, D. and HURVICH, L. *J. opt. Soc. Amer.*, 1956, **46**, 12.

PRESENTATION AND DISCUSSION OF PAPERS 14, 23, 16, 15, 26, 17, 10, 12, 32 AND 34

IN the absence of Dr. Crawford, who was indisposed, his paper (14) was read in title by the CHAIRMAN, PROF. Y. LE GRAND. DR. L. PLAZA summarised the paper by Drs. M. Dagher, A. Cruz and L. Plaza (23), and DR. ADRIANA FIORENTINI summarised the one by herself and Dr. Lucia Ronchi (16). Papers 15 and 26 were presented by their authors, PROFESSOR R. W. DITCHBURN and CDR. D. FARNSWORTH respectively.

PROFESSOR R. GRANIT stressed two points. Firstly on the nature of sensory clues, it was clear that both static and dynamic components of sensation must receive attention and that there were differences in the dynamics for different colours. Such facts as the faster conduction of red-sensitive elements in the optic nerve, and the slower conduction of blue, established electrophysiologically, were very relevant. In the second place, eye movements were evidently essential to the visual function, and the eye musculature had a special system for maintaining them - that had recently been proved. A successive extension and relaxation occurred - which could be observed as a spluttering discharge in the signal picked up by a microelectrode.

DR. R. W. G. HUNT showed diagrams he had made representing the MacAdam, Wright and Munsell discrimination data, in attempts at uniform chromaticity transformations. The diagrams brought out the point made by Cdr. Farnsworth about a relative foreshortening of the discrimination contours in the blue-yellow direction, the foreshortening showing a progressive change in going from the MacAdam, through the Wright to the Munsell data.

DR. R. A. WEALE presented his paper (17) and at the same time added a comment on the relative sensitivities of rods and cones, as the size of stimulus diminished, a point discussed in Session 2. He thought that there were reasons for thinking these sensitivities of the same order if certain allowances were made.

THE CHAIRMAN considered that there was really no answer to the question of the comparative sensitivities of a rod and a cone because their spectral sensitivities were entirely different.

PROFESSOR M. RICHTER, in summarising his paper (10), said that he had started from the proposition that the anomalous subject had just one fundamental response curve different from the normal. For the deuteranomalous he had assumed that the spectral transmission of the photosensitive element whose absorption of light produced the stimulation of the "green" mechanism equalled the spectral transmission of the normal "green" raised to a certain power c. He had made a colorimetric study of a deuteranomalous subject by two methods and the results pointed to a value of c greater than 2 and perhaps lying between 3 and 4. The Yustova fundamentals for the normal were taken as basis. He thought it might be possible to characterise any

deuteranomalous subject by his c value and to predict on that basis his colour-matching properties.

DR. M. A. BOUMAN explained that the work by Ing. P. L. Walraven and himself was directed ultimately to finding the aptitude of anomalous subjects for practical tasks in industry and in the Services. They had therefore concentrated on colour discrimination of different kinds. After outlining the paper (12), Dr. Bouman gave some later results. (These are included as an Addendum to the paper).

PROFESSOR E. N. YUSTOVA, through her interpreter MRS. MILNER, made the comments which follow on the paper by herself and Professor N. D. Nuberg (32). She said that they had carried out a series of investigations of the colour vision of dichromats using a trichromatic colorimeter. They were thus able to define the exact directions along which protanopes and deuteranopes did not distinguish colours. The method of measurement was described in Dr. Nuberg's report. Ten protanopes and twelve deuteranopes were tested. In the C.I.E. system the directions were characterised by the following specifications: for the axis B, x=0.750, y=0.250; for the axis G, x=1.70, y=-0.70. The direction of the axis B was defined by the position of the points R and G and by the position of the plane of the alychne, as shown by Dr. Nuberg. The main value of their investigation was that they had defined the exact direction of the axis G. Other authors encountered certain difficulties when determining these directions because they used the chromaticity triangle instead of the colour space. The specifications of x, y for the direction of the axis G obtained by the speaker and Dr. Nuberg differed substantially from those obtained by other authors and were rather similar to König's results. With regard to the determinations of the axes R and B, there was no disagreement.

It was known that there were two hypotheses explaining the dichromasy phenomenon: the hypothesis of the absence of one of the dichromat receptors, and the hypothesis of a fusion of two receptors into one. Both had their supporters. However, the first hypothesis enabled them (the authors) to identify the directions found in the course of experiments with dichromats, as the axes of the basic physiological system of the Young-Helmholtz receptors, and to determine the spectral response curves of these receptors. The second hypothesis did not give this possibility. They stood for the first hypothesis, and she (Professor Yustova) wished to take advantage of her presence there to say something in its favour, as many of her colleagues stood for the hypothesis of fusion, using it to explain deuteranopy. Naturally, colour experiments did not give the possibility of penetrating into the essence of colour vision phenomena but they gave criteria of validity for any physiological hypothesis.

I. Dichromats confirmed the colour matching of normal trichromats; that meant either that the two functional dichromat receptors were similar to those of normal trichromats, or that the fusion system must be according to

the linear law and could come about in only one way. If this were not so, there would be several forms of deuteranopy. They (the authors) considered the fulfilment of these two conditions to be rather unreal.

II. They thought that there was no value in considering deuteranopy as a special case conflicting with protanopy and tritanopy. There was no difference in principle in the experiments on the determination of axes *R* and *G*. They considered that the tendency to specialise deuteranopy arose from the difficulty of determining the axis *G*.

III. There was an important fact, refuting the fusion hypothesis, that was the postulate of the invariance of the colorimetric equalities of deuteranopes in different conditions of eye adaptation. They were convinced of that. In the fusion case, the change of adaptation would change the direction of the axis *G*.

The data obtained by them (the authors) independently of any interpretation were useful as they enabled one to develop rational tables, and anomaloscopes for colour vision tests.

The paper of Professor G. N. Rautian (34) was presented in title.

DR. W. A. H. RUSHTON remarked that in the fusion hypothesis discussed by Professor Yustova there could either be in the dichromat a fusion of two classes of receptors each containing one pigment, or the normal might have one class of receptors containing a mixture of pigments. In the latter case, symmetry among protanopes, deuteranopes and tritanopes would be preserved in the sense that they all lacked one class of receptors. On the mixture of pigments view, adaptation to very high intensities of red light - probably about 100,000 trolands - would be needed to modify the colour-matching properties of a deuteranope in the direction of protanopia.

DR. RUSHTON found surprising Professor Ditchburn's result that the stabilised image of a large uniform field ultimately went black; it did not seem to agree with what one saw when laying on one's back gazing at a cloudless blue sky. DR. R. W. DITCHBURN replied that the observation referred to a wide field with diffuse edges.

DR. G. S. BRINDLEY mentioned two points. Some earlier experiments on the subject by Dr. de Vries did show changes in a deuteranope's colour-matching after intense adaptation of the kind expected by Dr. Rushton. Dr. Richter's hypothesis on the modification of the "green" fundamental curve in deuteranomalous subjects might, he thought, coincide with that proposed by Dr. F. G. H. Pitt in the Cambridge Conference of 1947. DR. RICHTER said he had not had access to Dr. Pitt's paper. Behind his hypothesis was the idea that concentration changes of the photosensitive pigment might be the important factor, but, on that interpretation, the deuteranomalous would have a higher concentration than the normal, and he found it difficult to reconcile that with lower sensitivity.

PROFESSOR W. D. WRIGHT commented on a remark in the paper by Professor Yustova and Dr. Nuberg insisting that the V_λ curves for normals and

deuteranopes were different. He would say that, as an experimental finding, they were very similar. DR. D. B. JUDD recalled, on this question, observations by Dr. Willmer which led him to distinguish two kinds of deuteranope, one with the normal V_λ curve, the other with a V_λ curve displaced a little to longer wavelengths.

On Dr. Richter's paper, DR. JUDD said that the model used would imply that a deuteranope would accept the matches of a deuteranomalous subject, and he wondered whether the author had considered other hypotheses for explaining the colour-matching properties of deuteranopes. There was a suggestion by some Dutch workers (Dr. Schouten) that in anomalous vision the altered function was not centred on the normal *R* or *G* but lay somewhere in between and was broader. They thought that protanomalous and deuteranomalous subjects might both possess a curve centred there, but with its breadth modified in different cases by raising the "curve" to various powers, on the lines of Dr. Pitt's view.

DR. WEALE could not accept Dr. Moreland's suggestion of the complete monochromasy of the peripheral retina at, say, 40^0 or 70^0. He thought the level of adaptation must be taken into account. He also observed in reference to Cdr. Farnsworth's paper, that the blue mechanism in the periphery was very labile and adapted very rapidly, as shown by Auerbach and Wald. Dr. Moreland and Professor Wright quite agreed that it could not be said that under all conditions of adaptation the extreme periphery was monochromatic.

DR. J. M. BURCH mentioned an experiment in the N.P.L. colour-matching work which might be thought to support Cdr. Farnsworth's suggestion that, if the red receptors had a bimodal spectral response, the primary and secondary peaks might show different temporal effects. A colour match between two stimuli was made first in an ordinary 10^0 bipartite field, and then with a single field in which the stimuli alternately replaced each other at a controlled frequency. At frequencies of about one cycle per second, three-control matching was fatiguing but gave accurately repeatable results. In highly metameric matches, as when spectral blue-green with desaturating red was compared with a mixture of green and blue, the two methods gave different results: a match made under one condition was not accepted under the other, and it was the red control which required the greatest change.

PROFESSOR G. A. FRY said the dark field observed by Professor Ditchburn was presumably obtained in one eye, with the other eye covered. He would suggest that this might be a case of optical rivalry, and that what was seen was the field presented to the covered eye. PROFESSOR DITCHBURN replied that the difficult experiment of stabilising both refined images in binocular vision had been tried, and that the blackout did occur. Answering Dr. Pirenne, he said that measurements of increment thresholds as such had not been made, but cortical flicker frequency appeared to be unchanged by stabilisation.

PROFESSOR YUSTOVA, through her interpreter, said that the identity of V_λ for deuteranope and normal would be inconsistent with the direction of the *G* axis she had found. It would be possible only if the *G* axis lay on the alychne but that was not so. Actually the direct determination of V_λ was based on a quite different method of investigation than that of colour-mixture. PROFESSOR WRIGHT thought that conclusions on this point rested on one's theory of colour vision.

SESSION V

ELECTROPHYSIOLOGICAL ASPECTS OF VISION, PARTICULARLY COLOUR VISION

Chairman: PROFESSOR R. GRANIT, NOBEL INSTITUTE FOR NEUROPHYSIOLOGY, STOCKHOLM.

PAPER 18

ELECTROPHYSIOLOGY OF VISION; INTRODUCTORY REMARKS

By R. GRANIT

Ragnar Granit is Professor of Neurophysiology at the Caroline Institute in Stockholm and Director of the Nobel Institute for Neurophysiology which is a department of the Medical Nobel Institute. He obtained his M.D. from Helsinki University, where he was Professor of Physiology. In 1940 he was invited to Stockholm. He holds honorary degrees from Oxford and Oslo, and is Lecturer at the Rockefeller Institute for Medical Research, New York.

His neurophysiological work began at Oxford where he spent two years in the laboratory of Sir Charles Sherrington. He also spent two years as Fellow in Medical Physics at the Johnson Foundation, University of Pennsylvania, Philadelphia. His early work was chiefly devoted to vision and the retina. Later on, his interests turned towards general neurophysiology, chiefly to mechanisms for control of movement and posture as well as brain control of sense organs. The latter work has included muscle spindles and the retina. He completed in 1945 a monograph on the retina (Sensory Mechanisms of the Retina, Oxford University Press, 1947) and in 1954 delivered the Silliman Lectures at Yale University, published under the title Receptors and Sensory Perception (Yale University Press, 1955) reviewing and discussing the electrophysiological contributions to sensory physiology.

18. ELECTROPHYSIOLOGY OF VISION; INTRODUCTORY REMARKS

By R. GRANIT

THE psychophysical relationship between stimulus and sensation may be a simple one, yet the intermediate mechanisms - as proved by physiological research - are very complicated ones, and probably have to be complicated, or the final result could not be simple. One example should suffice: the sensory overlap at all stages, retina, geniculate body and visual cortex is stupendous, in spite of which the eye is a marvellous instrument for differentiation. This principle of overlap is general for the sense organs. Thus the olfactory bulb consists of secondary neurones to each of which some 25,000 olfactory receptors project. Nevertheless olfactory discrimination is of extraordinary acuteness.

With regard to the now universally applied techniques making use of capillary microelectrodes of high resistance and tip dimensions below 0.5μ, as introduced by Gerard and Ling, one of the major difficulties in retinal work consists in arriving at reliable criteria for identification of the site of recording. This technique was first successfully applied to the central nervous system by Professor J. C. Eccles and his colleagues in Canberra and they succeeded in making an important contribution in terms of intracellular records.

Let us consider how in their case the electrode site was identified, as it throws light on the problems facing those applying similar techniques to the study of the retina.

The Canberra group analyzed the responses of the large motor cells in the ventral horn of the spinal cord whose axons run out in peripheral nerves to muscle. By maintaining slow, repetitive, antidromic (or backward) stimulation with shocks applied to the motor nerves, they could make an impulse enter these cells from the 'back end' in response to each shock. Now, when the microelectrode is gradually advanced into the spinal cord, it would, when penetrating the membrane of a large motor horn cell, give the following cues for identification: (i) a sudden large shift of level of potential to something of the order of -70 mV; (ii) the antidromic impulse entering the cell would, at the same time, become very large and positive-going, in fact, of the order of 80-100 mV, and thus enormous in terms of what is customarily obtained with extracellular recording (a few millivolts); (iii) the reflex impulses set up by any normal or orthodromic input system would behave similarly; (iv) further criteria are provided by a formidable background of knowledge of general reflexology.

With this method Eccles and his colleagues have proved to the hilt - as since confirmed in many laboratories and also with other types of cell - that excitation generally coincides with depolarization, inhibition with hyper- or repolarization of the cell membrane.

Now, consider the retina. Firstly, the cells are not very large and the experience from other organs tends to show that small cells mostly explode with a burst of impulses producing a 'scream' in the loudspeaker while at the same time the membrane potential breaks down so that the instrument again records base line level. The ventral horn cells are 70μ across, the cones only a few μ. The horizontal and the ganglion cells would make a better target and the latter in particular could be tested antidromically. But if a cell does not produce an impulse, how is one to known where the tip of the microelectrode is located? A sudden relatively stable and large shift of level of potential does not as such suffice for identification because, as Brindley points out in his paper at this Symposium, such shifts take place across the high internal resistance of his R-membrane which, he suggests, is to be identified with *membrana limitans externa*. Let us, however, assume that a successful penetration of a cell has been carried out. What would, under the circumstances, opposite changes of potential signify? In the first instance one is forced to consider Eccles's results, confirmed, as I said, in many laboratories, that depolarization and hyperpolarization are electrical signs of excitation and inhibition respectively. I do not mean to say that other explanations are excluded, merely that new results in the first instance would have to be critically gauged against available knowledge from related fields of study.

Again, if no definite evidence establishes a record as intracellular, extracellular reversals of potential seen with different stimuli can be interpreted in many different ways unless further results are accumulated to show precisely how sinks and sources are distributed with respect to the pick-up electrode.

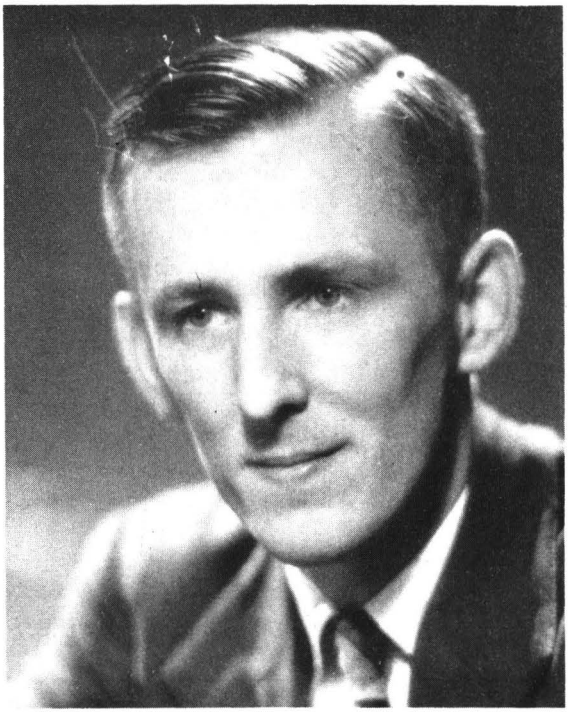
This should suffice to show that the problem of identification of electrode site is a formidable one and not solved by reading off a micrometer screw and asserting that the record is intracellular. Brindley has tried to attack it with the aid of his R-membrane and Tomita with a double microelectrode one of which is set at a distance from the other in the axis of penetration. MacNichol *et al.* have tried staining through the electrode.

The work of Donner and Rushton introduces new aspects to an old and well-known approach. Separation of cones from rods with the aid of the Stiles-Crawford effect seems to establish once more the physiological reality of the special blue-sensitive rods of Schwalbe and Kühne while Donner's application of Stiles's method of analysing colour reception by difference thresholds indicates great similarity of colour reception in the cones of frog and man.

PAPER 19

WORK ON THE ELECTRORETINOGRAM

By G. S. BRINDLEY



DR. G. S. BRINDLEY is a University Demonstrator in Physiology at Cambridge. He was Ophthalmic House Surgeon at the London Hospital in 1950-1951, and worked at the R.A.F. Institute of Aviation Medicine from 1952 to 1954. His work, mostly published in the Journal of Physiology, includes papers on colour vision, the quantum nature of visual threshold, the site of electrical excitation of the human eye, and the electrical activity of the frog's eye.

19. WORK ON THE ELECTRORETINOGRAM

By G. S. BRINDLEY

SUMMARY

1. Analyses of the human electroretinogram have clearly separated its photopic and scotopic components, but have not with certainty subdivided the photopic response into those of distinct colour-sensitive mechanisms. The responses analysed are those of large areas of the retina, and it is very unlikely that it will be possible to separate the response of the fovea from that of the peripheral retina.

2. Electrical responses to illumination recorded with micro-electrodes from within the frog's retina provide evidence that the whole of the e.r.g. in the frog is generated by a single layer of the retina, very probably the rods and cones. Electrical responses of comparable time-course, but apparently contributing nothing to the e.r.g., are generated in other layers of the retina. Components of these responses probably due to the horizontal cells and the bipolar cells can be distinguished, and there may perhaps be other components contributed by the amacrine cells.

3. The uses and limitations of the slow electrical responses of the retina as a means of investigating mechanisms of colour-discrimination are briefly discussed.

THE SLOW ELECTRICAL ACTIVITY OF THE RETINA AND ITS APPLICATION TO THE STUDY OF MECHANISMS OF COLOUR-DISCRIMINATION

WHEN the eye of any vertebrate is illuminated, a change can be detected in the difference of electrical potential between the front of the retina (or any point in good electrical contact with it, such as the cornea) and the back of the eye or any remote part of the animal's body. This electrical response to illumination is known as the electroretinogram (e.r.g.). The greater part of it, if not the whole, certainly arises from the retina, for it can be recorded from the isolated retina in the absence of any other part of the eye *(refs. 1, 1A)*. It has been extensively investigated by a variety of methods during the past 80 years, but until recently there has been no fully satisfactory evidence to decide what structures in the retina produce it. The present review describes first some observations on the human e.r.g. which provide limited information about mechanisms of colour-discrimination, even in the absence of sure knowledge of which structures in the retina generate the response; secondly, a number of recent experimental results which provide strong evidence that in the frog the whole of the e.r.g., with the possible exception of the extremely slow part known

as the c-wave, is generated by the rods and cones; and thirdly some speculations on the kinds of additions to our knowledge of colour-discriminating mechanisms which may be expected to come from further study of the slow electrical activity of the retina.

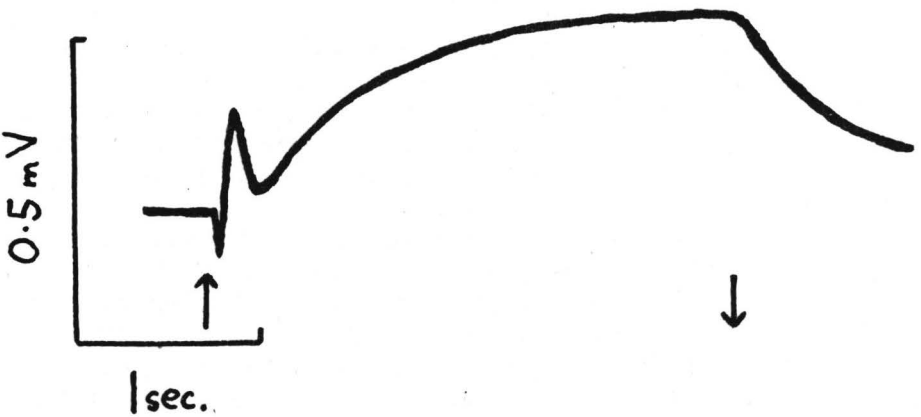


Fig. 1. Electrical response of the human eye to steady illumination lasting 3 seconds. Arrows mark the beginning and end of the stimulus. Compiled from the string galvanometer records of Hartline *(ref. 2)*.

THE HUMAN ELECTRORETINOGRAM

THE form of the electrical response of the light-adapted human eye to a light stimulus of three seconds' duration is shown in *fig. 1*. The beginning of the stimulus is followed, after a latency of roughly ten milliseconds, by a quick diphasic change in electrical potential, the cornea becoming first negative and then positive in relation to an "indifferent" electrode on the forehead, cheek or ear-lobe. The initial cornea-negative deflexion is known as the a-wave, and the immediately following cornea-positive deflexion as the b-wave. The b-wave is followed by a very much slower cornea-positive deflexion known as the c-wave. At the end of the stimulus, the potential declines slowly towards its resting level. In many vertebrate eyes, including that of the frog, extinction of the stimulus is followed, after a brief latency, by a third cornea-positive deflexion known as the d-wave, of similar time-course to the b-wave. In the human eye, d-waves are never conspicuous, and often, as in the records of Hartline *(ref. 2)* on which *fig. 1* is based, they are absent.

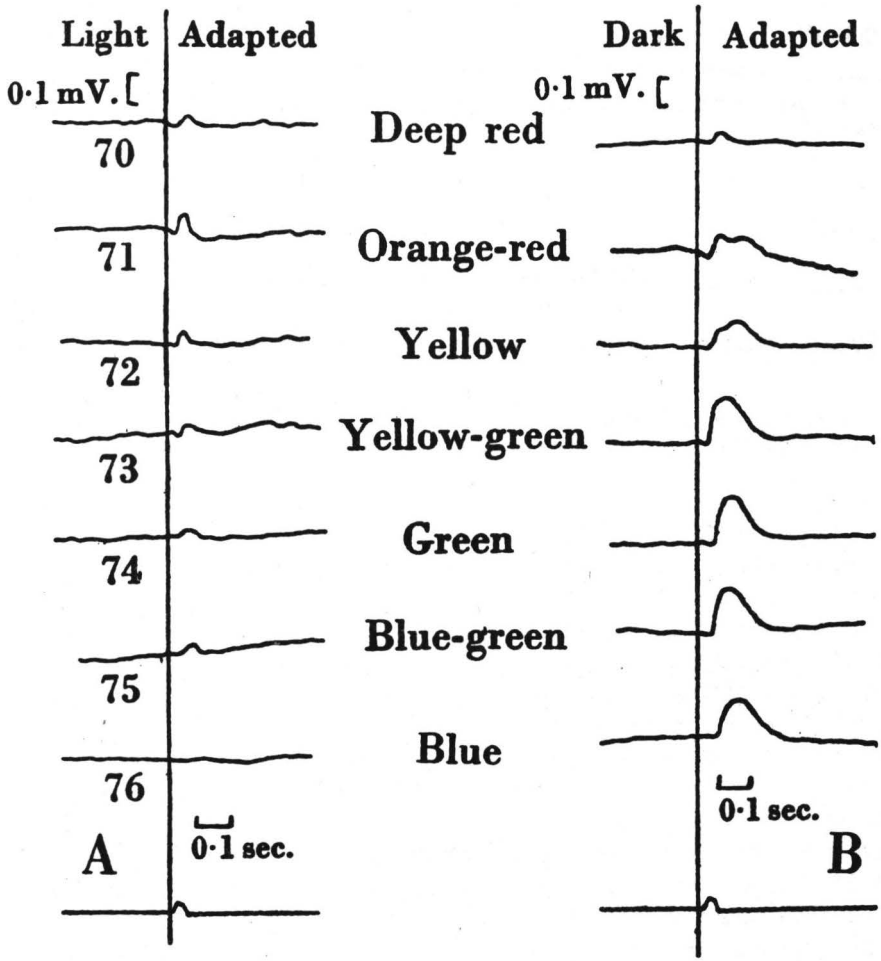


Fig. 2. Electrical responses of the human eye to brief flashes of light of various colours. From Adrian *(ref. 3)*.

In recording the human electroretinogram, movements of the eyes or eyelids may cause artifacts as large as, or larger than, the response of the eye in which the experimenter is interested (see *fig. 5)*. The longer is the stimulus, the more likely are these disturbances. Because of this, and of the practical convenience of using condenser-coupled amplifiers unresponsive to very slow changes in potential such as the c-wave, brief flashes of light have been used as stimuli in the greater part of recent research and in all clinical applications of electroretinography, and attention has been concentrated on the relatively rapid parts of the response. Responses to brief flashes of light of various colours recorded by Adrian *(ref. 3)* with a condenser-coupled amplifier and ink-writing oscilloscope, are shown in *fig. 2*.

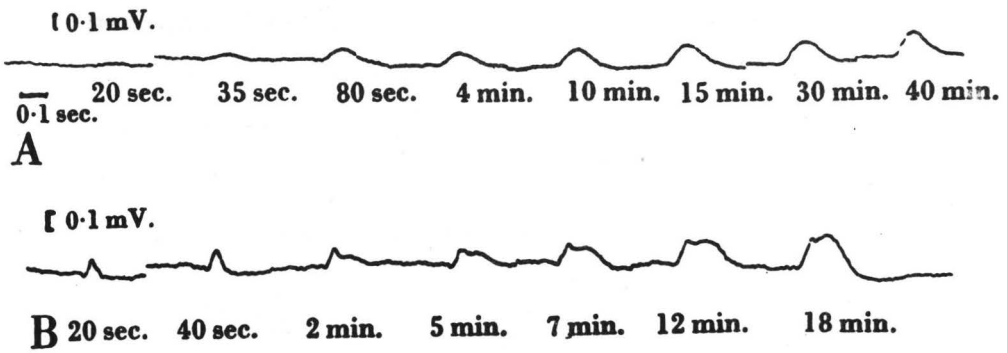


Fig. 3. Changes during dark-adaptation in the responses to brief flashes of light. A: blue light. B: orange-red light. From Adrian *(ref.3)*.

In the light-adapted eye the responses for all colours are brief and diphasic, a very small cornea-negative deflexion being followed by a larger cornea-positive one. The response to deep red light is the same in the dark-adapted eye as in the light-adapted, but with blue and green stimuli the brief diphasic response given by the light-adapted eye is replaced or masked, in the dark-adapted state, by a slower and much larger cornea-positive deflexion. Orange-red and yellow flashes give, in the dark-adapted eye, two-humped responses such as might be expected if the types of response produced by blue and by deep red light were being provoked simultaneously. Distinctions between these two types of response are clearly shown during the course of dark-adaptation *(fig. 3)*, and when a number of flashes are presented in rapid succession *(fig. 4)*; in the latter case the slow component of the response is much larger for the first than for later flashes, but the fast responses are approximately constant.

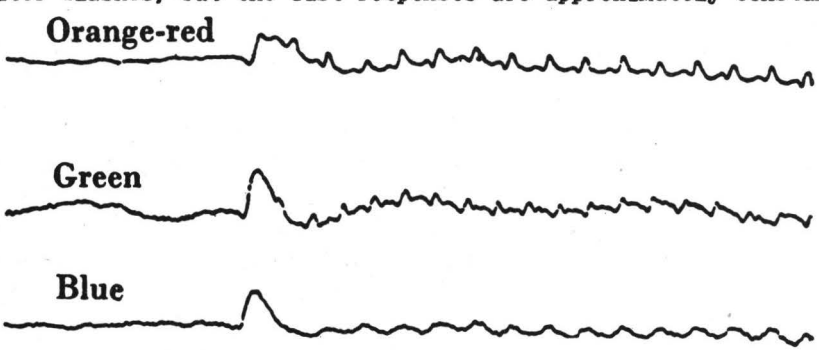


Fig. 4. Responses to series of flashes at a frequency of about twelve per second. Pupil dilated with "paredrine". From Adrian *(ref.3)*.

The effects of wavelength and of dark-adaptation strongly suggest that the slower responses in Adrian's experiments are produced by the scotopic mechanism of the eye, and the faster responses at least mainly by the photopic. More recent experiments, which have been much facilitated by L. A. Riggs's device of mounting the corneal electrode on a contact lens, have confirmed this distinction, but introduced some modifications. If stimuli of high intensity are used, it is possible to produce an initial cornea-negative deflexion even with blue light in the dark-adapted eye *(ref. 4)*.

In the response of the eye to bright flashes, this initial cornea-negative deflexion often consists of two clearly distinguishable troughs. For the second of these, which is much depressed by light-adaptation, the spectral sensitivity curve obtained by measuring the amount of light at different wavelengths required to produce a constant deflexion agrees, when the correction of Boynton *(ref. 5)* for the greater scattering of light of short wavelengths within the eye is applied, with the scotopic luminosity curve. The first trough has roughly the spectral sensitivity curve of photopic vision, and is very little affected by light-adaptation; it presumably corresponds to the initial cornea-negative phase of Adrian's brief diphasic response.

Fig. 5 shows the double initial cornea-negative deflexion. It also indicates how both parts of it are greatly increased in comparison with the cornea-positive deflexion by increasing the strength of the stimulus. This effect of the intensity of the stimulus on the relative size of two deflexions, the second cornea-negative, (called the a_2-wave by Auerbach and Burian, *(ref. 6)*), and the cornea-positive or b-wave, both of which have the spectral sensitivity curve of scotopic vision, is only one of the ways in which the electrical response of the scotopic mechanism can vary under varying conditions. The records of Riggs, Berry and Wayner *(ref. 7)* show that degrees of light-adaptation insufficient to convert the spectral sensitivity curve from the scotopic to the photopic are nevertheless sufficient to alter the shape of the b-wave making it shorter. This agrees with the known properties of other vertebrate eyes: in the guinea-pig, the form of the e.r.g. is much affected by the state of light-adaptation of the eye *(ref. 8)* although the retina contains very few cones, and no Purkinje shift can be detected *(ref. 9)*. Such variations in the response of a single mechanism make it very difficult to analyse the records obtained when more than one mechanism is active, even if it is assumed, (as cannot be known *a priori*, though there is now some experimental justification for it in the frog), that each such record is simply the sum of those that would be obtained from the several mechanisms concerned if they could be isolated from each other. However, even without any such analysis, a little may be learnt about mechanisms of colour-discrimination from study of the electroretinogram. In protanopia, the

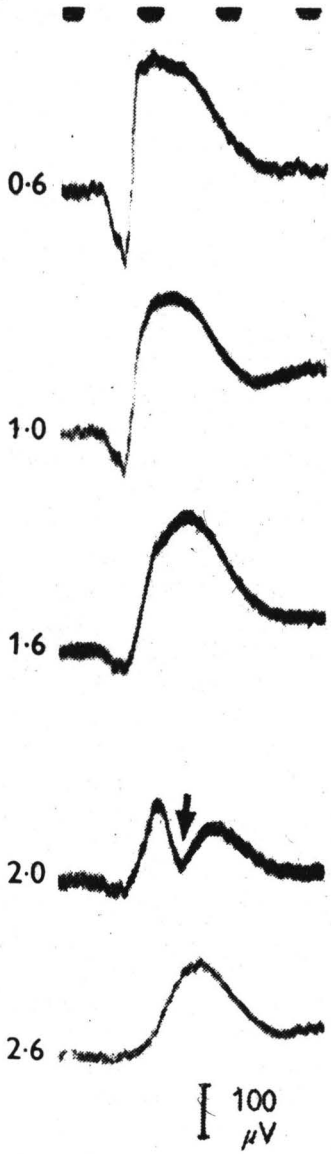


Fig. 5. Responses of the dark-adapted human eye to different intensities of white light. The figures opposite the curves are the densities of neutral filters inserted in the stimulating beam. At the arrow in the fourth record is shown the artifact produced when the subject blinks. Time-marks 0.1 sec. From Armington, Johnson and Riggs *(ref. 4)*.

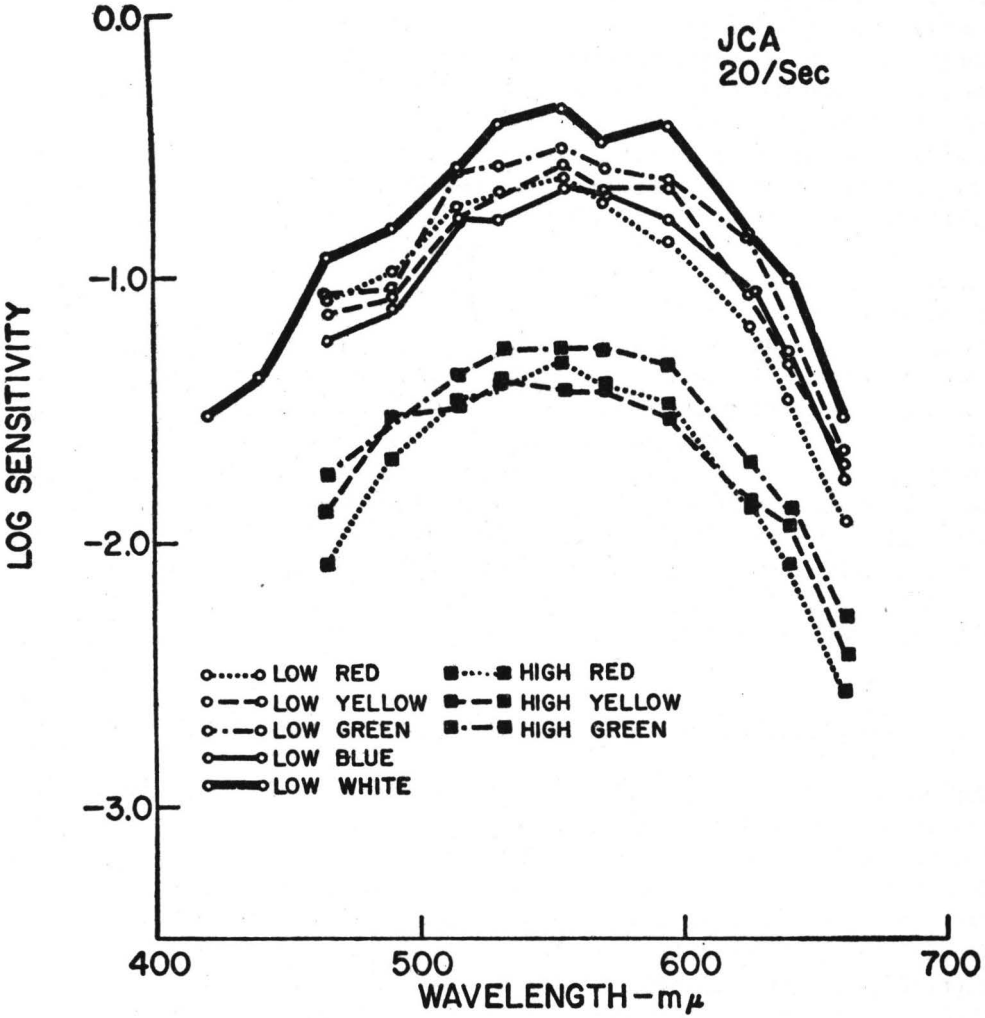


Fig. 6. Spectral sensitivity curves for the electrical response to a stimulus flickering at twenty flashes per second superimposed on a steady adapting field. From Armington & Biersdorf *(ref. 14)*.

response to red light is much smaller than normal *(refs. 10,11)*. This clearly establishes that protanopia involves a retinal abnormality, and is not a defect of the central part of the visual pathway only.

Johnson and Cornsweet *(ref. 12)* and Armington *(ref. 13)* have made use of Adrian's observation (see *fig. 4*), that the scotopic response is much reduced by giving a number of flashes in quick succession, to obtain spectral sensitivity curves for the photopic component of the e.r.g. with very

little contamination from the scotopic. The shape of the responses to twenty brief flashes per second is not detectably influenced by wavelength, and the spectral sensitivity curve for these responses has its maximum at about 550 mμ. Armington and Biersdorf *(ref. 14)* have examined the effect of superimposing the flickering stimulus on a steady coloured adapting field. Their results, some of which are shown in *fig. 6*, indicate that the colour of the adapting field has little if any effect on the shape of the spectral sensitivity curve. On reducing the frequency of stimulation to four per second, the responses were found to have two distinguishable cornea-positive peaks, of which the first had the same spectral sensitivity as the responses at 20/sec., and the second approximately that of scotopic vision. An attempt was made by Armington and Biersdorf to determine the effect of coloured adapting fields on the spectral sensitivity curve of the first peak. In contrast to the results at 20/sec., the shape of the curve was altered by adaptation, and differently by different colours; but the difficulty of separating by inspection two independently varying components in a compound response make the interpretation somewhat uncertain, and the effects of adaptation in these circumstances may perhaps result merely from differential effects on the photopic and scotopic mechanisms - at least no evidence is put forward by the authors which excludes this.

THE STRUCTURES WHICH GENERATE THE FROG'S ELECTRORETINOGRAM

THE retinae of most vertebrates contain, besides the rods and cones which are the light-sensitive elements, four principal kinds of nerve cells. Of these, the ganglion cells, whose axons are the fibres of the optic nerve, form a distinct layer close to the anterior surface of the retina. The cell bodies of the other three kinds of nerve cells, the horizontal, bipolar and amacrine cells, together form the "inner nuclear layer". The bipolar cells make synaptic connections with the rods and cones behind them and with the ganglion cells in front, and almost certainly provide the only direct link between them. The horizontal cells make synaptic connection with rods and cones, and possibly also with bipolar cells. The amacrine cells have processes which ramify in the "inner plexiform layer" which lie between the inner nuclear and the layer of ganglion cells. They probably make synaptic connection with bipolar cells and with ganglion cells. *Fig. 7* shows these four kinds of cells in the frog's retina, the bipolar and ganglion cells being shown in the upper figure and the horizontal and amacrine in the lower. It also indicates the distances of the several layers from the anterior surface of the retina and the resistance of certain structures to currents flowing perpendicularly to the surface.

All of these nerve cells, as well as the rods and cones, must be considered as possible contributors to the e.r.g. Evidence was, however,

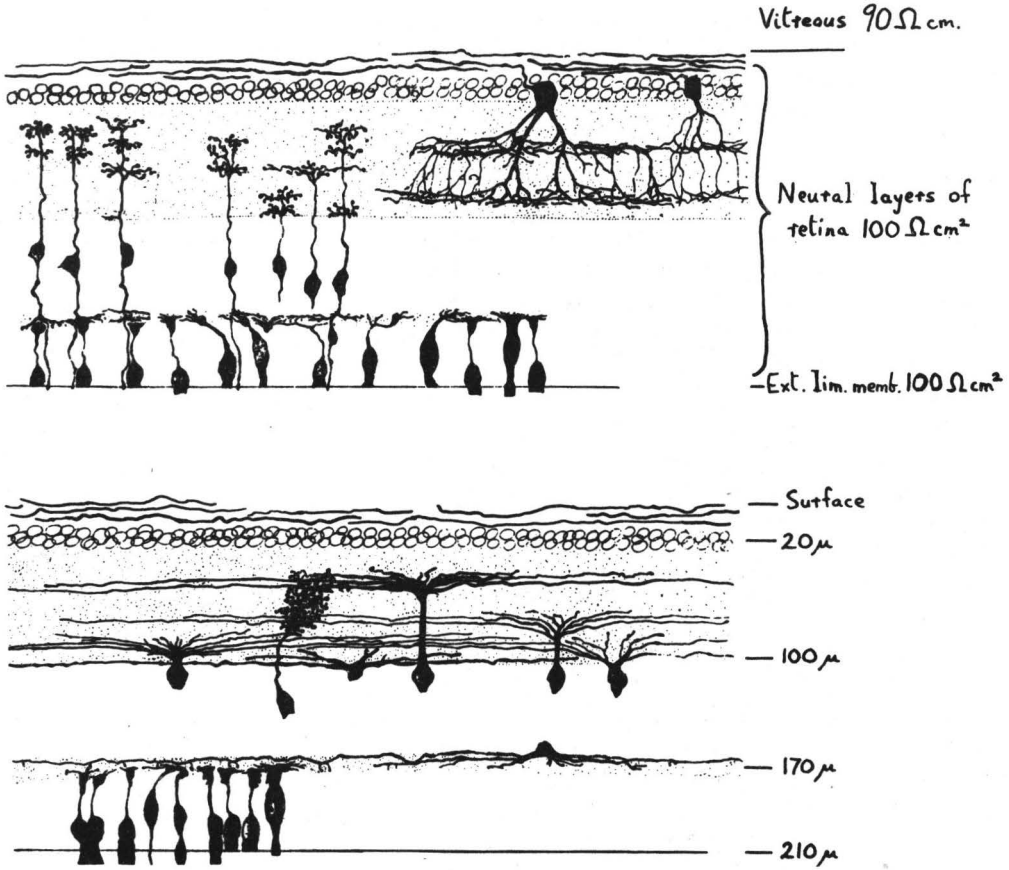


Fig. 7. Nerve cells in the frog's retina. The upper figure shows ganglion cells, bipolar cells and the cell bodies of some rods and a cone, the lower figure amacrine cells, a horizontal cell, and the cell bodies of some rods, a single cone and a double cone. The rods and cones proper are omitted from both figures. Compiled from the drawings of Cajal *(ref. 32)*.

provided by Granit and Helme *(ref. 15)* that the ganglion cells do not make a substantial contribution, since antidromic stimuli to the optic nerve, whether given before, during, or after illumination of the retina, have no influence on the form of the e.r.g. recorded. The insignificance of the ganglion cells was even more clearly shown by the observation of Ottoson and Svaetichin *(ref. 16)* that all spikes in the optic nerve (and hence presumably all activity of the ganglion cells) could be abolished by cocaine or urethane without producing any change in the e.r.g.

Experiments clearly distinguishing responses of the cells of the inner nuclear layer from those of the rods and cones have only been possible since methods have been available for recording with a very fine electrode

from within the retina, and for determining where in the retina the tip of the electrode lies. The first such experiments were those of Tomita *(ref. 17)* and of Ottoson and Svaetichin *(refs. 16,18)*. Tomita, in recording the responses to uniform illumination of the whole eye, with a microelectrode inserted into the retina of an opened excised frog's eye from its anterior surface, found complex changes in the form of the response with the depth of the electrode. Ottoson and Svaetichin, in an almost identical experiment, obtained a very simple pattern of responses: the e.r.g., recorded when the microelectrode lay in front of the retina, diminished in size and finally disappeared as the electrode was advanced through the retina, but nowhere changed in shape. Later experiments *(refs. 19,20)* have made it clear that both patterns of response can readily be obtained with the same experimental technique, the Tomita pattern being that of an eye in a nearly normal physiological state, and the Ottoson and Svaetichin pattern that of an eye which has lost many of the properties that it has in the living animal, but which retains a normal e.r.g. The two patterns of response are shown in *figs. 8* and *9*. With the microelectrode at the surface of the retina, a typical normal e.r.g., with a-, b- and d-waves is recorded. In the simple pattern of responses *(fig. 8)* this remains unchanged, except for a small decrease in size, until the electrode reaches a depth of 250 μ, when it suddenly decreases almost to nothing. In the complex pattern *(fig. 9)* the on-response of the e.r.g. is replaced, at depths of 155 and 205 μ, by a slow negative-going response upon which regular oscillations at about 12/sec. are superimposed. The off-response is at the same depths replaced by a large brief negative-going deflexion. As with the simple pattern, there is a sudden great decrease in the size of the response at a depth which in this experiment is 255 μ, and in nearly all experiments is between 200 and 275 μ. *Fig. 9* also shows the potential pulses recorded at each depth in the retina when square pulses of current of constant size are passed through it. Between 205 μ and 255 μ depth, the form of the potential pulse changes suddenly, indicating that the tip of the electrode has passed through a structure of high electrical resistance and capacity. The distance of this structure from the anterior surface of the retina and from the sclera makes it very probable that it is the external limiting membrane. It is regularly observed in experiments of this kind, and always coincides with a large, sudden decrease in size of response.

It would appear from superficial consideration of the records of *fig. 9* that the response recorded between electrodes on opposite sides of the whole retina must be the sum of a number of different responses generated in different layers of the retina. There are, however, very strong arguments against this conclusion, arguments which indicate that complex responses such as those seen at depths of 105, 155, and 205 μ in *fig. 9* make no significant contribution to the e.r.g., all or very nearly all of which is generated by structures which penetrate the external limiting membrane, almost certainly the rods and cones.

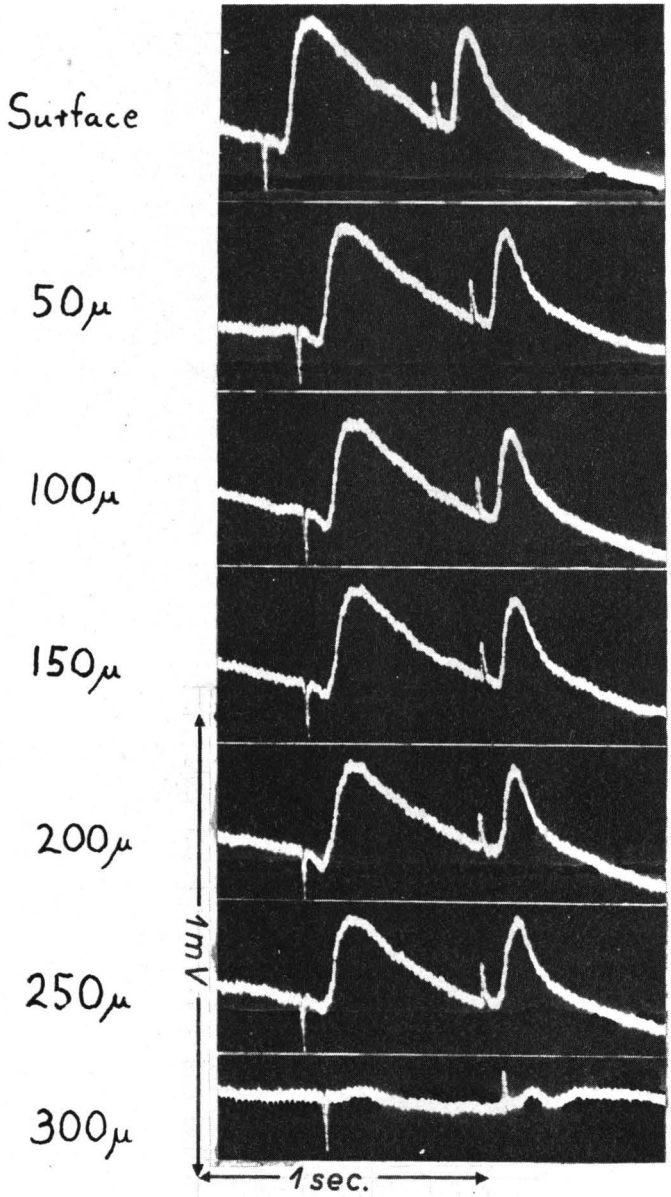


Fig. 8. Responses to uniform illumination of the whole retina, recorded with a microelectrode inserted from the anterior surface of the retina to the depths indicated. In this and the following figures, the beginning and end of the stimulus are shown by downward and upward artifacts respectively. From Brindley *(ref.33)*.

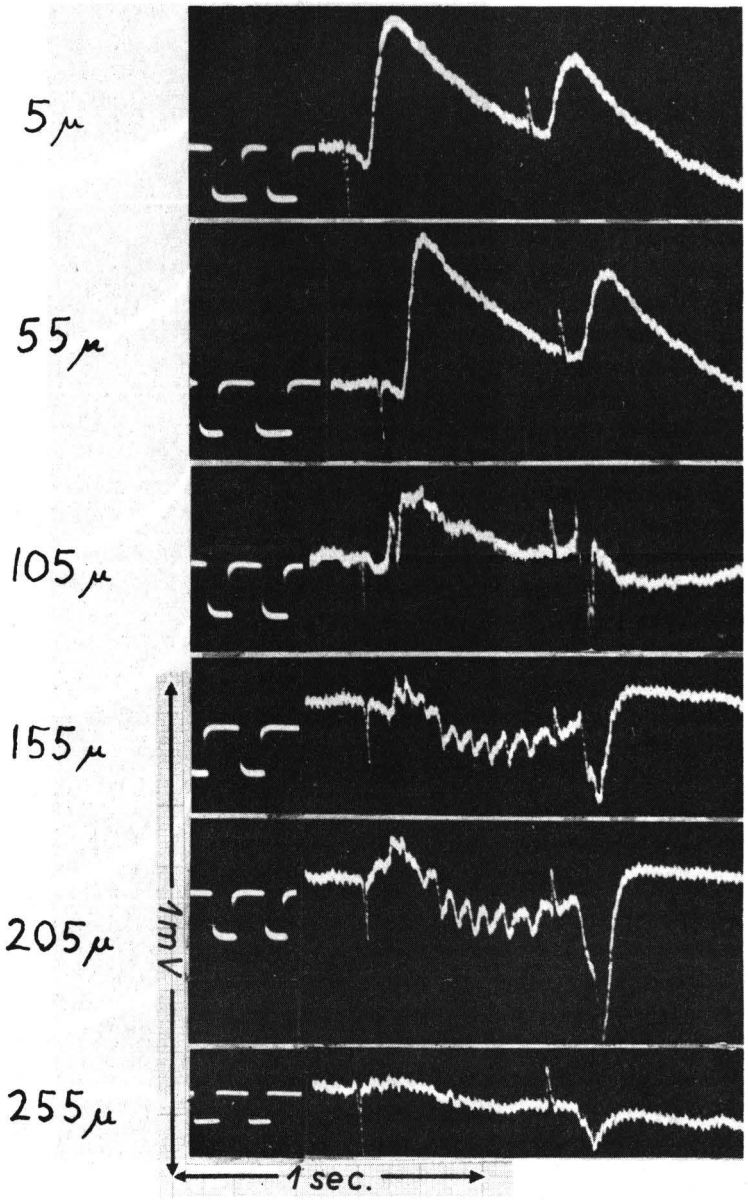


Fig. 9. Potential pulses produced by passing square current pulses of constant size through the retina, and responses to uniform illumination, recorded with a microelectrode inserted from the anterior surface to the depths indicated. From Brindley *(ref.33)*.

1. A completely normal e.r.g. can be obtained from a retina all parts of which give the simple pattern of responses.

It is essential for this argument that the simple pattern (i.e. that shown in *fig. 8)* be present *at all points* of the retina, for it would otherwise be possible that any point giving the simple pattern was an inactive region in a retina of which other regions were active, and generated an e.r.g. which was electrically conducted to the inactive region containing the recording electrode. Some evidence that the simple pattern could be present at all points of a retina was given by Brindley *(ref. 19)*. Tomita & Torihama *(ref. 20)* seem to have observed the same phenomenon, for they write: "The focal potentials are very susceptible to ageing at higher temperatures. At 17°C and above, they usually disappear in 10 minutes or less, while the e.r.g. does not change much," and later: "Once the focal potentials have disappeared at one site, punctures of other regions of the same retina usually fail to detect them, or, if detected, they are very feeble." The point was established beyond reasonable doubt by the work of Brindley *(ref. 21)*, in which, with special precautions to make the whole of a retina accessible to the microelectrode, as many as 25 points, scattered all over it, were investigated in detail, and in the majority of experiments the simple pattern of response found at all of them.

The possibility of obtaining a normal e.r.g. from a retina which gives the simple pattern of responses everywhere, even though such a retina is admittedly in some respects abnormal, implies that the complex responses seen at depths of 105, 155 and 205 μ in *fig. 9* are not necessary for the production of the e.r.g., and make no contribution to it, or at least no contribution which has any effect on its shape. It also implies that when the complex responses are lacking, a change of potential of the same time-course and nearly the same size as the e.r.g. appears across the structure of high electrical resistance and capacity (R membrane of Brindley, *(ref. 22)* which is probably the external limiting membrane. The current which crosses this membrane in order to produce the change of potential must be carried by structures which penetrate it. In mammalian retinae, the only cells which penetrate the external limiting membrane are the rods and cones. In the frog, however, it is also penetrated by processes of the bipolar cells, known as Landolt's clubs, five of which can be seen in *fig. 7*. If the identification of the R membrane with the external limiting membrane is correct, the current which polarises it with the time-course of the e.r.g. must be carried either by the rods and cones or by the Landolt's clubs of the bipolar cells, and the cells which carry the current presumably also generate it: if they passively carried current generated by other structures, these structures should also reveal themselves in the pattern of electrical responses. It is very unlikely that in experiments like that of *fig. 8* the observed potential change is the sum of responses of different time-course generated by the rods and cones on the one hand and the bipolar cells on the

other, for if so, the very different extent of these cells in front of the external limiting membrane should cause some spatial separation of the two responses.

Strong confirmation that the R membrane is not any structure *in front* of the external limiting membrane is provided by the observation that the retina has no electrical capacity when the choroid and pigment epithelium have been stripped from it *(ref. 21)*. Tomita and his colleagues interpret a feature (sudden great diminution in the size of the response), which in Brindley's experiments always corresponded to the R membrane, as occurring when the tip of the electrode was some 80 μ *behind* the external limiting membrane. It seems probable that this is an error arising from failure to allow for shrinkage in making histological preparations; but if it were correct, it would strengthen rather than weaken the conclusion that the nerve cells of the retina make no contribution to the e.r.g.

2. *Alteration in the strength of stimulus has a simple effect on the e.r.g., but a very complex effect on the Tomita pattern of intra-retinal responses.*

The effects of varying the strength of stimulus on the responses to uniform illumination recorded from within the retina are shown in *fig. 10*. The e.r.g., that is the response recorded at the anterior surface of the retina, increases steadily in size with increasing intensity and alters very little in shape, except for a steady decrease in the latency of both on- and off-effects. The complex responses recorded at depths of 100, 150 and 200 μ, on the contrary, alter in shape with intensity in a manner which differs for the on- and off-effects and for different depths: the large diphasic off-effect present at 100 and 150 μ with high-intensity stimuli is absent at low intensity. No trace of it appears in the e.r.g. at any intensity. The negative-going responses at 200 μ are larger at the intermediate intensity than at the high or low. Again no corresponding phenomenon appears in the e.r.g. This complexity in the behaviour of the intra-retinal responses without any counterpart in the e.r.g. provides further support for the conclusion that they make no important contribution to it.

3. *The e.r.g. obtained on illuminating a number of regions of the retina simultaneously is the sum of those obtained on illuminating them separately.*

This is true whether the regions are contiguous or not, provided that the effects of stray light are eliminated by superimposing the test fields on steady background of lower intensity; thus the response to illumination of a given total area of retina (confined to a region whose properties are uniform) is the same if that area is made up of many small fields as if it is concentrated in one large field *(refs. 21,23,24)*. Such additivity is to be expected if the structures which generate the electroretinogram do not interact with each other, provided that the passive electrical properties

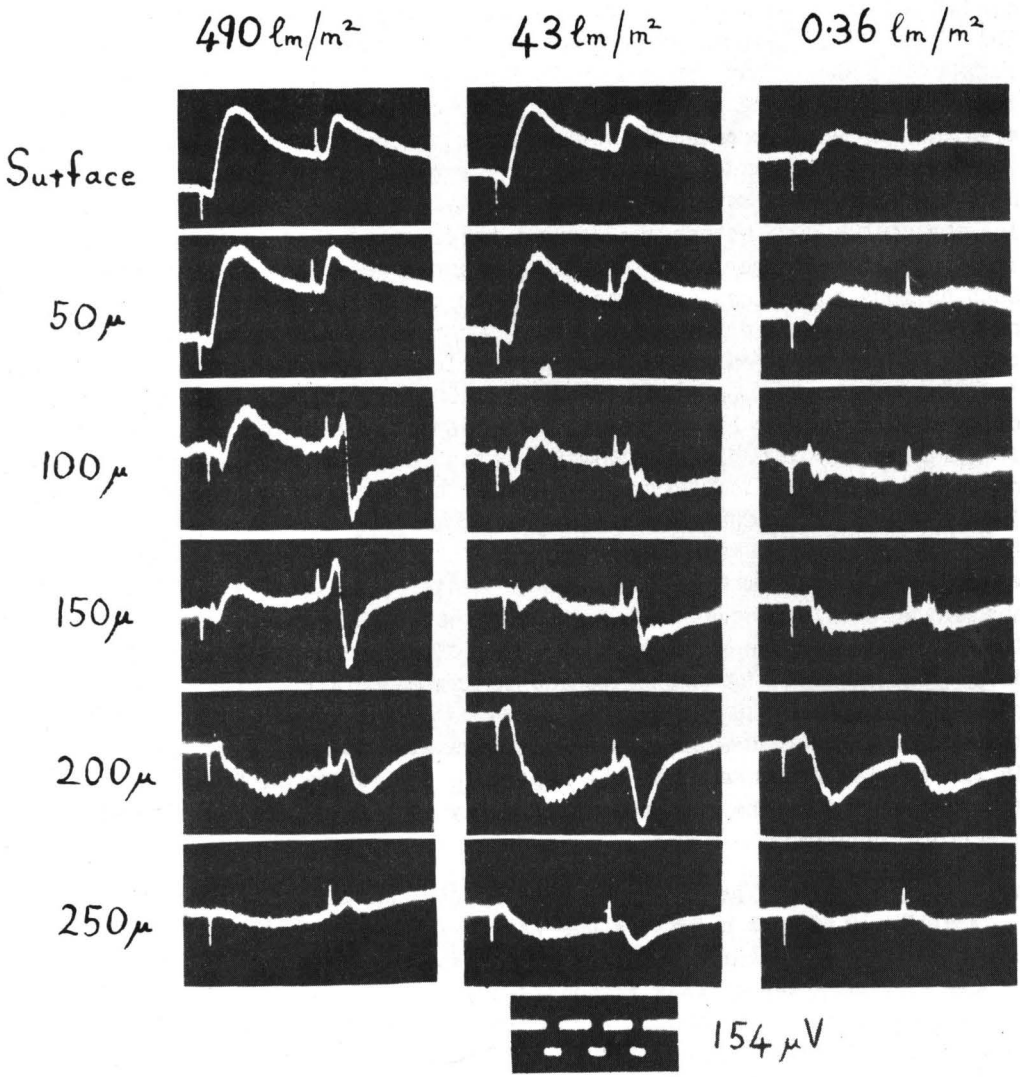


Fig. 10. Effect of varying the intensity of the stimulus on the e.r.g. and on the responses to uniform illumination recorded with a microelectrode inserted from the anterior surface of the retina.

of the retina are linear and not substantially altered by illumination. The linearity of passive electrical properties has been verified for the retina as a whole, and the change in impedance of illuminated areas of retina has been found to amount to no more than about 0.1% *(ref. 22)*. The electric currents produced by active areas of the retina are insufficiently large to modify to a detectable extent the electroretinogram produced by neighbouring areas *(refs. 15,21)*. Additivity is thus expected if the generating structures have no nervous connexions allowing them to interact (as is likely, though not certain, for the rods and cones), and is unexpected if such nervous connexions are present, as is certainly true for all classes of nerve cells in the retina. The expectation of non-additivity for the nerve cells is greatly strengthened by the conspicuous spatial interaction found in the spike potentials produced both by ganglion cells *(refs.25,26)* and by cells of the inner nuclear layer *(ref. 19)*, and especially by the large departures from additivity found in the slow responses recorded from the neural layers of the retina. A typical example of these departures from additivity is seen in *fig. 11*. Illumination of a small spot centred on the electrode produced large negative-going responses at "on" and "off". An annulus surrounding the electrode produced smaller responses of roughly similar shape. When spot and annulus were illuminated simultaneously, the responses were much smaller than the sum of those produced by the two stimuli separately, and differed in shape, the peak of the on-response coming much later. Similar discrepancies between the sum of the responses to two non-overlapping stimuli and the response obtained when both stimuli are given simultaneously are usual in the complex responses from all depths in the retina in front of the R membrane *(ref. 21)*. They contrast strikingly with the additivity found in the electroretinogram.

4. *The uniformity of the main features of the complex responses at 200 to 150 μ for different points on the retina indicates that these must be generated by bipolar cells, and hence probably that the bipolar cells are inactive when the complex responses are absent.*

In some of the intra-retinal responses to *local* illumination, negative-going deflexions within the illuminated area are associated with positive-going ones outside. Such responses must be generated, at least in part, by tangentially orientated elements, probably chiefly the horizontal cells. In responses to uniform illumination of the whole retina, however, the slow negative-going deflexion at "on" and the faster and larger one at "off" found at 150 to 200 μ depth are present, if the retina is in good condition, at all points *(ref. 24)*. These therefore cannot be generated by tangentially orientated elements. The only radially orientated nerve cells of appropriate extent in the retina are the bipolar cells, and there seems to be no tolerably plausible alternative to assuming that they are the generators. The failure of remote electrodes to detect the responses can be explained if the generating structures act as approximately symmetrical tripoles, a sink

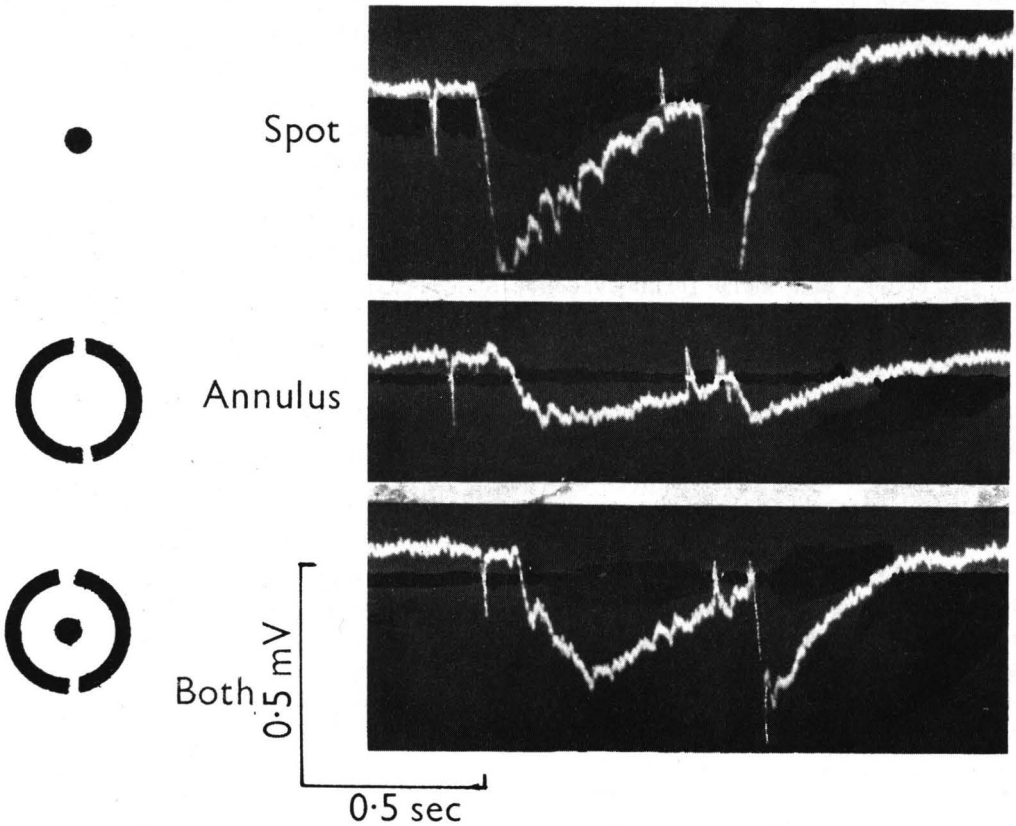


Fig. 11. Responses, recorded by a microelectrode inserted from the anterior surface of the retina to a depth of 150 μ, to illumination of a spot of diameter 180 μ centred on the electrode, of an annulus of internal diameter 680 μ, and external diameter 980 μ surrounding it, and of spot and annulus together. From Brindley *(ref. 19)*.

for current lying between two sources; and since the response appears across the R membrane, one of the sources for each bipolar cell must lie at least partly behind the R membrane, that is it must be the Landolt's club.

This identification of the generator of the main part of the response at 150 to 200 μ depth in the complex response-pattern with the bipolar cells provides a second reason for believing that the structures which generate the response appearing across the R membrane in the simple response-pattern must, if the R membrane is the external limiting membrane, be the rods and cones. If bipolar cells were to generate this response as well as the complex one, they would either have to be of two kinds, responding in very different ways and very differently sensitive to the factors which cause

disappearance of the complex response-pattern, or be each capable of two quite different kinds of activity, one of which could disappear without affecting the other. Whether generated by the same or different cells, the two kinds of activity would have to involve very different distribution of current flow across the cell membrane, one including the whole extent of the cell, and the other only its extreme posterior part. It is not altogether impossible that a substantially uniform population of bipolar cells should be capable of two such diverse activities, but it is a considerably more complex hypothesis than that the more stable activity is due to the rods and cones, and there is no evidence specifically supporting it.

5. *Sharply localised responses of similar time-course to the e.r.g. can be recorded from the exposed posterior ends of the rods and cones.*

The sharpness of localisation of these responses *(refs. 18, 19)* is inconsistent with their arising from structures substantially in front of the external limiting membrane, and accords much better with a generator which comes into contact with the electrode than with one which only just penetrates the external limiting membrane, though the latter hypothesis cannot be absolutely excluded in the absence of sure knowledge of the passive electrical properties of the layer of rods and cones for tangential currents. The polarity of the local responses is that of the e.r.g., and their time-course very similar, so that they could be the basis of it. They thus give some further support to the hypothesis that the rods and cones generate the e.r.g.

USES AND LIMITATIONS OF THE SLOW ELECTRICAL RESPONSES OF THE RETINA AS A MEANS OF INVESTIGATING MECHANISMS OF COLOUR DISCRIMINATION

THE scope of correlations between electroretinographic and psychophysical data on human colour vision is probably severely limited by the principle that the maximum electroretinographic response which can be obtained by illuminating part of the retina is proportional to the area of retina illuminated, provided that stray light is excluded, so that for fields of less than about 30° diameter no detectable response due to the image of the test field on the retina is to be expected. This principle is likely to be inexact, to the extent (probably slight) that different regions of the retina make different contributions, area for area, to the e.r.g.; but it is established as a very good approximation for the frog *(refs. 23, 24)*, and is strongly supported by the experiments of Boynton and Riggs *(ref. 27)*, Asher *(ref. 28)* and Boynton *(ref. 5)* for the human eye. If it is true, even very roughly, it implies that the colour discrimination of the fovea or of restricted regions of peripheral retina will never be accessible to electroretinographic investigation: the signal that such regions produce is too small.

For the retina as a whole, the analyses by Armington and Biersdorf *(ref. 14)* of photopic responses isolated by flicker provided no evidence of separate mechanisms with different spectral sensitivities when twenty stimuli per second were given; and the results obtained at four stimuli per second are not free from the possibility of scotopic contamination. The low gradient of the curves relating the size of e.r.g. to the adapting intensity for the human eye make the method of differential adaptation relatively inefficient at separating mechanisms whose spectral sensitivities differ by as little as is probable for the human "red" and "green" mechanisms, so that Armington and Biersdorf's failure to separate them in experiments at twenty stimuli per second does not necessarily imply that all the receptors concerned in their responses had the same spectral sensitivity. The responses to sudden replacement of one colour by another would probably provide a more sensitive test for the presence of more than one kind of photopic receptor in the peripheral retina; but it would not be likely to do very much more than prove the existence of more than one kind - exact information about their spectral sensitivities is scarcely to be expected.

Slow electrical responses recorded with intra-retinal electrodes from the eyes of animals provide the only objective evidence yet available (though at present still fragmentary) about how the nerve cells of the retina modify the information handed to them by the receptors before it is transmitted along the fibres of the optic nerve to the brain. The message transmitted by the optic nerve has been investigated in detail, but until the experiments summarised here, it was not possible to make any but histological observations on the cells of the inner nuclear layer. Exact separation of the contributions made to the slow intra-retinal potentials by horizontal, bipolar and amacrine cells is difficult but almost certainly possible, and should provide a fairly detailed picture of the activity of these cells and how it alters with the intensity, colour and spatial pattern of the stimulus and with the state of adaptation. It may, however, give little information on how the cells influence one another. It is unlikely that such influences are wholly electrical, and the effects on retinal nerve cells of currents produced by other nerve cells may well be of negligible importance compared with the effects of chemical substances liberated by those cells. A few experiments designed to provide information on such hypothetical chemical transmitters have been reported by Tomita, Funaishi and Shino *(ref. 29)* and Brindley *(ref. 21)*, but mainly with negative results; we know, for example, that atropine, which prevents the action of acetylcholine at certain kinds of junction, has no effect on the slow intra-retinal potentials, even in very high concentration. It seems probable that a systematic investigation of the action of applied chemical substances on the slow intra-retinal potentials of a retina with its blood supply intact, using both uniform and suitably designed focal illumination, would

provide, in conjunction with histochemical observations on the distribution of enzymes likely to be concerned in the destruction of chemical transmitters *(ref. 30, 31* and others*)*, a great amount of information on the chemical means whereby one retinal neurone may influence another.

REFERENCES

1. KÜHNE, W. and STEINER, J. *Untersuchungen aus dem physiol. Inst. der Univ. Heidelberg*, 1880, **3**, 327-377.
1A. FURUKAWA, T. and HANAWA, I. *Jap. J. Physiol.*, 1955, **5**, 289-300.
2. HARTLINE, H. K. *Amer. J. Physiol.*, 1925, **73**, 600-612.
3. ADRIAN, E. D. *J. Physiol.*, 1945, **104**, 84-104.
4. ARMINGTON, J. C., JOHNSON, E. P. and RIGGS, L. A. *J. Physiol.*, 1952, **118**, 289-298.
5. BOYNTON, R. M. *J. opt. Soc. Amer.*, 1953, **43**, 442-449.
6. AUERBACH, E. and BURIAN, H. M. *Amer. J. Ophthal.* 1955, **40**, 42-59.
7. RIGGS, L. A., BERRY, R. N. and WAYNER, M. *J. opt. Soc. Amer.*, 1949, **39**, 427.
8. BOEHM, F., SIGG. B. and MONNIER, M. *Helv. physiol. Acta.*, 1944, **2**, 481-493.
9. GRANIT, R. *Acta physiol. scand.*, 1942, **3**, 318-328.
10. SCHUBERT, G. and BORNSCHEIN, H. *Ophthalmologica, Basel*, 1952, **123**, 396-413.
11. ARMINGTON, J. C. *J. opt. Soc. Amer.*, 1952, **42**, 393-401.
12. JOHNSON, E. P. and CORNSWEET, T. N. *Nature, Lond.*, 1954, **174**, 614.
13. ARMINGTON, J. C. *J. opt. Soc. Amer.*, 1955, **45**, 1058-1064.
14. ARMINGTON, J. C. and BIERSDORF, W. R. *J. opt. Soc. Amer.*, 1956, **46**, 393-400.
15. GRANIT, R. and HELME, T. *J. Neurophysiol.*, 1939, **2**, 556-565.
16. OTTOSON, D. and SVAETICHIN, G. *Acta physiol. scand.*, 1953, **29**, Suppl. **106**, 538-564.
17. TOMITA, T. *Jap. J. Physiol.*, 1950, **1**, 110-117.
18. OTTOSON, D. and SVAETICHIN, G. *Cold Spr. Harb. Symp. quant. Biol.*, 1952, **17**, 165-173.
19. BRINDLEY, G. S. *J. Physiol.*, 1956, **134**, 360-384.
20. TOMITA, T. and TORIHAMA, Y. *Jap. J. Physiol.*, 1956, **6**, 118-136.
21. BRINDLEY, G. S. 1957, in preparation.
22. BRINDLEY, G. S. *J. Physiol.*, 1956, **134**, 339-352.
23. BRINDLEY, G. S. *J. Physiol.*, 1956, **134**, 353-359.
24. BRINDLEY, G. S. *J. Physiol.*, 1957, (in the press).
25. HARTLINE, H. K. *Amer. J. Physiol.*, 1940, **130**, 700-711.
26. BARLOW, H. B. *J. Physiol.*, 1953, **119**, 69-88.
27. BOYNTON, R. M. and RIGGS, L. A. *J. exp. Psychol.*, 1951, **42**, 217-226.
28. ASHER, H. *J. Physiol.*, 1951, **112**, 40P.
29. TOMITA, T., FUNAISHI, A. and SHINO, H. *Jap. J. Physiol.*, 1952, **2**, 147-153.
30. FRANCIS, C. M. *J. Physiol.*, 1953, **120**, 435-439.
31. WISLOCKI, G. B. and SIDMAN, R. L. *J. comp. Neurol.*, 1954, **101**, 53-100.
32. CAJAL, S. RAMON. Die Retina der Wirbelthiere. Wiesbaden: Bergmann, 1894.
33. BRINDLEY, G. S. *Bibl. ophth.* 1957, **48**, 24-31.

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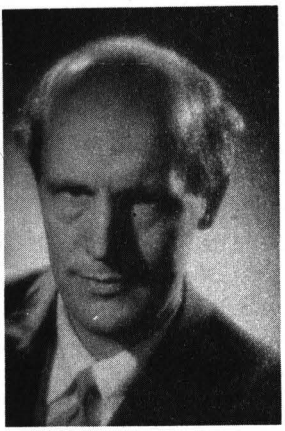
PAPER 39

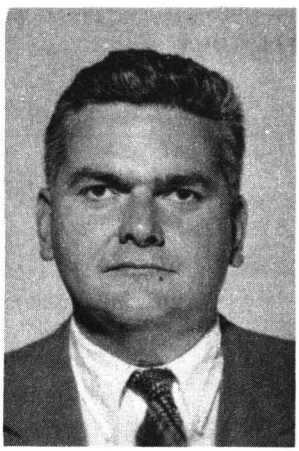
STUDIES ON SPECTRAL RESPONSE CURVES FROM THE FISH RETINA

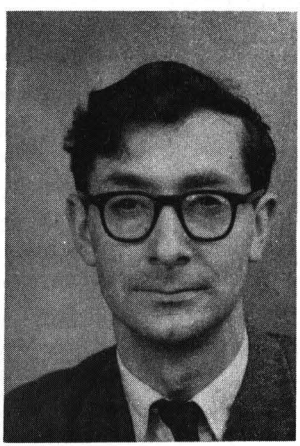
By E. F. MACNICHOL, Jr., L. MACPHERSON and G. SVAETICHIN, with the technical assistance of W. KRATTENMACHER.



Gunnar Svaetichin was born in Finland in 1915. Authorized physician in Finland. Army medical officer during the Finnish-Russian war. Doctor of medicine, Karolinska Institutet, Stockholm. Assistant professor of physiology and of medical physics, Karolinska Institutet. Since 1955 has been head of the department of Electrophysiology at the Instituto Venezolano de Neurologia e Investigaciones Cerebrales, Caracas, Venezuela.

Edward F. MacNichol, Jr., born Toledo, Ohio, U.S.A., October 24th, 1918. Graduate of Princeton University where he obtained his A.B. in Physics in June, 1941. Staff Member of Radiation Laboratory, Massachusetts Institute of Technology, July 1941-June 1946. Worked on range measuring equipment and special indicators for radar systems. Graduate student in Biophysics at the Johnson Foundation, University of Pennsylvania, June 1946 - January 1949. Held Committee on Growth Predoctoral Fellowship. Transferred to the Thomas C. Jenkins Department of Biophysics, Johns Hopkins University. Studied electrical activity of the receptors in the eye of Limulus under the direction of Dr. H. K. Hartline. Received Ph.D. in Biophysics, June 1952. At present an Assistant Professor of Biophysics at Johns Hopkins University. Active in the study of both vertebrate and invertebrate photoreceptors, also in instrumentation for biological research. Spent January to July 1957 as visiting Professor at IVNIC to work with Dr. Svaetichin.





L. Macpherson was born in London in 1925. He took the degree of B.Sc. in Physics and Mathematics at Chelsea and Northern Polytechnics, and subsequently worked for three years, as Research Assistant, with Professor A. V. Hill in the Physiology Dept. at University College, London. This was followed by one year at the Radio Biological Unit of Mount Vernon Hospital, Northwood, Middlesex, after which he went to Venezuela to join the Instituto Venezolano de Neurologia e Investigaciones Cerebrales.

1957

39. STUDIES ON SPECTRAL RESPONSE CURVES FROM THE FISH RETINA

By E. F. MACNICHOL, JR., L. MACPHERSON and G. SVAETICHIN, with the technical assistance of W. KRATTENMACHER

FISH CAUGHT AT A DEPTH OF 30–70 METRES ARE COLOUR BLIND

THE spectral response curve shown in row 1 of *fig. 1* represents a typical recording obtained from the retina of a fish caught at a depth of 30–70 metres in the Caribbean Sea. The spectral response curves obtained from fish inhabiting these depths were only of the Luminosity L type, having just one maximum in the blue-green region of the spectrum. Since sea water acts as a filter, which passes mainly blue-green light at depths greater than about 20 metres, it is very reasonable to find fish that possess a single receptor type having a single maximum in the blue-green region of the spectrum. It is unlikely that evolutionary selection would have maintained a mechanism of colour vision in a world where everything appears roughly monochromatic. The L type of cone apparently represents the receptor mechanism for achromatic vision. Further, it is a likely assumption that an animal lacking colour vision - like a totally colour blind human cone monochromat - only possess the Luminosity L type of cone.

FISH INHABITING SHALLOW WATER POSSESS A COLOUR VISION MECHANISM

FROM all the different species of fish investigated, which inhabit shallow water of about 1–2 metres, we obtained in addition to the Luminosity L type of spectral response curve, a response that had maxima of opposite polarities in two regions of the spectrum (rows 2, 3 and 4 of *fig. 1*). Some species of fish proved to have both the Red-Green R-G and Yellow-Blue Y-B type of receptors (row 4 of *fig. 1*), whereas certain species seemed to possess only the Y-B (row 2 of *fig. 1*) or R-G (row 3 of *fig. 1*) type.

It is suggested that the R-G and Y-B spectral response curves are expressions of the chromaticity signals delivered by the R-G and Y-B cones, the chromo-receptors which form the basic mechanism for colour vision, and that the L type of cone delivers the signal for the photopic luminosity. Yellow is the most luminous hue, a fact which well agrees with the observed close coincidence of the maxima of the L and the Y spectral response curves.

The R-G and Y-B spectral response curves bear a strong resemblance to the processes suggested by Hering in 1876 in his Opponent-colours theory. The R-G and Y-B spectral response curves correspond to the opponent colour

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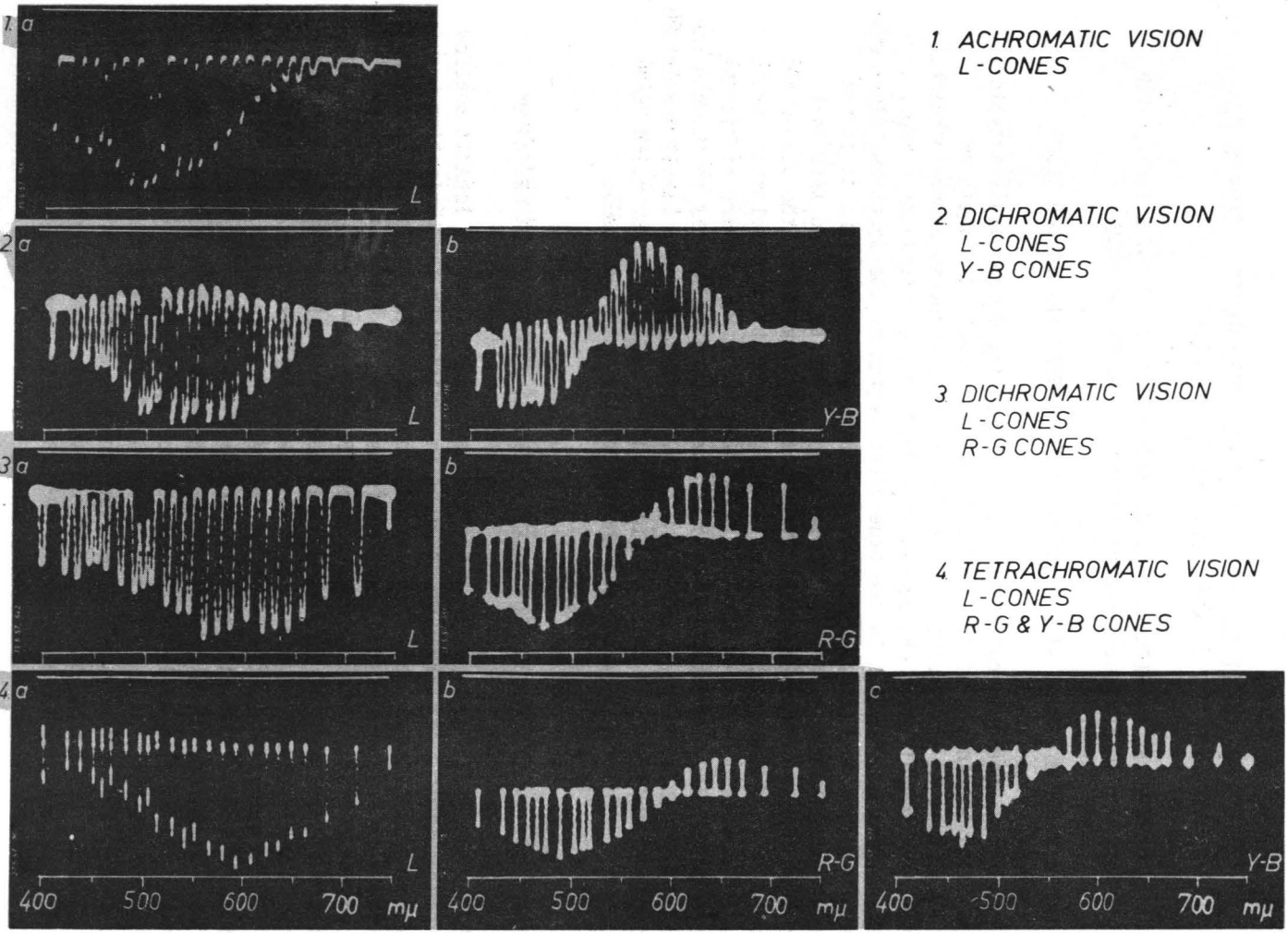

Fig.1.
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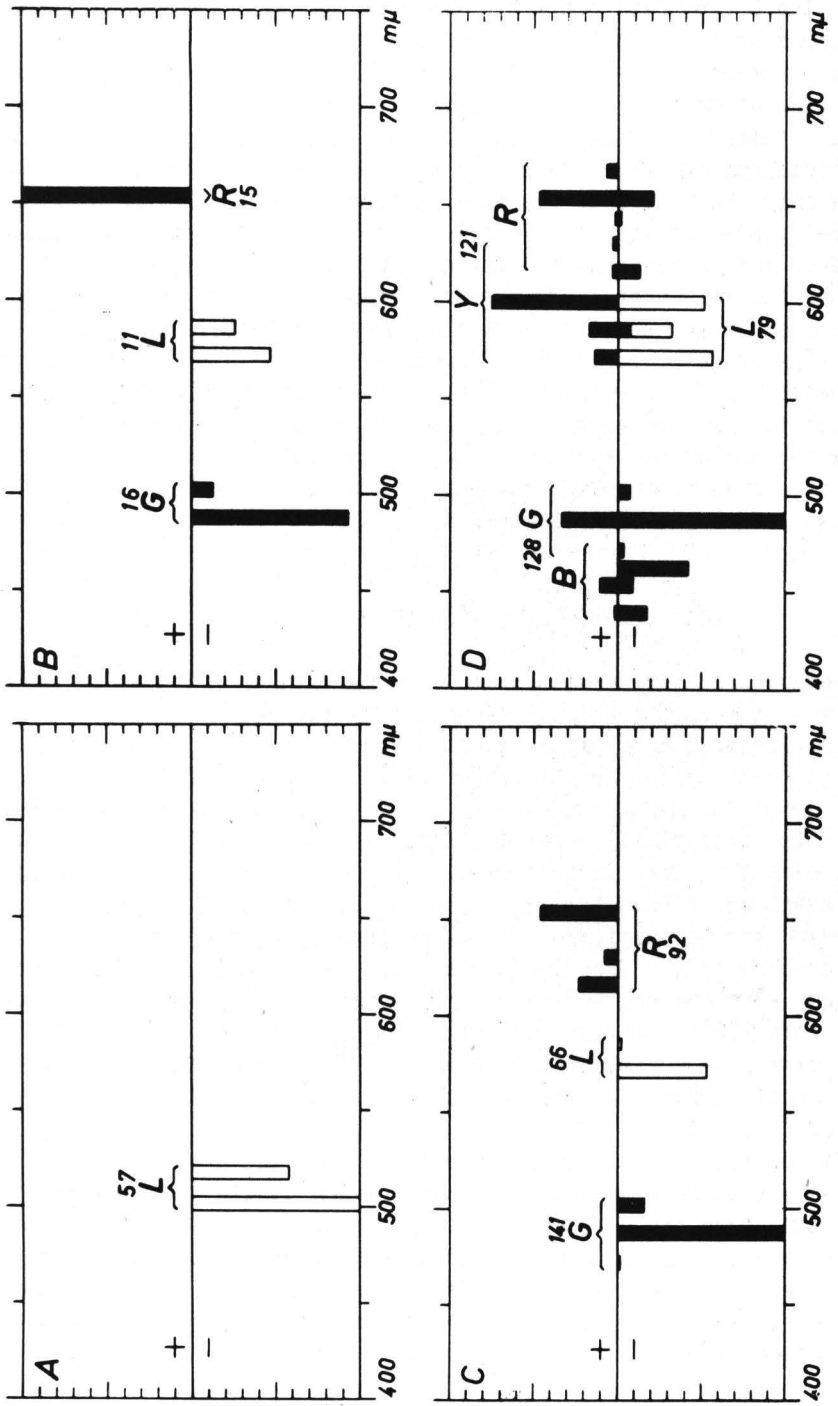
A
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141
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66
L
92
R
128
G
B
121
Y
R
79
L

Fig.2.

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pairs. The L type represents the separate photopic luminosity mechanism corresponding to Hering's black-white substance.

The diagrams in *fig. 2* show the spectral location, polarity, number and scattering of maxima of 498 photographically recorded spectral response curves obtained from the retinas of four different species of fish.

The diagram *fig. 2A* represents fish caught at a depth of 30-70 metres having only the L type of response (achromatic vision), the diagrams *fig. 2B-D* represent fish inhabiting shallow water (dichromatic vision *fig. 2B-C*, and tetrachromatic vision *fig. 2D*).

Among the well over 1,000 spectral response curves recorded, we have not observed any other type of curve than those presented here. The polarity of the L type of response corresponded always to a hyperpolarization of the cell membrane. The R-G and Y-B curves generally showed a hyperpolarization response in the blue-green portion and a depolarization potential in the yellow-red end of the spectrum. On a few occasions, in certain fish species, response curves of the R-G or Y-B type showing a polarity opposite to the one described above were obtained (*fig. 2D*).

LOCALIZATION OF THE ELECTRODE TIP IN THE RETINA

A common problem for physiologists working with microelectrode technique has been the accurate localization of the tip of the microelectrode in the nervous tissue. The total thickness of the fish retina is about 230 μ and the depth into which the electrode was inserted was originally judged from the readings on the micrometer gauge fitted to the micromanipulator. However, this earlier method was far from satisfactory. In a series of experiments the microelectrode was filled with crystal-violet solution, which stain after each typical recording electrophoretically was forced into the tissue around the tip of the microelectrode. After fixation, the retina was sectioned in the freezing microtome. Using a gelatine-glycerine technique described by Fernández-Morán *(ref. 1)* it was possible to obtain serial thin frozen sections of the material with a minimum of distortion. In the micrographs presented in *fig. 3* the centres of the violet spots seen in the sections have been marked with white crosses. The scale to the left in *fig. 3* is in 10 μ.

It is concluded from these experiments that the L type of spectral response curves were recorded from the region of the large synaptic endings of the cones and the horizontal cells, whereas the R-G and Y-B types of response curves were obtained 20-30 μ deeper, corresponding to the bipolar cell layer of the retina. In collaboration with Dr. H. Fernández-Morán experiments are in progress for a more accurate localization with the aid of the electron microscope.

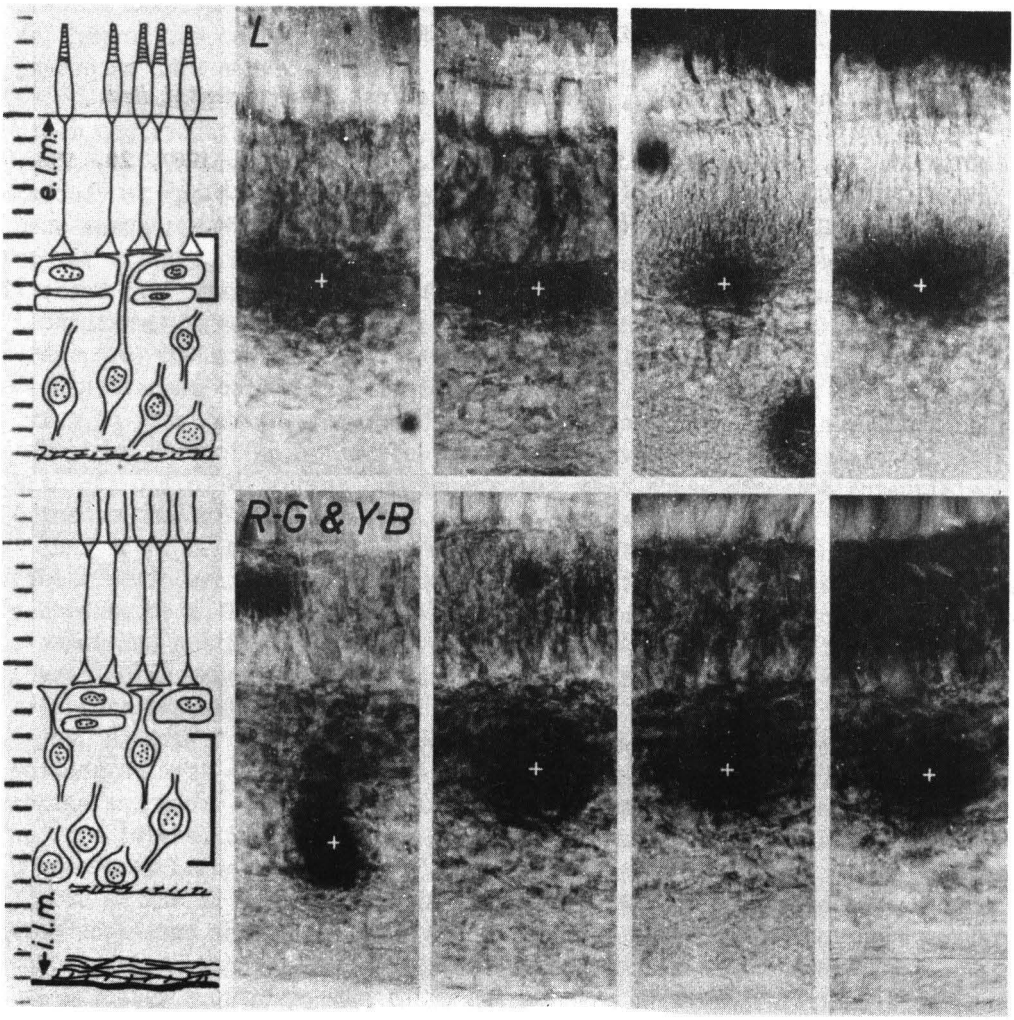

Fig.3.

REFERENCE

1. FERNÁNDEZ-MORÁN, H., *Exp.Cell Res.*, 1952, **3**, No.2.

GENERAL REFERENCES

MITARI, G. and YAGASAKI, Y., *Annual Rep.Res.Inst.Environmental Med., Nagoya Univ.*, 1955, 54.

MOTOKAWA, K., OIKAWA, T. and TASAKI, K., *J.Neurophysiol.*, 1957, **20**, 186.

SVAETICHIN, G., *Acta physiol.scand.*, 1953, **29**, Suppl., 106.

SVAETICHIN, G., *Acta physiol.scand.*, 1956, **39**, Suppl., 134.

TOMITA, T., *Jap.J.Physiol.*, 1957, **7**, 80.

PRESENTATION AND DISCUSSION OF PAPERS 18, 19 AND 39

THE CHAIRMAN, PROFESSOR R. GRANIT, opened with a general introduction on present developments in the electrophysiological work on vision (Paper 18). He then called on Dr. G. S. Brindley to give the first of the two review papers on this subject.

DR. BRINDLEY presented his paper (19) and added some remarks on two other contributions. He interpreted the results of Fiorentini and Ronchi (Paper 16) in which they found differences in the height, rate of rise and latency of the b-wave of the human electroretinogram as a function of the peak intensity of the stimulus with white and green as opposed to blue-violet stimuli, as differences between the scotopic and photopic mechanisms instead of as manifestations of the differences between separate chromatic mechanisms. Commenting on the paper by MacNichol, Macpherson and Svaetichin, (Paper 39) he said that the spike responses of opposite polarity obtained with different coloured stimuli were obtained from a part of the retina lying in front of the cones and are probably not intracellular. The results, therefore, do not mean that the cones themselves produce opposite potentials with stimuli of different wavelength but that these opposite potentials arise in the interacting nerve cells of the retina.

DR. F. H. C. MARRIOTT asked whether the off-response of the frog's electroretinogram could be produced by Landolt's clubs, since off-responses seemed to be a feature of cold-blooded eyes where Landolt's clubs were present and not of mammalian eyes where they were not. The off-response suggested nervous interaction and would therefore be unlikely to arise in receptors themselves.

DR. BRINDLEY replied that Professor Svaetichin had recorded an electro-retinogram with an off-response from the exposed posterior surface of the retina and under those circumstances it was improbable that he was picking up from interacting structures. The off-response was unlikely to be produced by Landolt's clubs.

DR. KATHERINE TANSLEY said that a large off-response could be recorded from pure-cone mammalian eyes in the squirrel family in which there appeared to be no Landolt's clubs. PROFESSOR G. WALD wished to know why, in Dr. Brindley's opinion, the responses obtained with intraretinal electrodes, were not intracellular, what was the reason for the hyperpolarisation obtained for some recordings by MacNichol, Macpherson and Svaetichin with short wavelength stimuli, and why Svaetichin's responses were graded ones. DR. BRINDLEY said the responses seemed not to be intracellular because Tomita got similar results which were unaltered by movements of the electrode too large to make it probable that the microelectrode could have remained within a cell. On the second point, it was true that the spinal cord hyper-polarisation and depolarisation tended to represent inhibition and excitation and by analogy this was probably their meaning in the retina, but one could

not be certain. The fact that MacNichol, Macpherson and Svaetichin got graded responses with different wavelength stimuli presented no difficulty if the recording electrode was extracellular as it probably was.

PROFESSOR GRANIT quoted experiments done by Elenius in which dark adaptation was followed by means of the electroretinogram in man. In normal subjects there was a long pause before the electroretinogram began to appear. In cone-blind (rod monochromat) subjects there was no such delay. This suggested that at the beginning of dark adaptation the cones inhibited the rod response and that the receptors were "set" by some horizontal interaction in the retina. DR. BRINDLEY wondered whether cone-blind subjects were really lacking in cones or only in cone function. If it was cone function, it might be possible to influence the delay in normal subjects by the use of red light which would stimulate the cones but not the rods. DR. W. A. H. RUSHTON said that one might test the suggestion that the cones inhibit the rods at the beginning of dark adaptation by comparing the effects in normal eyes when light adaptation was to blue and yellow lights matched with regard to their scotopic value. In this situation the effect of the two adapting lights would be equal for the rods but not for the cones. If the delay were due to an inhibition of rods by cones the effect would not be the same for the two adapting lights. His guess was that the effect would be the same.

PROFESSOR GRANIT, reverting to a previous point, said that if the records obtained with intraretinal microelectrodes in fact represented intracellular potentials then opposite signs in the potentials would represent excitation and inhibition. If the records were extracellular ones we should have, at present, no means of knowing whether a change in sign meant a change from excitation to inhibition or not.

PROFESSOR E. MARG mentioned that Sjöstrand had described large, closely-packed horizontal cells in a fish, the perch. In that retina it would appear to be impossible to record from that region of the retina without penetrating the cells.

PAPER 20

THE SPECTRAL SENSITIVITY OF VERTEBRATE RETINAL ELEMENTS

By K. O. DONNER

Donner, Kai Otto

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20. THE SPECTRAL SENSITIVITY OF VERTEBRATE RETINAL ELEMENTS

By K. O. DONNER

SUMMARY

1. The origin of the impulses recorded by the microelectrode technique from the surface of the retina is discussed.
2. The spectral sensitivity of the retinal elements can be described in terms of scotopic and photopic dominators, with broad spectral sensitivity curves. In addition, narrow-band modulator activity can be recorded in a number of elements, in some animals by direct threshold measurements, in others with indirect methods.
3. Utilizing the directional sensitivity of the cones, cone and rod contributions can be separated. This can also be done by the two-colour threshold technique as used by Stiles.
4. The nature of the dominator and modulator curves is discussed. The scotopic dominator shows agreement with known rod pigments, while the photopic dominator appears to represent the summed effect of at least two cone sensitivities. Neural processes seem to be responsible for the narrowness of the modulator response, but their spectral location probably indicates regions of maximum sensitivity for different types of receptors.

THE MICROELECTRODE TECHNIQUE

ALL the work on the spectral sensitivity of single retinal units so far published has been carried out with the microelectrode technique of recording as first used by Granit and Svaetichin *(ref. 1)*. The experiments have been performed on opened eyes, lacking lens and cornea; with cold-blooded animals on excised eyes, with birds and mammals on anaesthetized or decerebrate animals. Thus intra-ocular pressure has been removed and in excised eyes the blood supply has been cut off. The similarity between the results obtained with this technique and those from microelectrode experiments on intact eyes *(refs. 2,3,4)* suggests that the retina reacts in a normal way also in an excised and opened eye.

Granit introduced the term "retinal element" for the apparently single cell discharges recorded by the microelectrode from the surface of the retina. Direct evidence as to the origin of this discharge was given by

Rushton *(refs. 5,6)* who showed that the large impulses recorded from the cat's retina were in their properties consistent with the notion that they were derived from single cells. By a combination of histological and physiological techniques he was able to demonstrate that the impulses most likely were generated in large ganglion cells, 30 - 50 μ in diameter, with branches spreading over a circle about 1 mm in diameter. This established that the message recorded was that of the optic nerve fibres - the retinal ganglion cells being the source of these fibres. Later, Barlow *(refs. 7,8)* has examined this question and come to the same conclusion for the frog's retina. Two types of impulses are recorded from this retina: a fast triphasic and a slow diphasic impulse (compare also *ref. 9*, for the cat's retina). The slow type was shown by Barlow to be excited by a small spot of light near the tip of the electrode and was apparently produced by ganglion cells. The fast type probably originates from optic nerve fibres passing to the optic disk along the surface of the retina, since their receptive field is at some distance from the tip of the electrode and always in a direction away from the optic disk.

There is thus good evidence that what actually is recorded is the discharge from single ganglion cells. However, according to histological evidence *(ref. 10)* there are several varieties of ganglion cells, possibly with different functions and of different size. In microelectrode experiments there may be a selection in favour of the large ones, which can be expected to give a better isolation of the discharge. This criticism is probably to some extent justified for the cat's eye, although Kuffler *(ref. 4)* concludes from the frequency with which ganglion cell responses can be recorded from a restricted area that the selection cannot be extreme, probably only the very small cells are omitted. Barlow *(ref. 8)* has also observed that in the frog's eye ganglion cell impulses can be recorded from almost any point of the retina.

When trying to compare the results obtained with the microelectrode technique with data on the human eye, it must be observed that the results mainly refer to the periphery of the retina. However, Kuffler *(ref. 4)* found no essential difference between the elements in the periphery and those from the central area of the cat's eye. But a true fovea is absent in the cat and it is thus unlikely that single foveal ganglion cells have ever been studied, that is to say the midget ganglion cells connected to form private pathways for single foveal cones *(ref. 10)*.

The term "retinal element" as used by Granit thus refers to the retinal ganglion cell (or optic nerve fibre). Both on histological grounds *(ref. 10)* and from physiological experiments *(refs. 2,3,4,11,12)* it is evident that a very large number of receptors connect to the ganglion cells studied. The fields, inside which a small spot of light elicits a discharge (the receptive field) is mostly about 1 mm in diameter, the centre of this field being much more sensitive than the periphery.

THE typical result when spectral sensitivity curves are determined under fully dark-adapted conditions, measuring the threshold of the discharge at different wave-lengths, is shown in *figs. 1* and *2*. *Fig. 1* gives the spectral sensitivity of a single, particularly stable on-element from the cat's retina (circles) *(ref. 13)*. The curve given for comparison is the absorption curve for rhodopsin *(ref. 14)*. The second set of data (dots) gives the average scotopic sensitivity of the tench *(ref. 15)* compared with Dartnall's rhodopsin curve displaced to give maximum sensitivity at 533 mμ (compare *ref. 14*). The tench eye is known to contain visual violet (porphyropsin) with λmax at 533 mμ according to Dartnall *(ref. 14)* and 522 mμ according to Wald *(ref. 16)*.

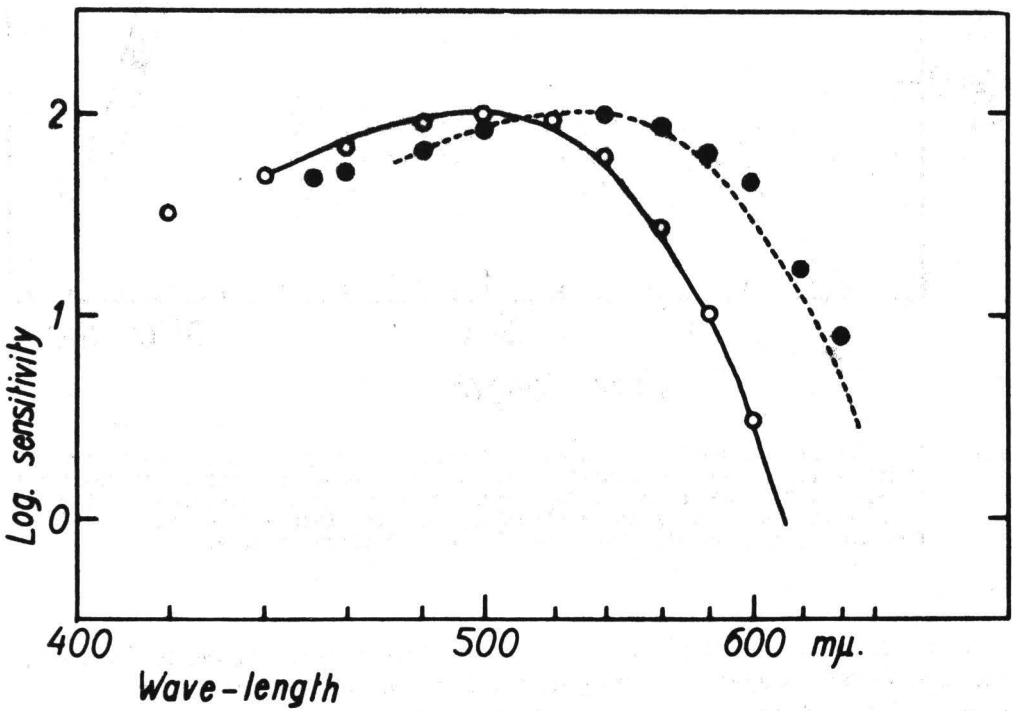


Fig. 1. Scotopic sensitivity for pure on-element (circles) from the cat's retina *(ref. 13)* compared with absorption curve for rhodopsin *(ref. 14)*. Dots: average scotopic sensitivity for the tench eye *(ref. 15)*. Dotted line: Dartnall's template curve displaced to give maximum at 533 mμ. Sensitivities in terms of reciprocal quanta in this and all the following figs.

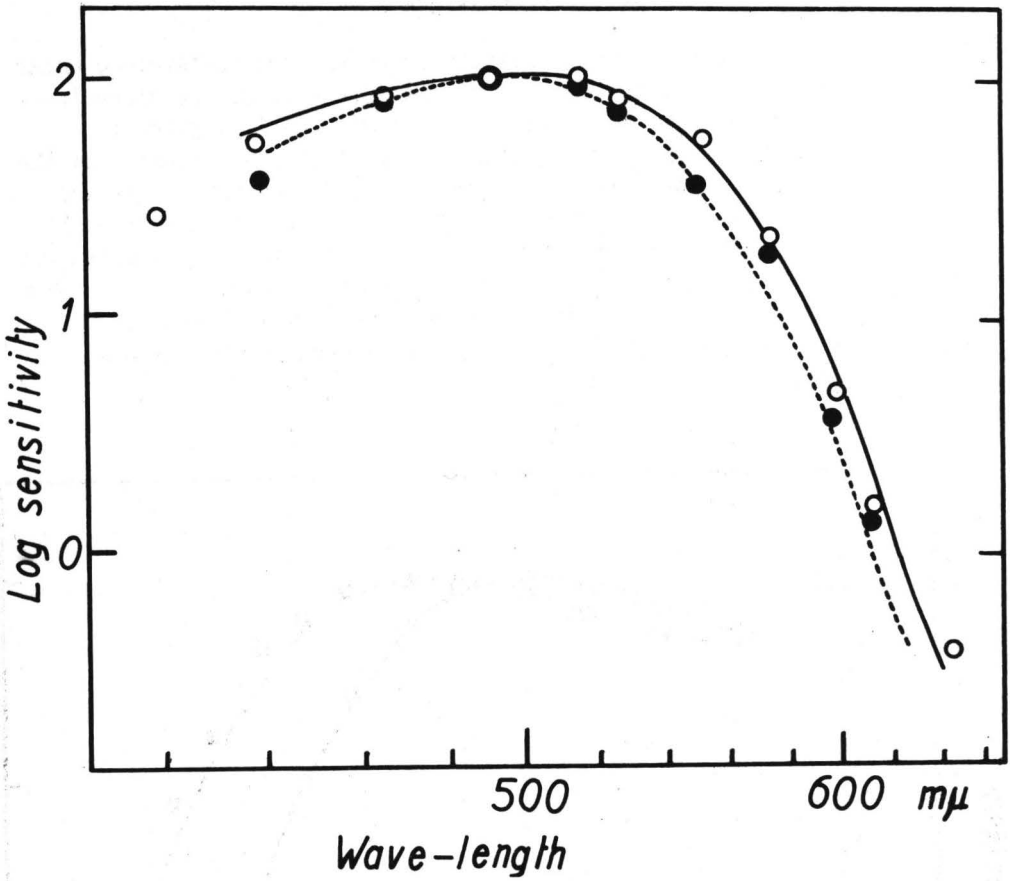


Fig. 2. Circles: sensitivity of fully dark-adapted frog's eyes, dissected in red light (average for 4 elements). Line in full: absorption curve for rhodopsin of density 0.75 at 500 mμ. Dots: sensitivity for eyes dark-adapted 1.5 hours after excision (average for 4 elements). Dotted line: absorption curve for frog rhodopsin *(ref.14)*. Data from Donner & Rushton *(ref.17)*.

Fig. 2 shows the scotopic sensitivity of frog retinal elements *(ref. 17)*. The dots refer to eyes dissected in daylight and dark-adapted after excision for 1.5 hours, the dotted curve is Dartnall's absorption curve for frog rhodopsin (V.P. 502). The circles show the average scotopic sensitivity for 4 elements, from eyes dark-adapted not less than 24 hours before the eye was excised. The dissection was performed in red light. The density of 500 mμ of rhodopsin in the rods ought in this case to be 0.75 as shown by Denton & Wyllie *(ref. 18)*. The curve (line in full) gives the spectral absorption of rhodopsin at density 0.75 calculated from Dartnall's curve

(compare *ref. 19*). Zewi *(ref. 20)* measured the regeneration of rhodopsin in the frog retina. From his data it can be concluded that those eyes, dark-adapted only after excision for 1.5 hours, would have a rhodopsin density of about 0.2 - 0.3 at 500 mμ. This value would give an absorption curve nearly identical with the curve for infinite dilution.

Scotopic sensitivity curves showing a similar agreement with the rhodopsin absorption curve have been obtained for guinea pigs *(ref. 21)* and for the pigeon *(ref. 22)*. Less exact agreement is shown by the results for albino rats *(ref. 23)* and albino rabbits *(refs. 24,25)*. In albino eyes, lacking retinal pigment, it is possible that absorption by haemoglobin and oxyhaemoglobin modifies the spectral sensitivity; in the rat, Granit *(ref. 23)* assumed that blood in the vitreous body caused the narrowness of the scotopic curves obtained.

Granit *(ref. 26)* found that in many cases the retinal elements of the cat did not show any change of the relative spectral sensitivity after adaptation with coloured lights. This is consistent with the interpretation that the scotopic sensitivity curve in pure rod or rod-cone eyes is mainly determined by the properties of a single visual pigment - rhodopsin, porphyropsin or other similar substances. However, in many elements, for example in the cat's retina, scotopic sensitivity deviates significantly from the simple curve shown in *figs. 1* and *2* (compare *fig. 13*) and is thus not referable in the above-mentioned simple way to the properties of rhodopsin alone *(ref. 13)*.

Results such as those shown in *figs. 1* and *2* also demonstrate that there are no absorbing substances present in the eyes used, that could modify the response - an important point when the more complicated results obtained under photopic conditions are considered.

Broad spectral sensitivity curves based on rod reactions and photopigments as described above, have been called scotopic dominators (compare *ref. 27*).

PHOTOPIC SENSITIVITY: PHOTOPIC DOMINATORS

UNDER photopic conditions the majority of retinal elements of mixed rod-cone eyes (cat, frog, pigeon, tench) and pure cone eyes (snake, tortoise) are maximally sensitive in the region 550 - 600 mμ. The most common spectral sensitivity curve obtained in the light adapted condition is the photopic dominator.

As shown in *fig. 3*, two main types have been recorded: (i) curves with maximum sensitivity at 560 mμ found in eyes giving the rhodopsin distribution of sensitivity in the scotopic state, the curves showing agreement with the human photopic visibility curve; (ii) curves with maximum sensitivity at 620 mμ found in eyes (tench, tortoise) giving the porphyropsin distribution of sensitivity in the scotopic state.

In *fig. 3* photopic dominators are compared with the absorption curves for iodopsin (λ max. 562 mμ, chicken) and cyanopsin (λ max 620 mμ).

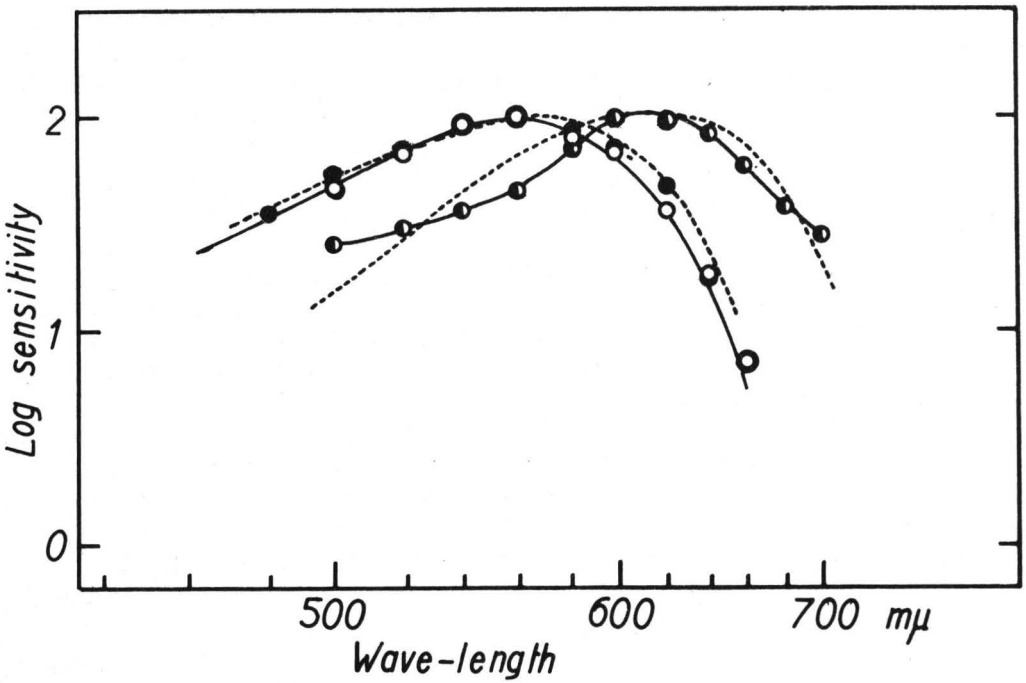


Fig.3. Photopic dominators. Circles: cat *(ref.52)*; dots: snake *(ref.15)*; half-filled circles: tench *(ref.15)*. Line in full: photopic dominator of frog *(ref.30)*. Dotted curves: absorption curves for iodopsin and cyanopsin *(refs.16,28)*.

According to Wald *(ref.16)* and Wald, Brown and Smith *(ref.28)* these are cone pigments corresponding to rhodopsin and porphyropsin respectively. Whereas iodopsin gives a fairly good fit to the common photopic dominator of cat, frog and snake, cyanopsin does not fit the data for the tench equally well. Dartnall *(ref.14)* concludes that the photopic dominators are too narrow to fit his template curve that on a wave-frequency abscissa might be expected to reproduce the absorption curves for broad-band visual pigments, irrespective of the location of their maxima.

In the eye of the pigeon Granit *(ref.29)* found a photopic dominator with its maximum at 580 mμ. He recorded the spectral sensitivity of the massed discharge from the retina, the result was, however, later confirmed for single elements by Donner *(ref.22)*. The cones in the pigeon's retina contain red, yellow and green oil droplets acting as filters in front of the external limbs of the cones - thus the shift of the maximum from 560 to 580 mμ can be explained, considering that the dark-adapted pigeon eye shows the rhodopsin distribution of sensitivity. All other eyes of this type give the 560 mμ photopic dominator.

PHOTOPIC SENSITIVITY: THE MODULATORS

IT has been stated above that the majority of retinal ganglion cells, for example in the frog *(ref. 30)*, when light-adapted show the distribution of sensitivity corresponding to the photopic dominator. In many of the eyes studied (compare summaries by Granit *refs. 27, 31, 32*), spectral sensitivity curves of a narrower type were also obtained - the modulators. Such curves were first recorded from the frog's retina *(refs. 1, 30)*. Later, similar results were obtained for the eyes of snake *(ref. 33)*, guinea pig *(ref. 21)*, rat *(ref. 23)*, pigeon *(ref. 22)*. As pointed out by Granit the maxima of these narrow curves are grouped in the regions 440 - 460 mμ, 520 - 540 mμ and 580 - 600 mμ.

As an example, the frog modulators as recorded by Granit *(ref. 30)* are shown in *fig. 4*. For comparison the scotopic and photopic dominators for the frog eye are given below in the diagram. Although the curves shown probably

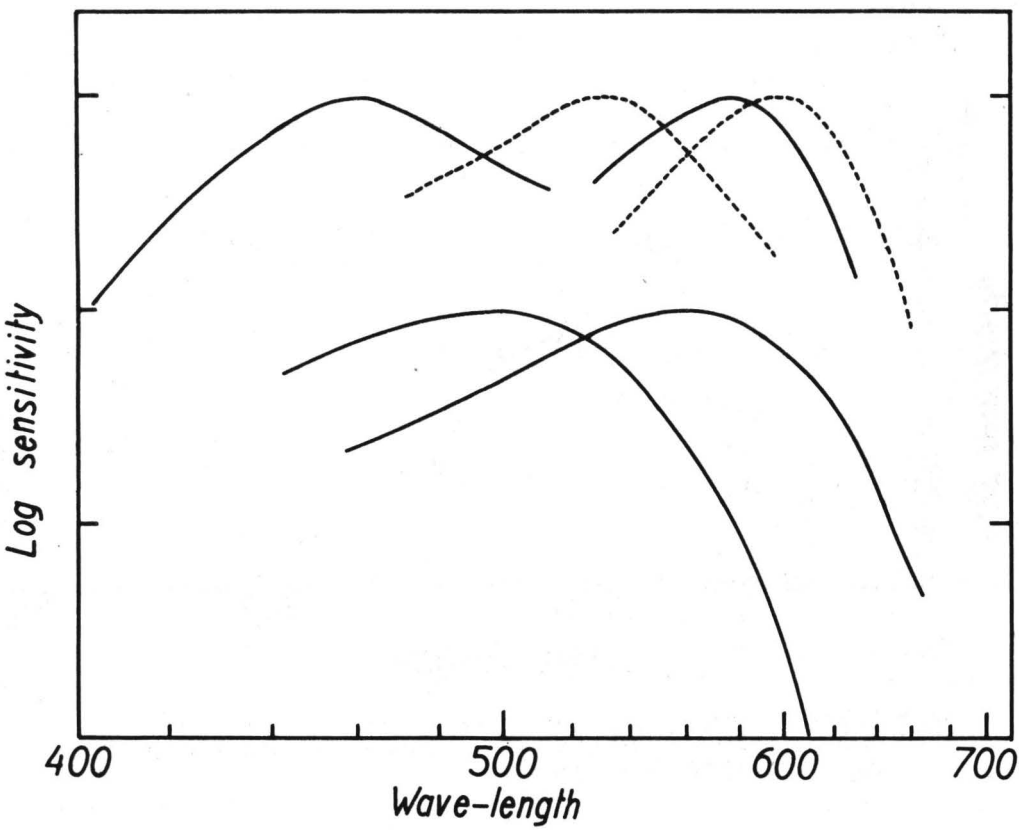


Fig. 4. Frog modulators from Granit *(ref. 30)*. Lower curves give scotopic and photopic dominators for comparison.

represent sensitivities of single ganglion cell discharges, it must be observed that in this work Granit partly used experiments where isolation was incomplete and the activity of a restricted number of units was recorded.

In many cases two modulator curves seem to be coupled together in the response from a single unit, or there is irregularity in the shape of the spectral sensitivity curve in those regions of the spectrum giving a low sensitivity for that particular unit. As an illustration the "red" modulator of the snake *(ref. 33)* and the "blue" modulator of the pigeon *(ref. 22)* are shown in *fig. 5*. As stated by Granit *(ref. 32, p. 120)*, it is actually more likely that a response of the type shown in *fig. 5* is obtained from a single unit, than to get narrow-band sensitivities without any indication of a secondary hump. In addition it has been found that the modulator curves show a greater variability between the results for individual elements than the results for the scotopic and photopic dominators *(refs. 22, 32)*.

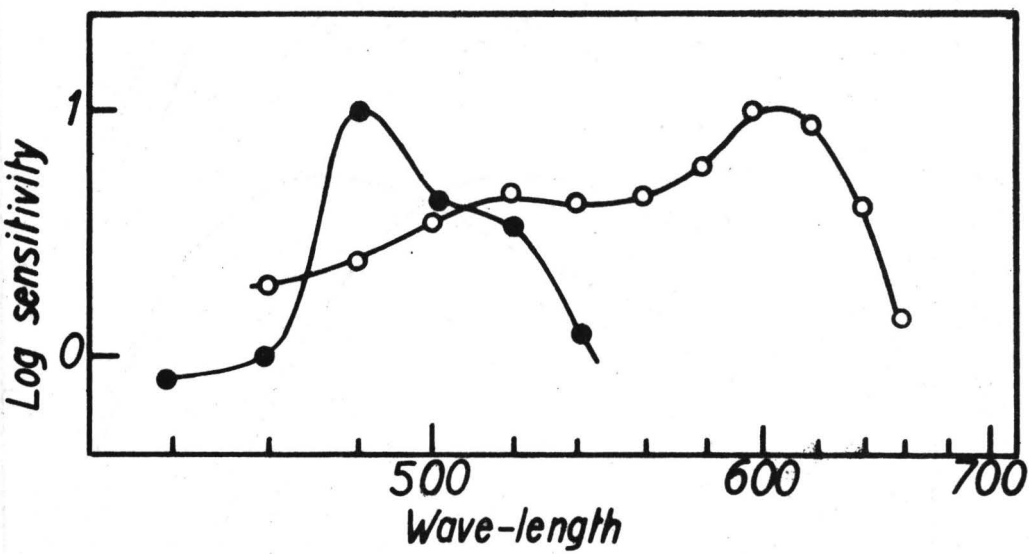


Fig. 5. Circles: snake, average spectral sensitivity of 7 series giving red modulator with additional hump in the green *(ref. 33)*. Dots: pigeon, single "blue" modulator *(ref. 22)*.

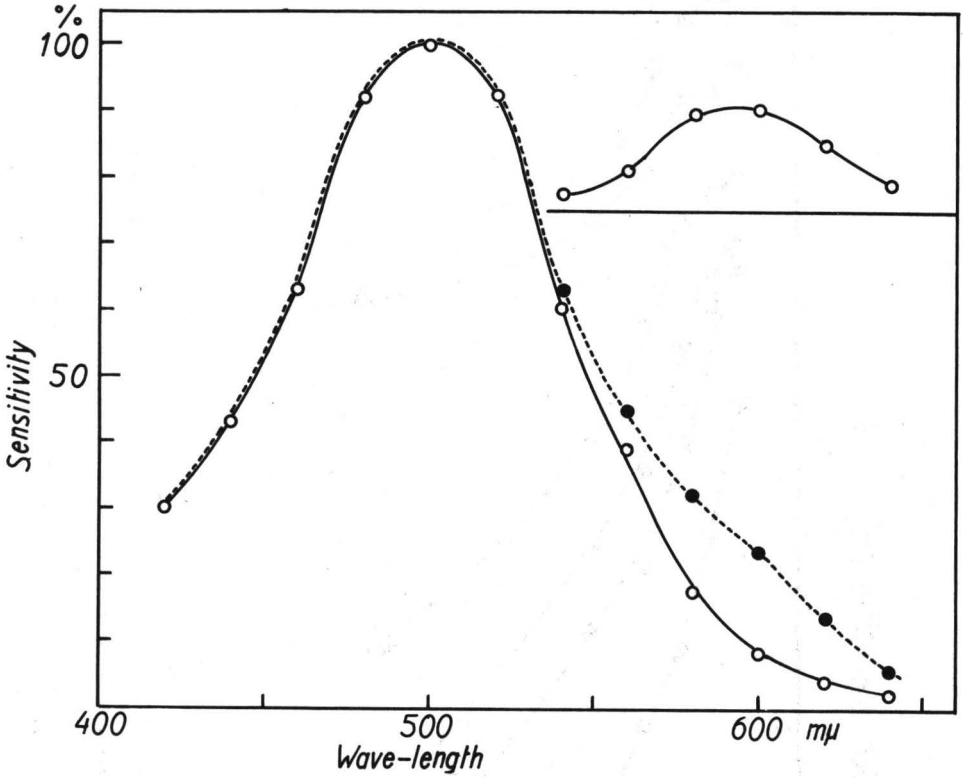


Fig. 6. Method of selective adaptation used to obtain cat modulators *(ref. 26)*. Full explanation in text.

Another type of modulator was derived by Granit *(ref. 26)* in experiments on the cat's eye using selective adaptation. The method is illustrated in *fig. 6*. The scotopic sensitivity of a single element was determined by threshold measurements, giving a spectral sensitivity curve of the scotopic dominator type *(fig. 6*, circles, line in full). Then the retina was illuminated by a strong, coloured light, red, green or blue, which was left on for some time. Thresholds were determined by interrupting the adaptation light and giving a test flash of variable wave-length and intensity. Thus a second sensitivity curve for the unit under investigation was obtained *(fig. 6*, dots, dotted line). In about 60% of the elements investigated the two curves were of different shape. From the data obtained, Granit calculated the difference between the sensitivity curves before and during adaptation, when the ordinates had been made equal for that region of the spectrum showing the greatest decrease of sensitivity. The difference between the ordinates was plotted against wave-length *(fig. 6*, above). In this way three types of

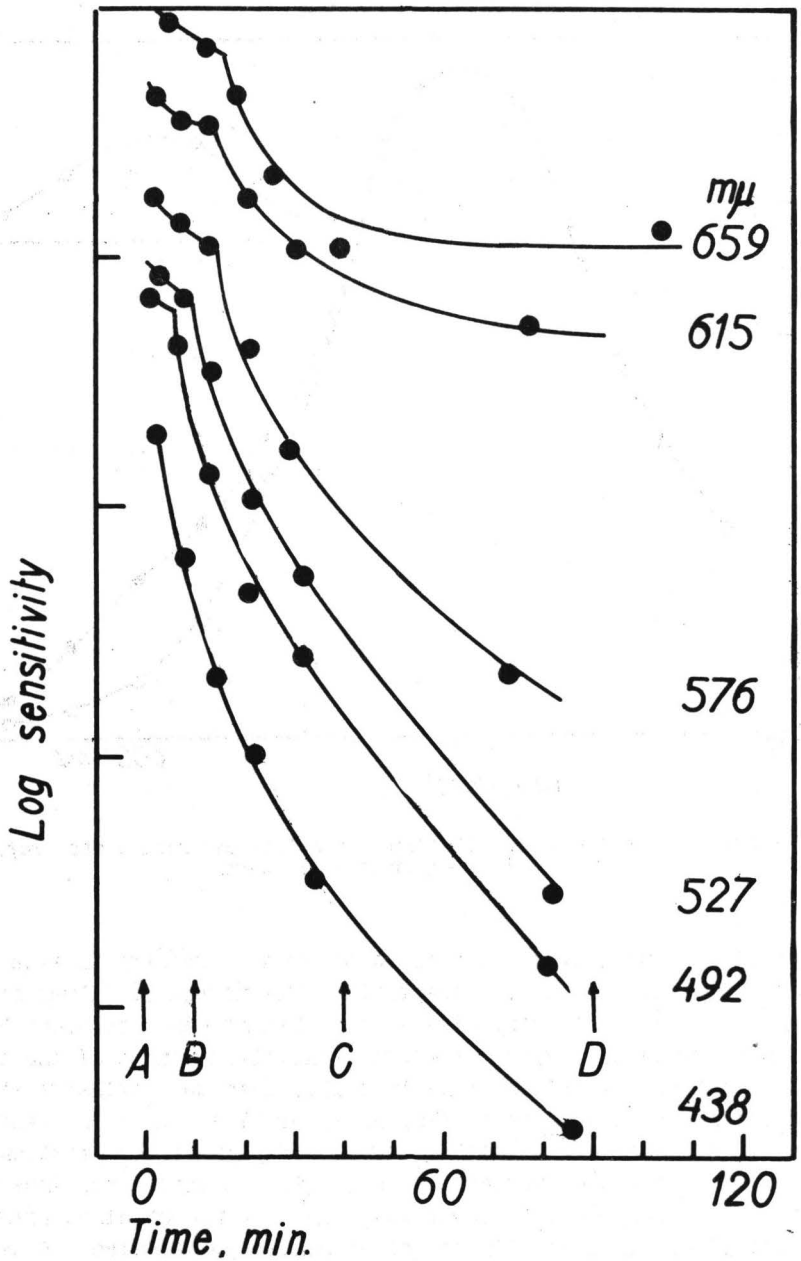


Fig.7. Dark-adaptation curves for single element of the frog's retina determined for wave-lengths indicated on right-hand side of graph. Curves arbitrarily displaced along the ordinate in relation to each other, *(ref.17)*.

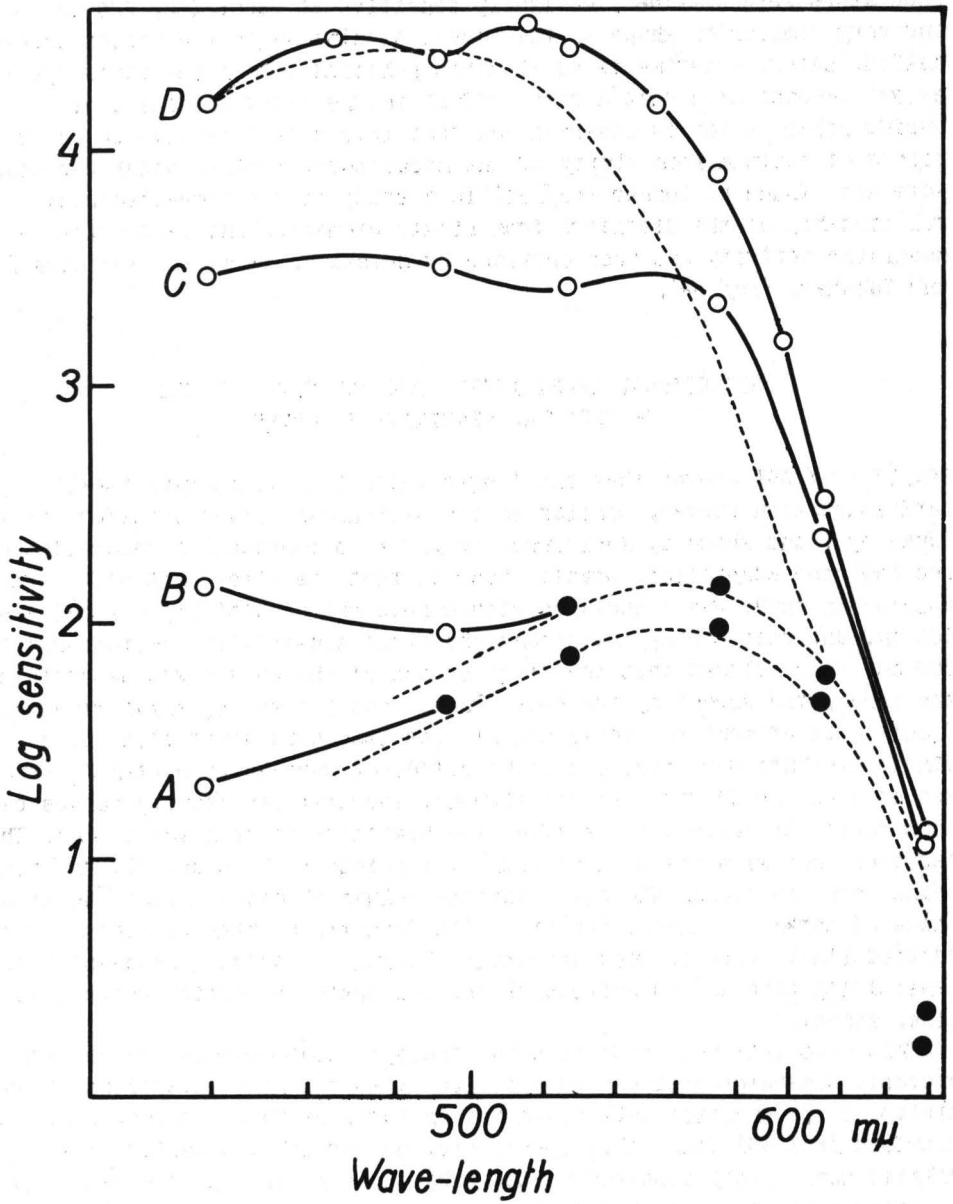


Fig. 8. Sensitivity curves derived from data of *fig. 7* at times indicated by arrows (A, B, C, D). Dots: values obtained for first phase of dark-adaptation. Circles: second phase. Dotted curves: frog photopic dominator *(ref. 30)*, absorption of frog rhodopsin *(ref. 14)*. (Donner and Rushton *(ref. 17)*).

modulators were obtained, maximally sensitive at about 460, 520 and 600 mμ and very similar in shape to the curves obtained with the direct threshold method. Later, experiments on electric polarization of the cat's eye *(refs. 34,35)* demonstrated that a rise or fall in the light threshold of an element during polarization is observed and that this effect mainly occurs at the points of maximum sensitivity of the modulators. Similar modulator effects were also found by Donner *(ref. 36)* in a study of the time-frequency relationship of the discharge from single elements. Indirect evidence for modulator activity has been obtained by Motokawa, Iwama and Tukahara *(ref.37)* and Tukahara *(ref. 38)*.

DIRECTIONAL SENSITIVITY. ROD AND CONE EFFECTS IN SPECTRAL SENSITIVITY CURVES

GRANIT *(ref. 30)* showed that the frog's retinal elements gave two-branched dark-adaptation curves, similar to the well-known curves obtained for the human eye, and shown by Kohlrausch *(ref. 39)* to represent a separation of rod and cone adaptation. Granit observed that the first part of the dark-adaptation curve was associated with a spectral sensitivity maximal around 560 mμ, and that during the second phase the sensitivity maximum shifted to 500 mμ. He concluded that the first branch of the curves was determined by the cones, the second by the rods. Donner and Rushton *(ref. 17)* repeated Granit's experiment and confirmed his results. Dark-adaptation curves for single elements were recorded using different wave-lengths *(fig. 7)*. From a set of such curves for a single element, spectral sensitivity curves can be constructed at various times after the beginning of dark-adaptation. This has been done with the data of *fig. 7* (at points A, B, C and D), the result being shown in *fig. 8*. The dots indicate values obtained during the first phase of dark-adaptation. Compared with Granit's average photopic dominator (dotted line) there is good agreement. During the second phase spectral sensitivity changes and approaches the rhodopsin absorption curve (dotted line, above).

This association of rods with the scotopic dominator and cones with the photopic dominator provides an opportunity to test the directional sensitivity of the ganglion cell discharge in terms of rods and cones. Stiles and Crawford *(ref. 40)* found that light entering through the centre of the dilated human pupil appeared to the subject brighter than the same light entering near the edge. Later, it was shown by Crawford *(ref. 41)*, Stiles *(ref. 42)* and Flamant and Stiles *(ref. 43)* that the effect applied chiefly to the cones and could therefore be used to distinguish between rod and cone effects. Donner and Rushton *(refs. 17,44)* found that during photopic conditions a directional sensitivity is exhibited by the frog retinal elements as shown in *fig. 9*. In the photopic state the spectral sensitivity of this element is that of the photopic dominator (dotted line, Granit, *(ref. 30)*)

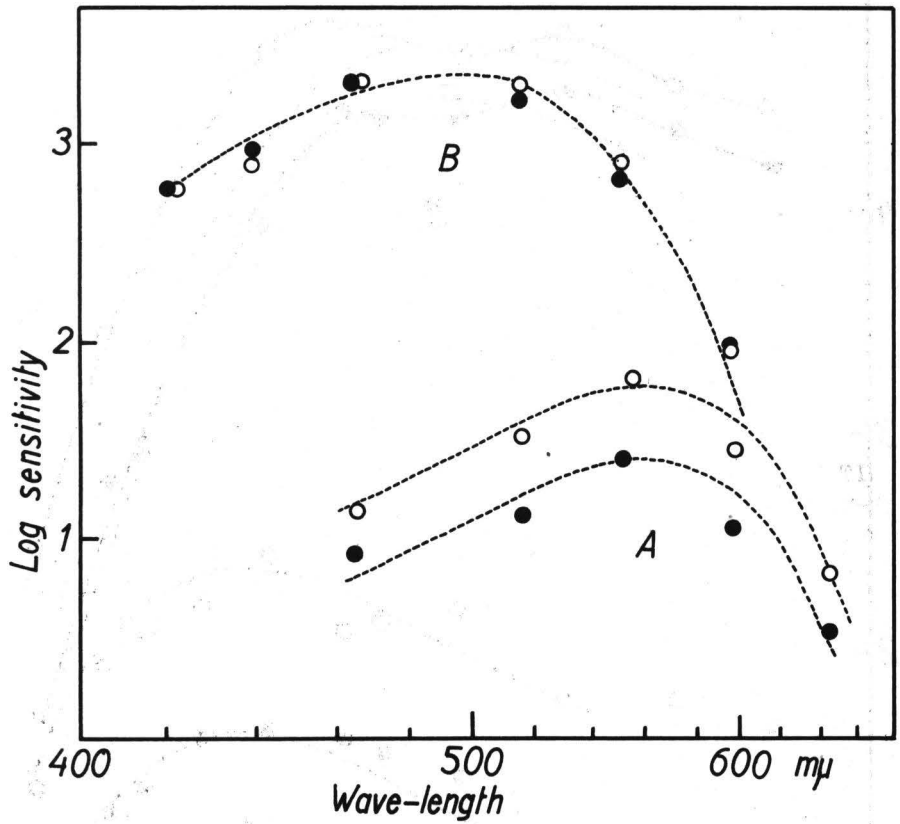


Fig. 9. Experiment on directional sensitivity. Single element, frog. A, photopic conditions, B, scotopic conditions. Circles: sensitivity for more perpendicular incidence of light. Dots: oblique incidence. *(ref. 17)*. Dotted curves, compare *fig. 8*.

but there is a general reduction of sensitivity when the incidence of light is made more oblique. This property did not occur in the scotopic state when spectral sensitivity is determined by the rods *(fig. 9, B)*. These results thus give additional evidence that directional sensitivity is a property of the cones. It can be used to analyse the rod and cone contributions to the ganglion cell discharge. An example of this is shown in *fig. 10*, where a more complex sensitivity curve has been recorded for two angles of incidence, the circles referring to a more perpendicular incidence. Curves B refer to a state of less complete dark-adaptation, frequently found in the frog's eye. This type of curve is described by Granit *(ref. 30)*, who particularly noted the high and rapidly adapting blue-sensitivity. It is seen that a change to a more oblique incidence of the light very much reduces the hump maximal

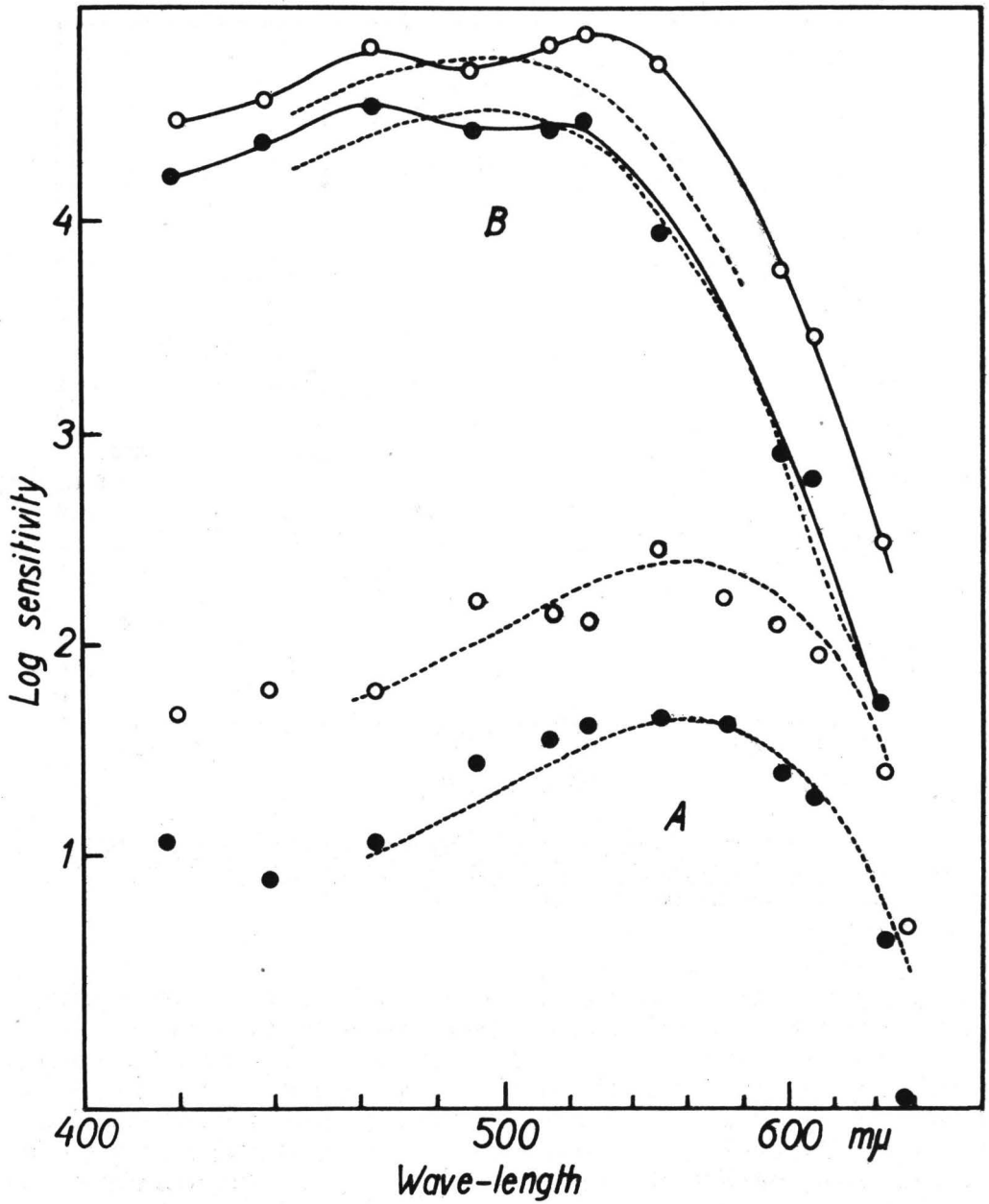


Fig. 10. Same as Fig. 9. Single element, frog. Full explanation in text, *(ref. 17)*

around 530 mμ , whereas on the blue side no change is observed in relation to sensitivity at 500 mμ. The conclusion is that the "green" hump has been produced by cones, the "blue" by a receptor not showing directional sensitivity. The rod properties of the special blue-sensitivity of many of the frog's retinal elements thus present evidence in favour of the interpretation, already suggested by Granit and Munsterhjelm *(ref. 45)* that this effect is due to the green rods. According to the measurements of Denton and Wyllie *(ref. 18)* the green rods absorb light heavily in the region 400 - 440 mμ and practically none in 490 - 520 mμ. The number of these rods is by no means negligible; Denton and Wyllie state that they cover 8% of the total retinal area, the rhodopsin rods covering about 60%. It might be added that Donner and Rushton *(ref. 17)* showed that the blue-sensitivity is depressed by selective adaptation with blue light and is then probably due to a special pigment.

Experiments like those shown in *figs. 8* and *10*, clearly demonstrate that in the retinal elements investigated a cone sensitivity like that of the photopic dominator, by summation with the rod response produces intermediate sensitivity curves, assuming that the spectral sensitivity of the cones does not change during the process of dark-adaptation.

THE TWO-COLOUR THRESHOLD TECHNIQUE

THE two-colour threshold technique, as used in work on the human eye *(refs. 46,47,48)*, involves measurement of the least perceptible intensity (increment threshold) of a small test flash superimposed on a large conditioning field. Using monochromatic lights of different wave-lengths and plotting log (conditioning intensity) against log (increment threshold), families of curves can be obtained which show a definite division into branches allowing separation of rod and cone mechanisms *(ref. 43)* and a division of the cone response into several component mechanisms (compare summaries by Stiles *refs. 47,48*). In preliminary experiments this technique has been applied to single retinal elements of the frog *(ref. 49)*. Although incomplete, the results seem worth mentioning here because they show essentially the same features as the results for the human eye and thus seem to provide a basis for the comparison between human and electrophysiological results. *Fig. 11* shows typical curves obtained for a well isolated unit using a conditioning field of wave-length 464 mμ of variable intensity and determining the increment threshold for a test flash of variable wave-length. The data have here been analysed with the method used by Stiles. As seen from the diagram evidence is obtained in this case for the presence of two components: the low-intensity response apparently shows the rhodopsin distribution of sensitivity, and the high-intensity component appears to be maximally sensitive at about 550 mμ. The spectral

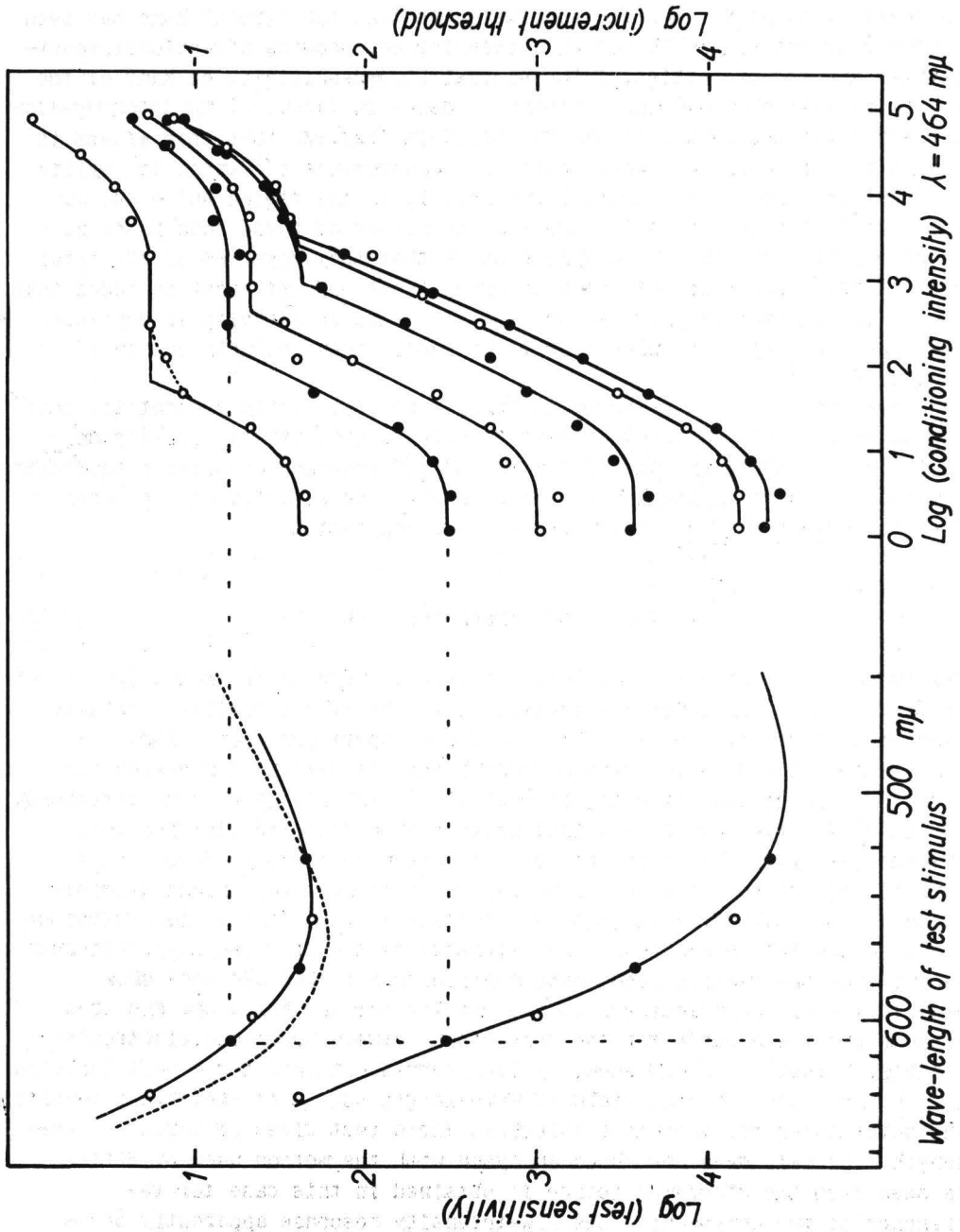


Fig. 11. Single element, frog. Analysis of data obtained by two-colour threshold method (compare *(ref. 47)*). Wave-length of conditioning stimulus 464 mμ. *(ref. 49)*.

sensitivity of this process agrees well with Dartnall's template curve when placed to give maximum at 550 mμ.

The fact that the shape of the second branch of the curves in *fig. 11* is not the same for all wave-lengths of the test flash, indicates the presence of a second high-intensity more red-sensitive component. Other less complete data show that with a red test flash on a blue conditioning field, increment threshold curves with three branches can be obtained.

The two-colour threshold technique rests on the assumption that a conditioning field of a certain wave-length depresses the sensitivity of the receptors maximally sensitive in that spectral region, and that the response to the test flash is due to stimulation of receptors or a certain receptor not very much affected by the field. It was shown above (*figs. 8* and *10*) that under certain conditions summation of the effects from rods and cones occur. Under the present conditions summation would be seen as a less well marked transition between the different branches of the increment threshold curves (compare *ref.46*). This in fact occurs in many elements showing only a very gradual change from one branch to another. On these grounds the 550 mμ curve in *fig. 11* cannot with certainty be said to represent a primary process before more material has been collected. It is, however, noteworthy that its spectral sensitivity deviates significantly from the photopic dominator (*fig. 11*, dotted curve).

In a less exact way the method can be used for a study of the homogeneity of the photopic dominator curve. Using strong constant conditioning fields and measuring the spectral sensitivity it is seen that the photopic dominator is changed (*fig. 12*). The two uppermost curves refer to the same unit, and give the sensitivity for a test flash superimposed on (i) a blue conditioning field (464 mμ) of the maximum intensity available and, (ii) (dots) a still stronger blue field using an Ilford spectral blue filter. There is a clear shift of sensitivity towards the red. The lowermost curve gives for another element the result of the same experiment, illustrating the highest red-sensitivity obtained. The two upper sets of data are compared with Granit's photopic dominator (*ref. 30*), the lower results with the 580 mμ modulator of the frog. Although the results indicate that a photopic receptor (cone) exists in the frog's retina with a maximum sensitivity at about 580 mμ, experiments of the type shown in *fig. 12* do not allow the conclusion that the isolated and unmodified sensitivity curve of that receptor has been obtained.

NATURE OF DOMINATOR AND MODULATOR CURVES

The scotopic dominator: Most elements in mixed rod-cone and rod eyes give this response in the scotopic state, and there is good evidence that the effect is due to the retinal rods and is wholly determined by the spectral properties of the known rod photopigments.

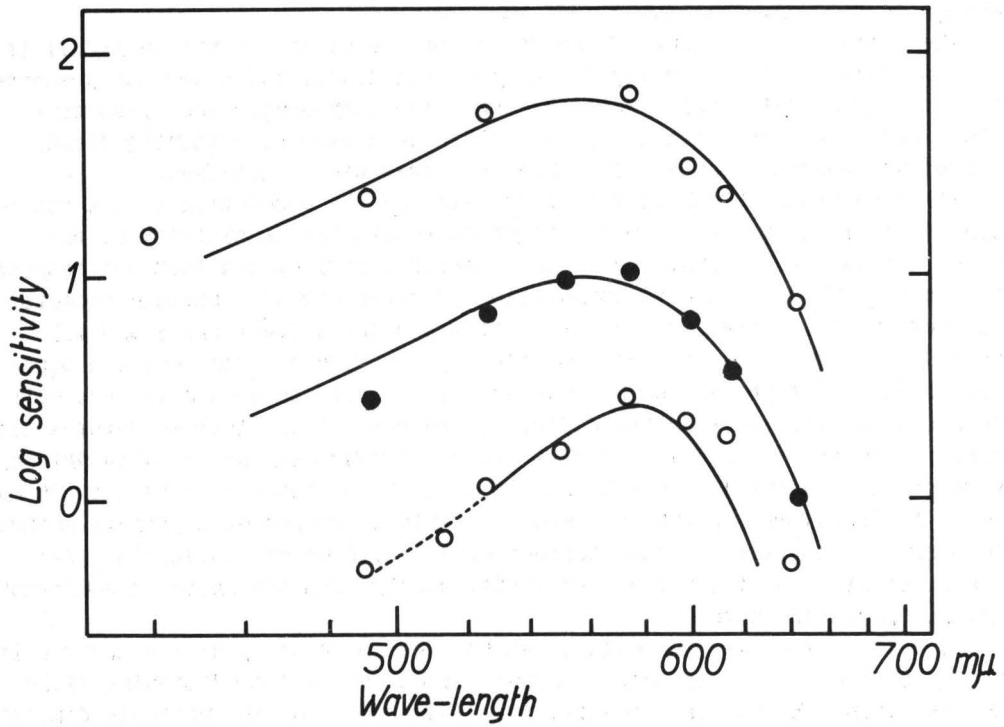


Fig. 12. Frog. Spectral sensitivity measured with blue conditioning field. Explanation in text.

The photopic dominator. Concerning the origin of this type of spectral sensitivity curve there are the following alternative possibilities: (i) the curves recorded represent the properties of a single pigment, not quite identical with those already known; (ii) the photopic dominator is produced by summation or other kinds of interaction of two or more types of cones with different photopigments; and (iii) there is a single type of cone provided with a mixture of two or more pigments giving the dominator sensitivity.

From the experiments on directional sensitivity *(ref. 17)*, it is concluded that the photopic dominator is a pure cone effect. Granit (compare *ref. 27*) found that the 560 mμ photopic dominator curve in many cases has a notch around 570 - 590 mμ and suggested on these grounds that it is a composite curve produced by summation of the modulators. On the other hand there is an approximate agreement with the absorption curve of Wald's iodopsin.

The results on the two-colour threshold technique suggest the presence of two cone effects with different spectral sensitivities, with sensitivity maxima at approximately 550 and 580 mμ. It also seems clear that the

photopic dominator curve depending, for example, on the effect of a coloured conditioning field, is altered. These results suggest that interpretations according to alternatives (ii) or (iii) are more likely to be true, although the main effect may be derived from the 550 mμ component.

In the frog's retina there are found, according to Saxén *(ref. 50)*, one main type of single cone and the double cone. The latter consists of a component similar to the single cone and an accessory component, with a large paraboloid and showing some rodlike features during its development *(ref. 51)*. Such double cones constitute about 10% of the total number of visual cells. The accessory component is geometrically of a shape that would be expected to give a rather low directional sensitivity. On histological grounds an explanation according to alternative (ii) would then seem natural for the frog's retina.

The modulators. Here we are faced with two possibilities: (i) narrow-band visual pigments are directly producing the spectral sensitivity curves; (ii) neural interaction is modifying the response of receptors with broader sensitivity curves.

As pointed out above, there are signs in many of the experiments where modulators have been recorded, of the participation of more than one kind of receptor in the discharge as judged from the irregularities in the shape of the spectral sensitivity curves recorded. Alternatively the modulator curves have been derived by calculation from originally fairly broad sensitivity curves.

What interaction can do is illustrated in *fig. 8*, where the response presumably is determined by cones, giving the photopic dominator response, and the red and green rods. Further information on the transforming effect of the neural layers of the retina on receptor sensitivity is given by experiments where narrow curves with maxima at 500 mμ have been obtained. Granit *(ref. 23)* found a narrow rhodopsin modulator in experiments on the rat retina and similar curves were recorded for some elements in the dark-adapted cat's eye by Donner and Granit *(ref. 13)*. These curves are essentially narrower than the rhodopsin absorption curve for infinite dilution *(fig. 13)*. Donner and Granit also observed that modest light-adaptation in some elements tended to make the curves even narrower. As it is unlikely that such effects are due to a change in the spectral sensitivity of the rods, one is left with the conclusion that the scotopic dominator curve is changed by some neural mechanism into a narrower sensitivity curve.

Donner *(ref. 22)* showed that the modulators in the pigeon's eye were shifted towards the long wave-lengths as compared with the corresponding curves for the frog's eye. This was explained as an effect of selective absorption by the coloured oil droplets in the cones. These droplets absorb in the short wave-lengths and the limits of absorption coincide approximately with the steepest slope of the modulator curves on the short-wave side of the sensitivity maximum. If this explanation is valid, one is forced to accept that the spectral maxima of the modulators approximately

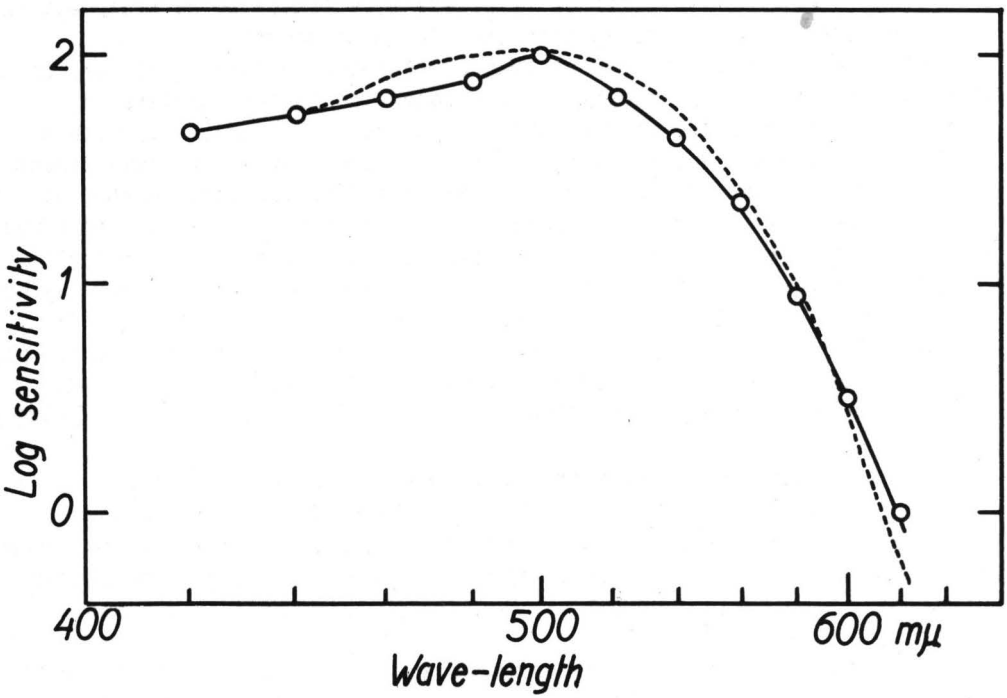


Fig. 13. Cat. Scotopic sensitivity of pure off-element. Dotted line: rhodopsin. *(ref.13)*

coincide with the spectral maxima of receptors responsible for the modulator effects, since if the modulators were produced by such processes of interaction that their spectral location was very much different from the actual receptor maxima, the relation mentioned would hardly have been obtained.

The evidence then suggests that the narrowness of the modulator curves is essentially a result of neural interaction. But the fact that a modulator curve is recorded in some part of the spectrum probably indicates that there is a receptor type, maximally sensitive in that particular region, but having a broader spectral sensitivity curve. Presumably such primary, relatively broad cone sensitivities could either produce a broad photopic dominator response or narrow modulator curves, depending on the type of connexions to the ganglion cell.

REFERENCES

1. GRANIT, R. and SVAETICHIN, G., Principles and technique of the electrophysiological analysis of colour reception with the aid of microelectrodes. *Uppsala LäkFören. Förh.*, 1939, **45**, 161-177.
2. THOMSON, L. C., The localization of function in the rabbit retina. *J.Physiol.*, 1953, **119**, 191-209.
3. KUFFLER, S. W., Neurons in the retina: organization, inhibition and excitation problems. *Cold Spr.Harb.Symp.quant.Biol.*, 1952, **17**, 281-292.
4. KUFFLER, S. W., Discharge patterns and functional organization of mammalian retina. *J.Neurophysiol.*, 1953, **16**, 37-68.
5. RUSHTON, W. A. H., The structure responsible for action potential spikes in the cat's retina. *Nature*, 1949, **164**, 743-744.
6. RUSHTON, W. A. H., Electric records from the vertebrate optic nerve. *Brit.med.Bull.*, 1953, **9**, 68-74.
7. BARLOW, H. B., XVIII International Physiological Congress, Copenhagen, 1950. Abstracts of communications p.88.
8. BARLOW, H. B., Action potentials from the frog's retina. *J.Physiol.*, 1953, **119**, 58-68.
9. GERNANDT, B. E., The form variations of the spike recorded by a microelectrode applied on to the mammalian retina. *Acta physiol.scand.*, 1948, **15**, 88-92.
10. POLYAK, S. L., The retina. Chicago, Univ. Press, 1941, p.607.
11. HARTLINE, H. K., The receptive field of the optic nerve fibers. *Amer.J.Physiol.*, 1940, **130**, 690-699.
12. BARLOW, H. B., Summation and inhibition in the frog's retina. *J.Physiol.*, 1953, **119**, 69-88.
13. DONNER, K. O., and GRANIT, R., Scotopic dominator and state of visual purple in the retina. *Acta physiol.scand.*, 1949, **17**, 161-169.
14. DARTNALL, H. J. A., The interpretation of spectral sensitivity curves. *Brit.med.Bull.*, 1953, **9**, 24-30.
15. GRANIT, R., A relation between rod and cone substances, based on scotopic and photopic spectra of *Cyprinus*, *Tinca*, *Anguilla* and *Testudo*. *Acta physiol.scand.*, 1941, **2**, 334-346.
16. WALD, G. W., The biochemistry of vision. *Annu.Rev.Biochem.*, 1953, **22**, 497-526.
17. DONNER, K. O., and RUSHTON, W. A. H., *J.Physiol.*, 1957, (in the press).
18. DENTON, E. J., and WYLLIE, J. H., Study of the photosensitive pigments in the pink and green rods of the frog. *J.Physiol.*, 1955, **127**, 81-89.
19. HECHT, S., SHLAER, S. and PIRENNE M. H., Energy, quanta and vision. *J.gen.Physiol.*, 1942, **25**, 819-840.
20. ZEWI, M., On the regeneration of visual purple. *Acta Soc.Sci.fenn.*, 1939, N.S.B, 2:4. p.56.

21. GRANIT, R., Spectral properties of the visual receptor elements of the guinea pig. *Acta physiol. scand.*, 1942, **3**, 318-328.
22. DONNER, K. O., The spectral sensitivity of the pigeon's retinal elements. *J. Physiol.*, 1953. **122**, 524-537.
23. GRANIT, R., Isolation of colour-sensitive elements in a mammalian retina. *Acta physiol. scand.*, 1941, **2**, 93-109.
24. DODT, E. and ELENIUS V., Spektrale Sensitivität einzelner Elemente der Kaninchennetzhaut. *Pflüg arch. ges. Physiol.*, 1956, **262**, 301-306.
25. DODT, E., Generalized inhibition of the retinal ganglion cells in relation to wave-length and state of adaptation. *Acta physiol. scand.*, 1956, **36**, 219-228.
26. GRANIT, R., The colour receptors of the mammalian retina. *J. Neurophysiol.*, 1945, **8**, 195-210.
27. GRANIT, R., Sensory mechanisms of the retina. London, Oxford Univ. Press, 1947, p. 412.
28. WALD, G., BROWN, P. K., and SMITH, P. H., Cyanopsin, a new pigment of cone vision. *Science*, 1953, **118**, 505-508.
29. GRANIT, R., The photopic spectrum of the pigeon. *Acta physiol. scand.*, 1942, **4**, 118-124.
30. GRANIT, R., Colour receptors of the frog's retina. *Acta physiol. scand.*, 1942, **3**, 137-151.
31. GRANIT, R., The organization of the vertebrate retinal elements. *Ergebn. Physiol.*, 1950, **46**, 31-70.
32. GRANIT, R., Research on chromatic vision by electrophysiological means. *Coloquio sobre problemas opticos de la vision, Madrid*, 1953, 105-134.
33. GRANIT, R., "Red" and "green" receptors in the retina of Tropidonotus. *Acta physiol. scand.*, 1943, **5**, 108-113.
34. GERNANDT, B. E., Colour sensitivity, contrast and polarity of the retinal elements. *J. Neurophysiol.*, 1947, **10**, 303-308.
35. GRANIT, R., The mammalian colour modulators. *J. Neurophysiol.*, 1948, **11**, 253-260.
36. DONNER, K. O., The spike frequencies of mammalian retinal elements as a function of wave-length of light. *Acta physiol. scand.*, 1950, **21**, Suppl. 72, p. 59.
37. MOTOKAWA, K., IWAMA K. and TUKAHARA S., Colour processes in single retinal elements. *Tohoku J. exp. Med.*, 1951, **53**, 399-416.
38. TUKAHARA, S., Modulators and dominators of the toad's retina. *Tohoku J. exp. Med.*, 1951, **54**, 11-20.
39. KOHLRAUSCH, A., Untersuchungen mit farbigen Schwellenprüflichter über den Dunkeladaptationsverlauf des normalen Auges. *Pflüg. Arch. ges. Physiol.*, 1922, **196**, 113-117.
40. STILES, W. S. and CRAWFORD, B. H., *Proc. roy. Soc. B.*, 1933, **112**, 428.

41. CRAWFORD, B. H. The luminous efficiency of light entering the eye pupil at different points and its relation to brightness threshold measurements. *Proc.Roy.Soc.B.*, 1937, **124**, 81-96.
42. STILES, W. S., The directional sensitivity of the retina. *Sci.Progr.*, 1939, **33**, 676-689.
43. FLAMMANT, F. and STILES, W. S., The directional and spectral sensitivities of the retinal rods to adapting fields of different wave-lengths. *J.Physiol.*, 1948, **107**, 187-202.
44. DONNER, K. O. and RUSHTON, W. A. H., *J.Physiol.*, 1956, **132**, 37P.
45. GRANIT, R. and MUNSTERHJELM, A., The electrical responses of dark-adapted frog's eyes to monochromatic stimuli. *J.Physiol.*, 1937, **88**, 436-458.
46. STILES, W. S., Investigations of the scotopic and trichromatic mechanisms of vision by the two-colour threshold technique. *Rev.Opt. (theor. instrum)*, 1949, **28**, 215-237.
47. STILES, W. S., Visual properties studied by subjective measurements on the colour-adapted eye. *Brit.med.Bull.*, 1953, **9**, 41-49.
48. STILES, W. S., Further studies of visual mechanisms by the two-colour threshold technique. *Coloquio sobre problemas opticos de la vision.* Madrid, 1953, 65-103.
49. DONNER, K. O., Unpublished observations, 1957.
50. SAXÉN, L., The development of the visual cells. *Ann.Acad.Sci.fenn., Ser.A.IV Biologica*, 1954, **23**, 1-95.
51. SAXÉN, L., The initial formation and subsequent development of the double visual cells in amphibia. *J.Embryol.Exp.Morphol.*, 1956, **4**, 57-65.
52. GRANIT, R., The spectral properties of the visual receptors of the cat. *Acta physiol.scand.*, 1943, **5**, 219-229.

THE review paper (20) was presented by DR. K. O. DONNER.

DR. R. A. WEALE said there was a discrepancy between the concentration of visual purple found by Denton and Wyllie *in situ* in the frog retina and the width of the sensitivity curve of the frog as measured electrophysiologically. The curve was too narrow. Donner and Rushton's results suggested that the frogs in the earlier electrophysiological experiments were not sufficiently dark-adapted. There was a possibility that not all the visual purple was physiologically active but Donner and Rushton's results had made this less likely.

DR. MARGARET LENNOX asked what kind of units Donner used in his experiments. Were they on-elements or off-elements, or what on/off ratio did they have? In the cat, recording from the higher centres, there was no evidence that colour was determined by excitation and inhibition. On the other hand there was evidence for a temporal factor.

DR. H. REMBERG noted that Dr. Donner had mentioned the experiments of Granit on the fully dark-adapted cat's retina (first published 1945; *fig. 6* of Paper 20). These experimental data by no means proved the existence of narrow-banded colour receptors, as would be seen from the argument which followed. In these experiments the fully dark-adapted retina of the cat was illuminated with nearly spectral red, green and blue adapting-lights. The effect of that illumination on a receptor unit which contained rods and cones simultaneously had to be a Purkinje shift of the sensitivity curve towards the red end of the spectrum, and in such a way that the extent of the shift was smallest for the red adapting-light, greater for the green and greatest for the blue adapting-light. If the differences of the ordinates of the unshifted and the shifted (post-adaptation) sensitivity curves were regarded as proportional to modulator sensitivity (as Granit assumed) one obtained narrow-banded curves with maxima in different parts of the spectrum as he (Dr. Remberg) had pointed out in 1953 in *Pflügers Archiv.*

DR. H. B. BARLOW asked about Dr. Donner's measurements by the two-colour threshold method. Was he using short and small or long and large stimuli? In the explanation of modulator curves, there was a third possibility, in addition to those already mentioned. In retinas where lateral movements of the receptors could occur (amphibians particularly), there might be a shielding of receptors by other receptors containing the same or different pigments. That would be a photic interaction not simply a neural one. Donner and Rushton's curves on the effect of obliquity of the light seemed to show that the magnitude of the effect was the same except when the curve changed from one receptor response to another. If that were so it would be important in the Stiles-Crawford effect in the human eye.

DR. W. S. STILES asked Dr. Donner if there was a possibility of applying the two-colour threshold method to animals possessing a rod-free fovea. In the human eye it was the blue cone mechanism which was easiest to distinguish from other cone mechanisms by that method, but it was almost essential to work at the fovea to avoid the masking effect of rod response. On the wavelength dependence of directional sensitivity mentioned by Dr. Barlow, the evidence for the human eye was that different cone types gave effects of different magnitude, but, in addition, the effect for each type did vary with wavelength.

Replying to the discussion, DR. DONNER said, as regards the elements studied, that they were all on-off ones and the more sensitive component (usually the on-effect) was used as the index. To Dr. Barlow, he would reply that for the threshold-intensity curves the circular adapting field was 2mm in diameter with a central test spot of 0.2mm diameter. The duration of the stimulus was one second. Shielding effects were quite possible since the retina was slightly deformed by the pressure exerted on its surface by the electrode.

PROFESSOR GRANIT quoted Ingvar's unpublished work on the measurement of spectral sensitivity in the optic cortex of the cat. The sensitivity curves obtained (potential developed plotted against stimulus energy) differed from the dominator curves obtained from the eye. The main variation was a large narrow hump in the blue. These observations were made on the "cerveau isolé" of Bremer and the blue hump was destroyed by anaesthesia.

SESSION VI

COLOUR THEORIES

Chairman: DR. W. S. STILES, N.P.L.

PAPER 21

COLOUR THEORIES AND THEIR IMPLICATIONS IN COLOUR VISION

By Y. LE GRAND

Professor Yves Le Grand, born in Paris in 1908, engineer from Polytechnic School (1926-1928), assistant in physics of the late Prof. Charles Fabry and of the late Prof. Jean Becquerel, Professor in the Muséum d'Histoire Naturelle (Paris) since 1949 and Director of the Laboratory of Applied Physics in this Institute; the specialities of this laboratory are Optics of vision and Optics of natural media (air and sea). Honorary Secretary of the International Commission on Illumination (C.I.E.) since 1955.

21. COLOUR THEORIES AND THEIR IMPLICATIONS IN COLOUR VISION

By Y. LE GRAND

SUMMARY

THE general features of colour theories are reviewed and the most probable mechanisms discussed at the three main levels (retina, transmission line, cortex).

COLOUR THEORIES AND THEIR IMPLICATIONS IN COLOUR VISION

IN every theory of colour vision, it is necessary to postulate at least three successive mechanisms:

(1) a peripheral "colour unit", that is the smallest retinal area the stimulation of which gives a fully developed colour sensation;

(2) a transmission line, with possibilities of amplification and modifications of the signal;

(3) a cortical "colour receptor", the spatial character of colour necessitating at least as many receptors as there are peripheral units.

In addition, there are certainly co-operation phenomena, either positive (facilitation) or negative (inhibition); although they are of great importance in colour perception, we shall neglect them for the sake of simplicity.

COLOUR UNIT

FROM Aubert onwards it has been known that a very small coloured object on a neutral background of the same luminance appears colourless (it is not true for point sources in the dark, owing to aberrations and scattering). This fact suggests that a colour unit must contain a rather large number of cones, some of them presenting individual differences as regards spectral sensitivity.

These differences may be due to various photosensitive pigments, or to physical filters with one single pigment (coloured oil droplets like those of birds and tortoises, or laminated structure of the outer limb producing interference phenomena); the first hypothesis seems most probable and explains the approximate invariance of colour sensation when light strikes

the retina at various obliquities, for example by transcleral illumination or after diffusion by the blind spot.

As to the number of different types of cones, it is at least three for normal subjects (experimental trivariance of vision) but any number n is mathematically possible if we suppose $n - 3$ additional relations between the n responses. However, the stability of colour matches over a fairly large range of illumination values and of adaptation conditions supposes that linear laws (such as Grassman's and von Kries') are, at least approximately, valid for the 3 independent responses. It is easy to understand why a linear law governs the initial action of light on photosensitive substances, but linearity is lost as soon as a nervous message is sent from the cone to the bipolar cell; it then seems necessary to suppose that the $n - 3$ relations are of a physical and not a physiological kind; the only way of obtaining such relations by physics seems the mixture of 3 different photosensitive pigments into each cone: if the maximum absorption of each pigment remains low, the relations are very nearly linear.

It is easy to understand why all the experimental laws of colorimetry result immediately from the existence of three pigments, whatever is the mixture made with them: equivalent stimuli are such that the three initial photochemical actions are identical, and anything which occurs afterwards cannot alter this identity. As all colorimetry is founded upon equivalent stimuli and not upon colour sensations, it is unaffected by any mixture of the pigments or by nervous phenomena. This distinction has been frequently ignored; in particular it was missed by Helmholtz who thought that the transmission of the three elementary responses of Young's theory to the brain ought to be free from any interference.

We see that trivariance of vision may coexist with the presence in the retina of any number n of different kinds of cones. In particular n may be infinite (more exactly equal to the total number of cones in the retina) if mixing of the three pigments is made at random between the cones; the colour unit will then contain a majority of cones in which the three pigments are mixed approximately in equal concentrations; their spectral response will be roughly the photopic luminous efficiency curve (Granit's "dominators"); a small number of cones would contain a relatively high concentration of one or two of the pigments ("modulators") and, although the spectral sensitivity of such elements varies continuously, in a first approximation it would be possible to classify them into 6 groups.

TRANSMISSION LINE

IT is known that the passage of a stimulus along a fibre of any sensory nerve is associated with a series of spike potentials, all of the same amplitude, only their frequency varying with the intensity of the stimulus.

This fact is hard to fit into any schema of opponent-colour theories such as Hering's, and the only physiological basis for two retinal mechanisms in opposition might be looked for in the duality of the 'on' and 'off' responses that certain modern researches in electrophysiology ascribe to a single retinal receptor.

The main question that is still open about the visual transmission line is the following: is there any peculiarity of a fibre in the optic nerve that might indicate that this fibre transmits the response from one type of modulator rather than from another? Erlanger thought that it might be the diameter of the nerve fibre, the red modulators making use of the thickest fibres (this would also explain the smaller latent period of the red sensation, as found by Piéron). Troland suggested that the spike potentials may succeed with a rhythm peculiar to each type of receptor. Other suggestions have been made, but none settled by experiment.

If there were such a "colour characteristic" of a nervous fibre or of its response, it would moreover be necessary to explain how it may be elicited merely by the fact that a given cone contains more of a given pigment. For example, Polyak suggests that the photochemical decomposition of the pigments produces different changes in the cone, these being accepted electively by the different bipolars.

I am not sure that it is necessary to postulate anything about the nervous fibre of the transmission line. This problem bears some analogy with the famous problem of the "corresponding points" in the retinae. The old concept of a "local sign" transmitted to the cortex has been abandoned; experiment shows that there exists an innate geometrical correspondence between a given point on the retina and some neurons of the "cortical retina", the corresponding projection area in the brain; in addition, there are slight physiological and perhaps anatomical adjustments that allow the extraordinary precision of binocular vision; these adjustments are made during the development of space perception in the young child, as studied in particular by Piaget. It is now generally agreed that location in space with all its complexity may be achieved by these rather simple means. Why should not location in "colour space" follow the same lines? We will now examine this last point.

COLOUR RECEPTOR

EXPERIMENTAL evidence about colour phenomena in the cortex (electrical records) has until now been rather poor, and we are reduced to hypotheses. If it seems necessary to put colorimetry at the very beginning of the visual chain, in the cones themselves, it remains uncertain how to interpret the psychological laws of colour vision, i.e. for monochromatic radiations: the apparently simple character of certain radiations, their varied saturation

and the Bezold-Brücke effect; for complex radiations: the neutralization, partial or complete, of the attribute of colour, variations of hue and the effects of adaptation. As the retina is a peripheral part of the brain, and a very complicated one, it would be equally plausible to locate either in the cortex or in the retina some of the interactions that are the physiological basis of these psychological laws; the only difference would be that the activity of the optic nerve may or may not reflect something of the trivariant nature of the first luminous reaction.

In the correspondence between any retinal colour unit and its associate cortical receptor, spatial discrimination is achieved by luminance differences much more than by colour phenomena, as has been demonstrated by experiments undertaken for colour television; so it is unnecessary to postulate that the response of a single cone specially sensitive to long wave-lengths (for example) would by itself be sufficient to arouse the sensation of red; it is much simpler to suppose that colour sensation is a differential effect due to the cortical synthesis of messages coming from all the cones of the colour unit. The objection that red seems a simple and direct sensation and not a complex perception is of no value: depth also is an intuitive and familiar notion, "a specific experiential response - a sensation - directly arising from physiologic stimuli "(Ogle), and yet we know that it involves the differences of the two retinal images. In modern psychology, the old distinction between sensations and perceptions has quite faded away. All laws of "colour constancy" show that the naive colour sensation is actually a complex phenomenon and it seems reasonable to explain the psychology of colour vision by integration of all responses coming from the colour unit (and from the others also to a smaller extent).

There still remains a difficulty which we have already met: if there is no "frequency code" nor other means of giving a colour specification to each nervous message, apart from its retinal origin from a given modulator, how can "red" sensation correspond to some of these messages and not to others? Amongst the ways of solving this problem, the most biological is perhaps to think in terms of embryogeny: even if the visual system of a newborn child were definitively settled (which is not the case), we must remember that it is only the end of a long development in which heredity plays an important role (colour anomalies). Let us suppose, for example, that at a certain stage of foetal development all nervous cells are in place, from the cones to the last neurons of the visual chain, but that there is still no photopigment in the retina. Then a first pigment begins to appear, and is fixed at random, some of the cones being rich and others poor, perhaps because of slight anatomical differences. We know from electrophysiology that, even in total darkness, there is a spontaneous activity all along the transmission line. It is plausible to imagine that the presence of a large amount of pigment in some cones gives to them the possibility of sending to the cortex nervous information and, in this very

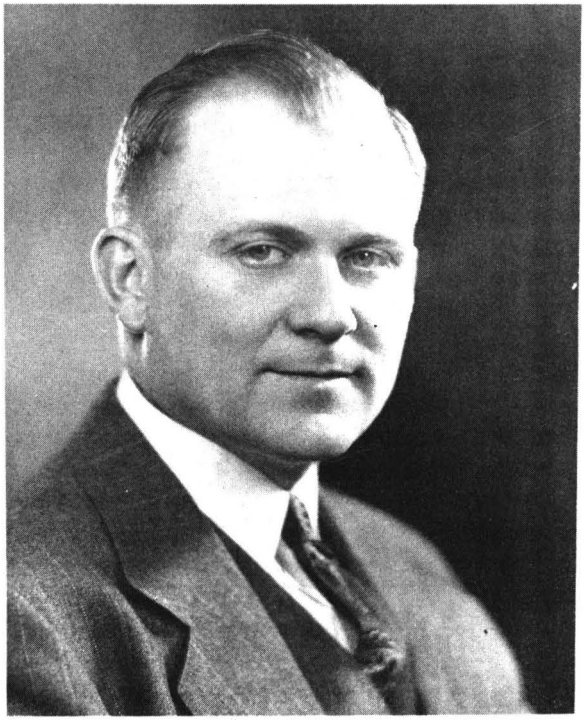
labile state of the brain, these messages may build the necessary synapses between the terminal neurons and the "red" centre, for example, Possibly also, some of these building processes might continue after birth, and psychologists agree generally that red is the only colour that the newborn baby seems to perceive.

I give this schema only as one among many possibilities, but it involves facts that are not biologically absurd, because we know that mechanisms of the same kind exist in vision for the stereoscopic sense. Although colour vision is a very old field of work, it is still a mystery and undoubtedly this helps to increase our interest in the problem.

PAPER 25

BEAT-FREQUENCY HYPOTHESIS OF COLOUR PERCEPTION

By D. L. MACADAM



David Lewis MacAdam

Born in Philadelphia, Pennsylvania, July 1, 1910. Awarded B. S. in Engineering Physics at the Lehigh University, 1932; Ph. D. in Physics at Massachusetts Institute of Technology, 1936. Employed in Research Laboratories, Eastman Kodak Company, Rochester, New York, continuously since 1936. Research on colour measurement and applications: colour photography, colour television, packaging, and whiteness. Research in colour vision: discrimination, adaptation, relations between colour specification and perceptions, brightness versus luminance, and dependence of visual acuity on colour contrast. Co-author of "Handbook of Colorimetry," and "Science of Color." Member and contributor to Journals of Optical Society of America, and Society of Motion Picture and Television Engineers.

25. BEAT-FREQUENCY HYPOTHESIS OF COLOUR PERCEPTION

By D. L. MACADAM

SUMMARY

PRODUCTION of beat frequencies, accompanying combinations of trains of visual nerve impulses that originate in a "trichromatic" retina, is suggested as a possible origin of the phenomena invoked by the "opponent-colours" theory and by the second stage of the Müller zone theory of colour vision. The present hypothesis offers unified explanations for diverse and apparently conflicting phenomena, such as: persistence of metameric colour matches, chromatic adaptation, colour discrimination, the Bézold-Brücke effect, the Abney effect, and the failure of the Abney "law" of additivity of heterochromatic brightnesses.

BEAT-FREQUENCY HYPOTHESIS OF COLOUR PERCEPTION

THE following hypothesis of visual response combination is based on the premise that nerve impulses are essentially as described by Hartline — trains of pulses of constant amplitude *(ref. 1)*. In some cases, their frequency increases rapidly to a constant value that is maintained throughout the period of constant stimulation. This constant frequency is related, approximately logarithmically, to the intensity of the stimulus. At the end of stimulation, the frequency decreases rapidly, but not abruptly, to zero. In other cases, a brief burst of pulses occurs at the beginning of stimulation, followed by inactivity, despite continuance of the stimulus, until the end of stimulation, which is followed by another brief burst of pulses. In these cases, even slight changes in stimulation cause bursts — the greater the change, the more numerous the pulses in the burst. In other cases, no pulses are recorded at the beginning, or while the stimulus continues unchanged, but a brief burst of pulses occurs only at the end of stimulation.

The essence of the present hypothesis is that, when two simultaneous series of pulses are combined, their beat frequency plays an important role in perception. According to this hypothesis, the initial result of photostimulation is of Hartline's first type — constant frequency (after a brief build-up) — continuing so long as the stimulus continues at constant intensity. According to the hypothesis, the second type of response — "on-off" — is the beat frequency between two identical trains of pulses, originating in the same photosensitive cell but transmitted

along two different paths which differ slightly in transmission time. Or, some combination of synapses may (1) regenerate the incoming train of pulses with time delay, (2) combine the regenerated train with the incoming train, and (3) relay the beat frequency to subsequent stages of the visual nervous system. The process might be described as 100% negative feedback. The intricacy of synaptic arrangement (Polyak *(ref. 2)*) suggests ample possibilities for such functioning. As Hartline wrote, "the importance of this type of response is obvious."

The third type of response described by Hartline would result if the incoming signal inhibited the relaying synapse. After the incoming signal ceased, the lagging end of the regenerated signal would be transmitted. Hartline mentioned that this "off" burst can be cut short by quickly resuming the stimulation, which, according to the hypothesis, would renew the inhibition.

Since the pulses are not even approximately sinusoidal, the concept of "beats" is not strictly appropriate. The same effect, so far as this discussion is concerned, would be produced if each pulse from either train inhibits a synapse in such a manner that the inhibiting pulse and also the next succeeding pulse of the other train are both blocked, and if a second and all succeeding pulses of either train are transmitted, so long as no pulse of the other train intervenes. The "off" type of response described by Hartline would result if the pulses of only the earliest train could initiate this inhibiting effect. The "off" burst would then consist of the second and all succeeding pulses of the delayed train, after any one of the decreasingly frequent inhibiting pulses, and, finally, all the delayed pulses after the one immediately following the last inhibiting pulse. An "on" effect, sometimes reported, in which a brief burst accompanies the beginning of stimulation, but in which there are no pulses during or at the cessation of stimulation, would be produced if only the delayed (or regenerated, or "feedback") train of pulses had the inhibiting effect. Although "difference-frequency" would, strictly speaking, be more appropriate with reference to such inhibition of pulses, the term "beat" seems more descriptive and will be used.

Beat frequencies resulting from the combination of the steady type of response of neighbouring receptors would be concentrated along contours of spatial variation of stimulation. This would have the effect of increasing the noticeability of slightly different neighbouring luminances. Similar functions have been proposed and used to some extent in television systems, where the effect is called "crispening" *(refs. 3, 4)*. However, some experiments indicate that the noticeability of slight luminance differences may be largely dependent upon eye and head movements. When the retinal image is stabilized by optical compensation for such movements, then, after the initial few seconds of observation, no steady pattern can be seen *(refs. 5, 6)*. This suggests that beat frequencies between trains of pulses

from neighbouring visual receptors play no role in visual-form-perception. But the possibility may be mentioned and the question kept open until further research finally establishes for vision the absolute necessity of retinal image motion.

The most interesting possibilities of the beat-frequency hypothesis relate to colour vision. Regardless of how they originate, at least three spectrally differentiated responses from each elementary area of the retina are necessary to account for normal colour vision. If "steady" trains of pulses, whose frequencies are roughly logarithmically related to the "red" and "green" stimulations, are combined, their beat frequency would be an indication of the "redness" or "greenness" of the sensation. Consequently, if that beat frequency is low in comparison with the separate "red" and "green" frequencies, and if the "blue" frequency is also low, the perception should be of "yellow". High beat frequencies would indicate greenness or redness, more or less free of yellowness. Which of the two opposed hues would be perceived would depend upon which of the two frequencies was high and which was low.

It may be that beat frequencies are produced in the retina, or they may be produced only as part of the functioning of the central nervous system. In any case, the "inhibition", or any other process that produces such beats, need not preclude transmission of the original "steady" trains also, along separate channels, to the perceiving centres. Nor need separate beat frequencies be produced for each elementary area of the retina, since colour discrimination in fine-grained patterns is very poor *(ref. 7)*, and chromatic differences, in the absence of luminance differences, provide very low spatial acuity *(ref. 8)*.

According to the present hypothesis, the sum of combined frequencies plays no role in visual perception. On the basis that the frequencies are approximately proportional to the logarithms of the stimulations, such a sum of frequencies would violate the Abney law of additivity of brightnesses in the sense opposite to the discrepancies from that law which are actually found *(refs. 9, 10)*. On the other hand, according to Willmer *(ref. 11)*, "there is evidence obtained from recording the ganglion cells in the frog that stimuli given to different parts of the receptive field of a ganglion cell can sum together on a linear or almost linear basis" *(refs. 12, 13)*. He suggests that "it is simpler to imagine that the polysynaptic bipolar cells collect their information on a strictly additive basis." According to this conception, the additive combination of the red and green stimulations would subsequently produce a frequency of pulses approximately logarithmically dependent upon the sum of the red and green stimulations. Slight departures from strict additivity could account for the observed discrepancies from the Abney brightness-additivity law.

In the case of yellow, just discussed, this frequency would have to be high compared with the "blue" frequency. When these two frequencies are,

in turn, combined, their beat frequency would be an indication of the "yellowness" or "blueness" of the sensation. A low beat frequency, if associated with low "red-*versus*-green" beat frequency, might correspond to white or gray. If associated with high "green" frequency, such low "yellow-*versus*-blue" beat frequency would correspond to a sensation of "non-yellowish" green, or cyan. If associated with high "red" frequency, low "yellow-*versus*-blue" beat frequency would correspond to a "non-yellowish" red sensation, or magenta. High "yellow-*versus*-blue" beat frequency, associated with low "red-*versus*-green" beat frequency would indicate either yellowness or blueness. Which hue of the two would be perceived would depend upon which of the two interfering frequencies was high and which was low.

It may be noted, that, if the original frequencies were strictly proportional to the logarithms of the stimulations, even if only within a restricted range of stimulations, then the two beat frequencies would be constant for any one chromaticity, regardless of its intensity, within the aforesaid range. Departures from a strictly logarithmic relation would result in a dependence of the beat frequencies on intensity for any one chromaticity and presumably in variations of the chromatic attributes of the resulting sensation--the Bézold-Brücke phenomenon. Departures from a strictly logarithmic relation between frequency and stimulation would also account for the curvatures of most loci of constant hue (Abney effect). Those well-established loci may provide the most useful data for determining these relationships and other parameters in a quantitative formulation of the present hypothesis.

If, for any reason, neighbouring receptor cells have slightly different spectral sensitivities, and if their responses are combined, then the beat frequency produced would have a spectral dependence proportional to the difference of the log spectral sensitivity curves of the neighbouring cells. If those spectral sensitivities were nearly alike, the spectral dependence of the recorded beat frequency would be quite narrow, resembling the spectral sensitivities of the "modulators" recorded by Granit *(ref. 14)*. Chromatic adaptation data, which indicated a fourth *(ref. 15)*, a fifth, and even a sixth receptor *(ref. 16)*, with spectral sensitivities not linearly related to the three required for a "trichromatic" retina, may also be accounted for in the same manner. Such an explanation would eliminate the apparent conflict *(ref. 16)* between the results of studies of corresponding colours for different chromatic adaptations and the persistence of metameric colour matches for a wide variety of chromatic adaptations.

Modes of functioning essentially like that postulated could arise from many conceivable arrangements and behaviour of nerves and synapses. The complex phenomena of consciousness and mental life must result from

unbelievably intricate arrangements and functioning in the central nervous system, whereof the postulated manner of combination of visual nerve pulses would be a potent and not excessively fantastic representative. The present hypothesis, however, does not assert that such *is* the manner of combination of visual nerve pulses. The present suggestion is merely that this hypothesis seems to unify many previously incoherent facts about vision in general, and colour vision in particular. This hypothesis seems to simplify thought and suggests unified explanations for previously unassimilable data, such as those of metameric colour matching, chromatic adaptation, colour discrimination, the Bézold-Brücke effect, the Abney effect, and the failure of the Abney "law" of additivity of heterochromatic brightnesses.

This hypothesis shares many features with previous theories. It suggests a mechanism to account for functioning such as is described by the Müller zone theory of colour vision *(ref. 17)*. Like the Müller theory, the present hypothesis attributes to the initial, photosensitive stages of colour vision a structure and function resembling those postulated by the Young-Helmholtz trichromatic theory and, to the later sensory or interpretive stages, functions similar to those postulated by Hering's opponent-colours theory *(ref. 18)*. The "red-*versus*-green" beat frequency is analogous to the chromatic value $(V_X - V_Y)$ employed by E. Q. Adams *(ref. 19)*, who used the Munsell value function in the role assigned by this hypothesis to the relation between pulse frequency and photoreceptor stimulation. Similar nonlinear functions were invoked by Stiles *(ref. 20)* and by LeGrand *(ref. 21)* in their attempts to account for colour discrimination. Such convergence of the best thoughts of many workers towards a unity suggested by a single, relatively simple hypothesis may indicate that we are approaching a basic understanding of the processes responsible for the diverse phenomena of colour vision.

MUCH of the material in my preceding paper, which seemed sensible when submitted, now seems unacceptable.

However, even after it became apparent that the beat-frequency hypothesis is untenable, I applied ideas suggested by it to several previously baffling problems of colour. In the first place, I attempted to account for the curvatures of constant-hue loci in the chromaticity diagram, such as those published by the Optical Society Sub-committee on the spacing of the Munsell colours *(ref. 22)*. Second, I attempted to account for the shapes and variations with lightness of the Munsell constant-chroma loci. Finally, I tried to account, in a manner which I think should be more acceptable to Dr. Hunt *(ref. 23)* than my original attempt, for the systematic discrepancies of results of chromatic adaptation experiments *(ref. 24)* from predictions based on the von Kries coefficient law.

These attempts were surprisingly successful, especially in view of the unacceptability, on neurophysiological grounds, of the hypothesis which suggested the successful analysis.

Fig. 1 shows constant-hue loci computed by a straightforward and relatively simple mathematical embodiment of the beat-frequency hypothesis. These loci are remarkably similar, not only in shape, but also in separation, and in variation with lightness, to the subjectively determined constant-hue loci of the Munsell system *(ref. 22)*. *Fig. 2* shows constant-saturation loci computed on the same basis. Again, the shapes, separations, and variations with lightness are quite similar to the Munsell constant-chroma loci. *Fig. 3* shows chromaticities of the discrepancies of corresponding colours for adaptations to tungsten and daylight, as predicted by the beat-frequency hypothesis, from those predicted by the von Kries coefficient law. These lie close to a straight line, in a manner very similar to the discrepancy chromaticities found experimentally.

Finally, *fig. 4* shows chromaticity-discrimination ellipses computed on the same basis.

Now, having perhaps piqued your curiosity, I should outline briefly the specific manner in which I employed the beat-frequency hypothesis to get these results. Then I shall tell you why I consider the beat-frequency hypothesis untenable and which features of it must be shared by any hypothesis that purports to inherit its good fortune. Finally, I shall call attention to experiments which seem to provide physiological basis for such a hypothesis.

I assumed that there are three independent retinal responses to colours, equivalent to the three primaries shown in *fig. 5*. The "red" primary is the same as that which Judd determined as the common intersection of confusion loci for protanopes *(ref. 25)*. The "blue" primary is that which Judd suggested as the common intersection of confusion loci for tritanopes. The

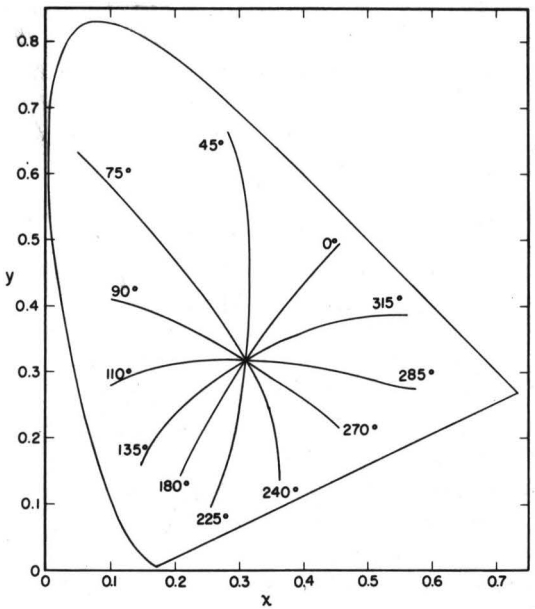


Fig. 1. Constant-hue loci.

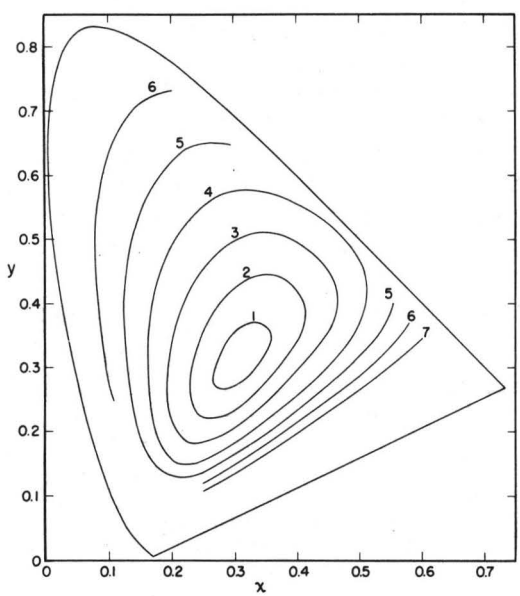


Fig. 2. Constant-saturation loci.

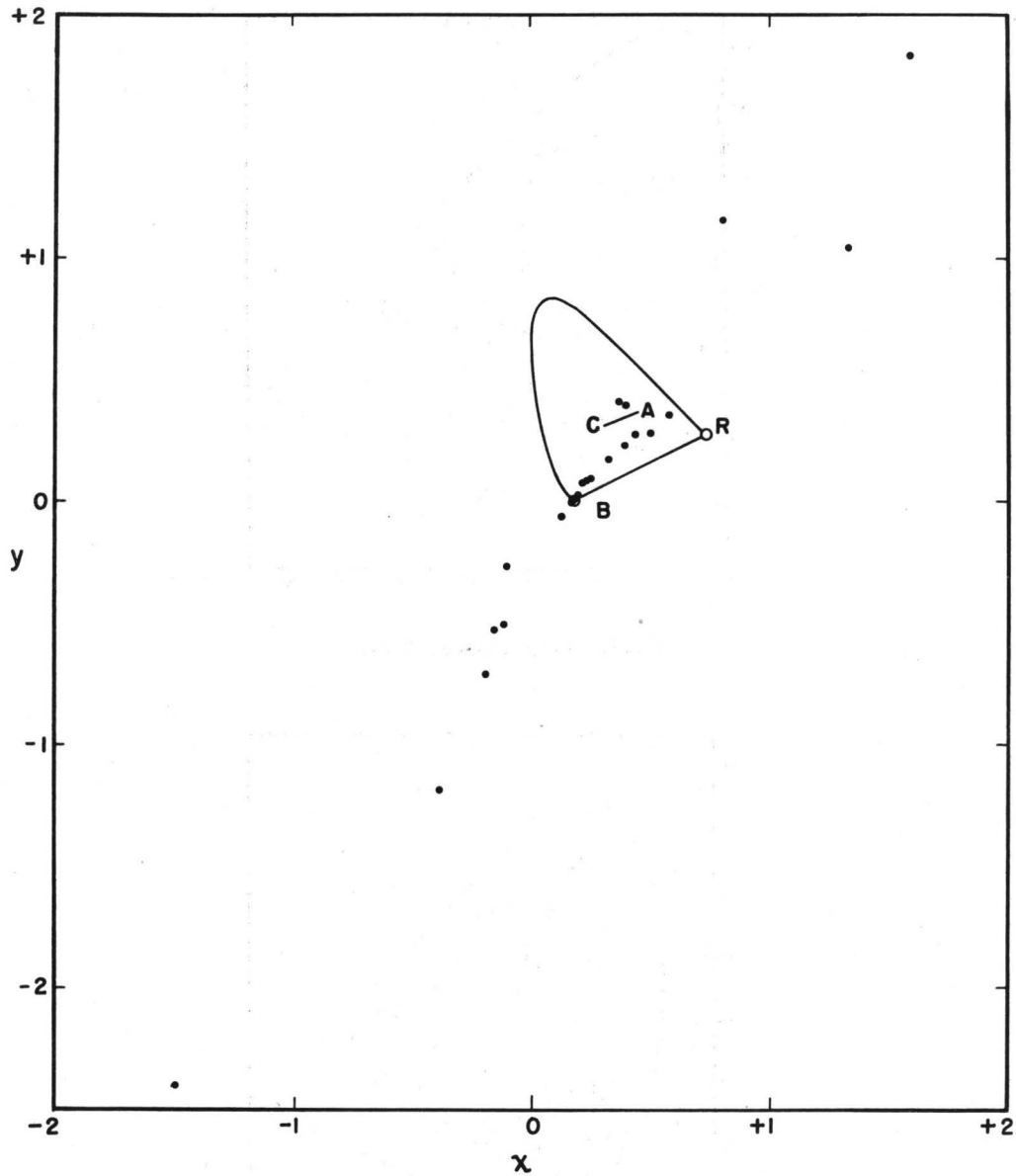


Fig.3. Discrepancies of von Kries predictions from corresponding colours according to hypothesis.

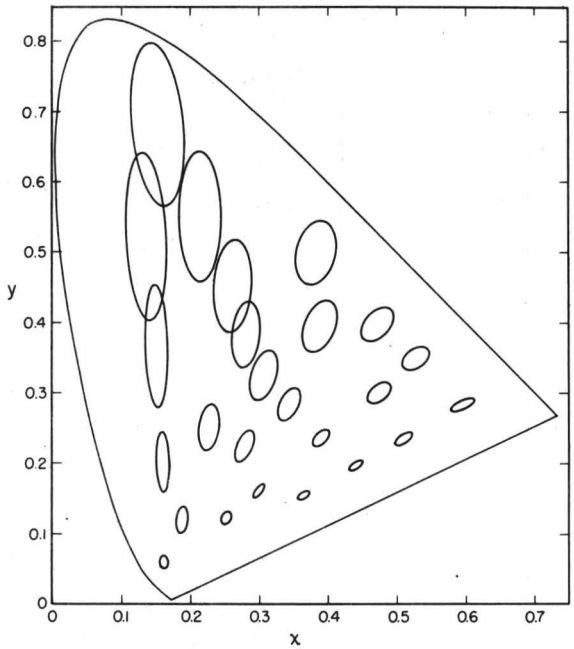


Fig. 4. Chromaticity discrimination ellipses.

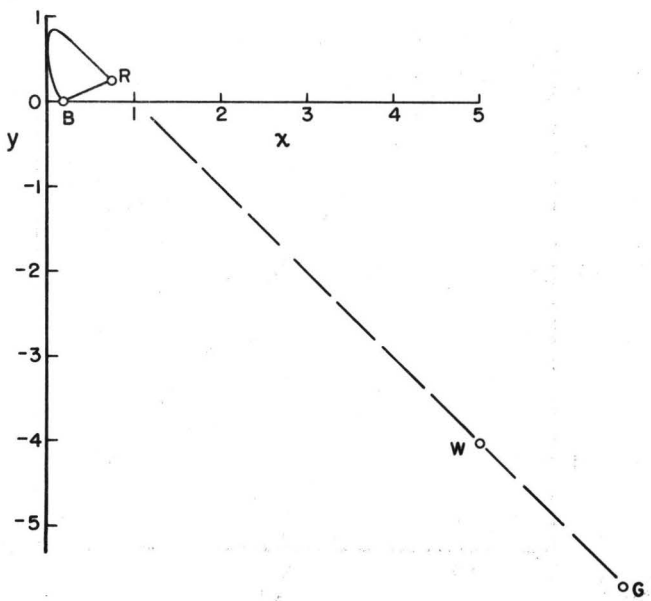


Fig. 5. Primaries assumed, shown in C.I.E. diagram.

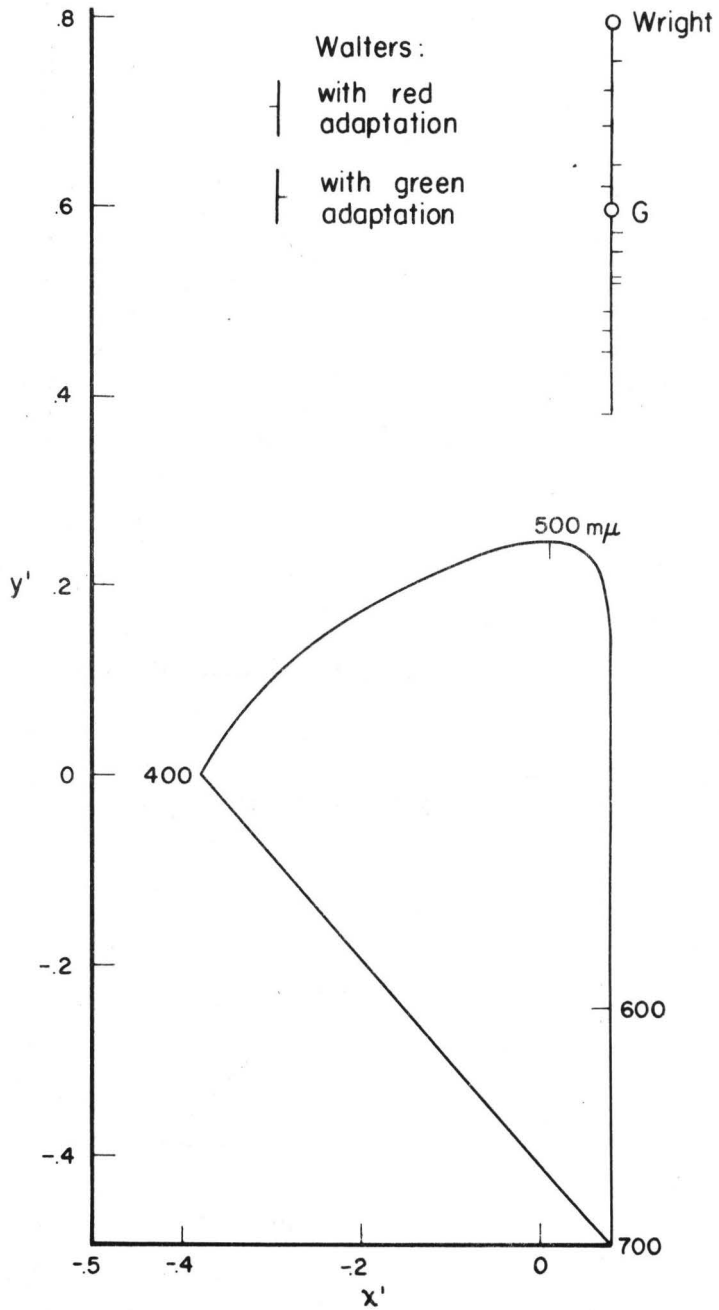


Fig.6. Primaries assumed, shown on Breckenridge and Schaub diagram.

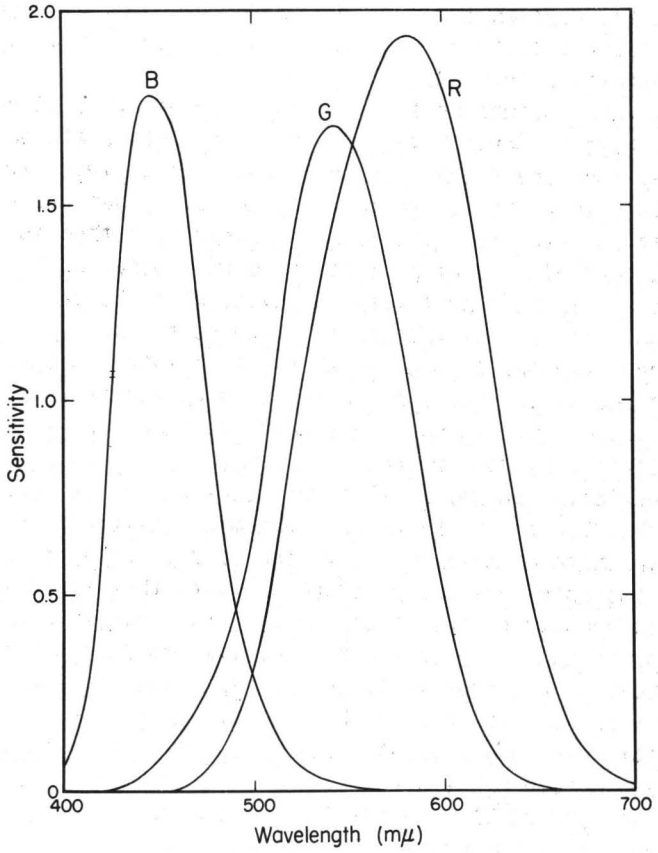


Fig.7. Spectral sensitivities assumed.

"green" primary is rather far from the point (at 1.0 on the x-axis) which Judd suggested as the common intersection of confusion loci for deuteranopes. Those loci are nearly parallel, and admittedly they do not clearly indicate any common intersection. The "green" primary I have adopted agrees rather well with those which Walters *(ref. 26)* and Wright *(ref. 27)* deduced from adaptation experiments. This resemblance is not apparent on examination of Wright's publication, because he used a different projection of the chromaticity diagram. But when the suitable transformation is applied to locate Wright's "green" primary on the customary C.I.E. diagram, it is found to be at the point W shown in *fig. 5*, in comparison with the "green" primary I assumed. The unconventional locations, and the differences among these suggested green primaries are, perhaps, exaggerated by the C.I.E. diagram. The locations and separation between Wright's primary and mine are possibly

shown better on the Breckenridge and Schaub diagram, which Wright used *(fig. 6)*. The earlier results of Walters are also shown, in excellent agreement with the primary I assumed.

As a set, my three primaries imply spectral sensitivity curves, *fig. 7*, consistent with Ségal's three-layer hypothesis of colour vision *(ref. 28)*. Ségal postulates that the "red" receptors, which he believes are buried in the pigment epithelium, are, by themselves, uniformly sensitive throughout the visible spectrum, but that the light incident upon them is filtered by the overlying layers of macular pigment, rods and cones, so that they have, in effect, practically no sensitivity to wavelengths shorter than about 520 mμ. Ségal postulates that the cones, which he thinks are only the "green" receptors, are sensitized by relatively dilute rhodopsin, which does not absorb and which therefore cannot produce sensitivity, for wavelengths longer than about 650 mμ. Ségal suggests that the light reaching the cones is filtered by rather dense yellow materials, including macular pigment and transitory orange, so that the cones cannot be appreciably stimulated by blue light, but have their maximum sensitivity shifted from 505 mμ, the wavelength of maximum absorption of rhodopsin, to about 555 mμ, the maximum of photopic luminosity. Ségal suggests that the "blue" receptors are the synaptic boutons of the cones, which extrafoveally constitute a sharply defined, compact, single layer about 1/10 mm in front of the layer of rods and cones. He believes that, in the light-adapted eye, they are sensitized (by transient orange) to the very low degree that any nerve tissue is sensitized by any light-absorbing constituent. Transient orange does not strongly absorb wavelengths longer than about 500 mμ, and therefore it can produce no appreciable sensitivity for longer wavelengths.

I have worked with tristimulus values based on these spectral sensitivities, or, in other words, based on the set of primaries shown in *fig. 5*. I have, furthermore, assumed that, very early in the visual process, the independent colour stimulations of three such classes of receptors are converted to signals whose intensities are related to the corresponding tristimulus values in an only quasi-logarithmic manner. If this dependence were truly logarithmic the resulting loci of constant hue would be straight lines and would be independent of lightness. I have used formulas of the type $\rho = a + b\,R^{p}$, where R is a tristimulus value representative of the stimulation of one of my primaries, p is an exponent whose value lies between 0.25 and 0.50, ρ is the intensity of the transmitted nerve signal, and a and b are constants that provide the best least-squares fit of ρ to the Munsell value function. Hunt *(ref. 29)* and others, as far back as Plateau about 1872 *(ref. 30)*, have proposed cube-root formulas, corresponding to $p = 1/3$. Ladd and Pinney *(ref. 31)* have shown that the Munsell value function from $V = 1$ to $V = 9$ is best fitted, with $\sigma_V = 0.018$, when $p = 0.352$. They have also reported that for $p = 1/3$, $\sigma_V = 0.029$; that for $p = 1/4$, $\sigma_V = 0.12$; and that for $p = 1/2$, $\sigma_V = 0.17$. Ladd and Pinney report

that if V is assumed to be of the form $a + b \log R$, then $\sigma_y = 0.43$. I have tried various values of p, ranging from 1/4 to 1/2, and have obtained the best results for $p = 1/3$ for the responses ρ and γ based on the stimulation of the red and green receptors, and $p = 0.42$ for the response β based on stimulation of the blue receptor.

I then assumed the difference $(\rho - \gamma)$ to play the role which I originally described as the "beat frequency" resulting from the combination of the red and green responses. As in the original form of the hypothesis, the resultant, $(\rho - \gamma)$, is zero for all nongreenish, nonreddish colours. These, of course, include yellow, blue, white, gray, and all their subjective intermediates. I computed a similar difference $(\iota - \beta)$, where ι was the response ($p = 1/3$) to a pseudolinear combination of the red and green tristimulus values, R and G. I tried alternative formulas for this "yellow" stimulation, including linear, quadratic, and cubic combinations of the "red" and "green" tristimulus values. The formula that proved most successful in matching the curved cyan to magenta, i.e., the nonyellowish, nonbluish locus, was found to be

$$G + R\ [0.288(\rho - \gamma) - 0.0287(\rho - \gamma)^2].$$

It is of interest to note that the coefficient of R is zero along the "blue" and "yellow" loci, for which $\rho - \gamma = 0$. The coefficient of R is positive for "reddish" colours, $\rho - \gamma > 0$, and negative for "greenish" colours, $\rho - \gamma < 0$.

Attempts were made to fit Munsell constant-chroma loci, by computing chromaticities (at constant luminance) for which the sum of the squares $(\rho - \gamma)^2 + (\beta - \iota)^2$ is constant. It was quickly found that equal differences of $(\rho - \gamma)$ and $(\beta - \iota)$ are not equally noticeable. The closest fit was obtained by multiplying $(\rho - \gamma)$ by 3. This factor is very similar, in effect and magnitude, to the factor 5, suggested by T. Smith at the Cambridge Discussion on Vision a quarter of a century ago, when he discussed the properties of the constant luminance, (X, Z) diagram *(ref. 32)*. He expanded the scale on the X-axis by 5 to obtain a diagram which he considered to be subjectively uniform in spacing colours. In 1942, E. Q. Adams, who anticipated several features of the present hypothesis, employed in the construction of his chromatic value diagram *(ref. 19)* a factor 2.61, very similar in effect to the factor 3 used here. At the last meeting of the Optical Society of America, Farnsworth *(ref. 33)* suggested that such factors, relating red-green differences to yellow-blue differences, depend upon the time of observation. He reported factors ranging from 2 to 5. For calculating the colour-discrimination ellipses shown in *fig. 4*, I modified my factor from 3 to 6.4. That change was required for the best fit of the calculated ellipses with the experimental ellipses I published some years ago *(ref. 34)*.

It may be mentioned that Adams applied the Munsell value function directly to the C.I.E. tristimulus values, a procedure that is not equivalent to the present, in which approximations for the Munsell value function are applied

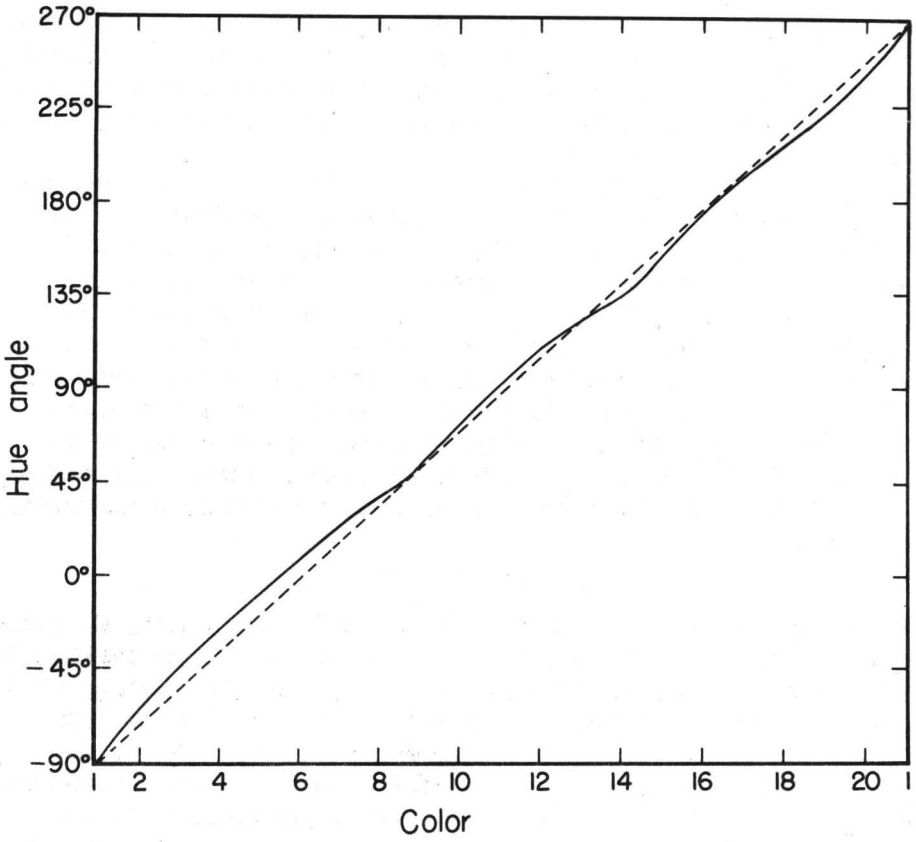


Fig.8. Hue specifications of twenty subjectively equally spaced hues.

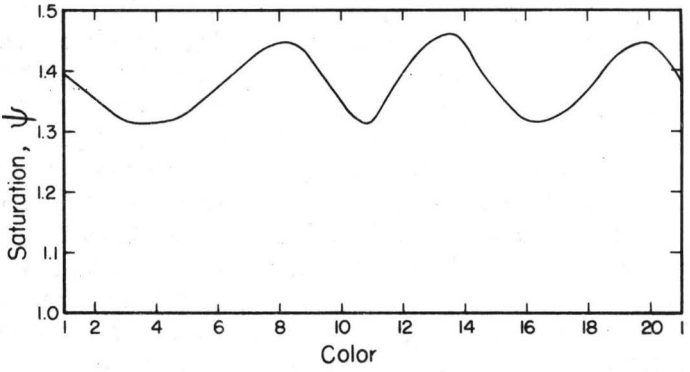


Fig.9. Saturation specifications of twenty hues, subjectively equal in saturation.

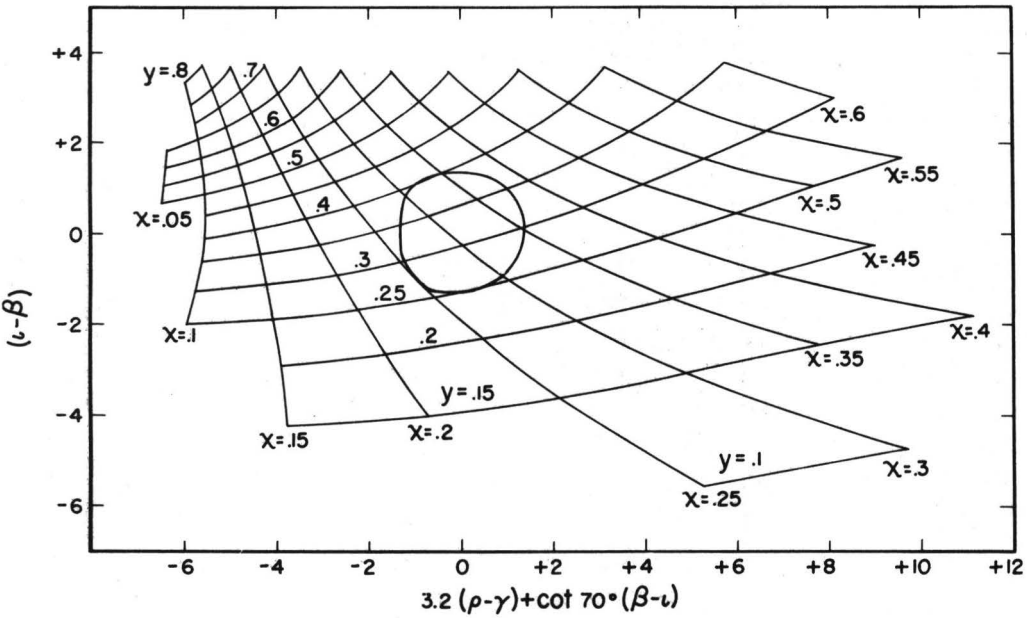


Fig.10. Twenty equally saturated, equally different hues, shown on net response diagram.

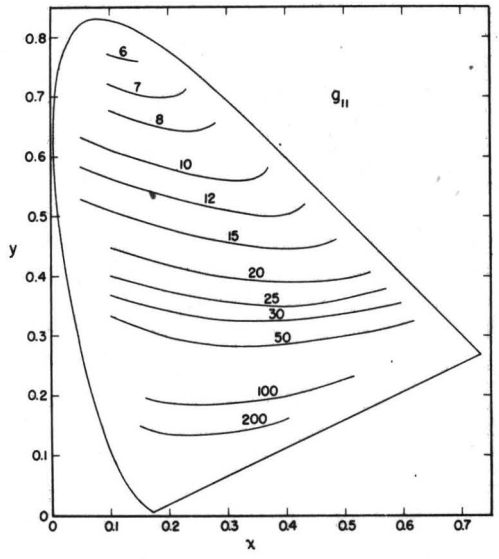


Fig.11. Colour metric coefficients.

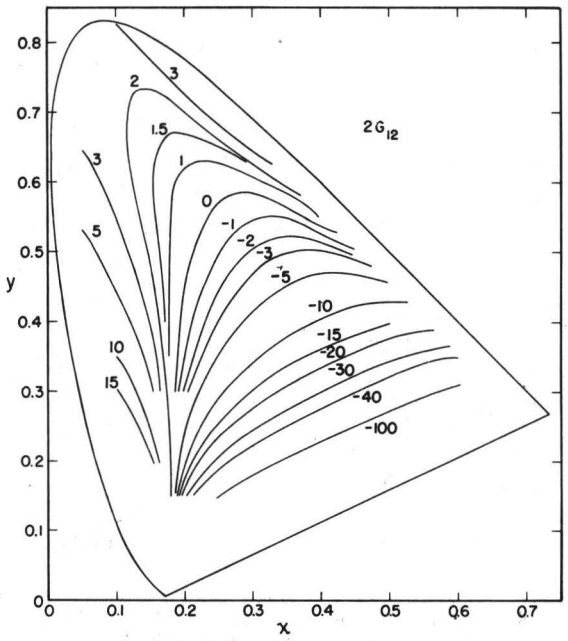


Fig. 12. Colour metric coefficients.

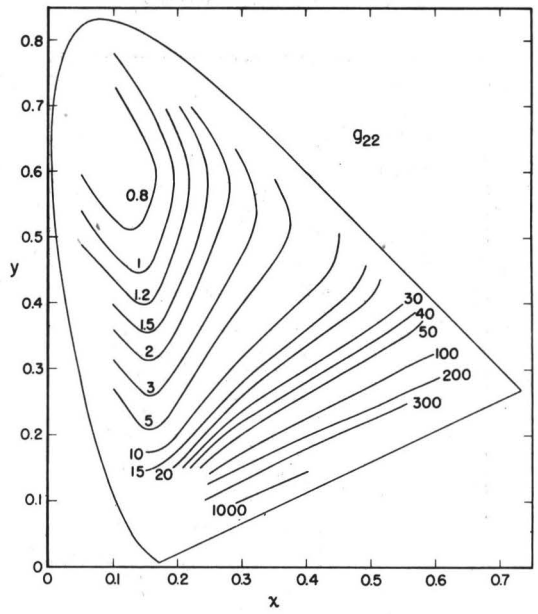


Fig. 13. Colour metric coefficients.

to modern estimates of the actual stimulation of the photo-receptors involved in human colour vision. Also, at the last meeting of the Optical Society of America, Glasser and three co-authors described a "cube-root colour co-ordinate system" essentially the same as Adams's, except for the replacement of the Munsell value function by a cube-root formula *(ref. 35)*. Taguti and Sato *(ref. 36)*, in Japan, have also used "exponential functions", in which, however, the exponents depend upon the C.I.E. tristimulus values, to replace the Munsell value function in the construction of Adams's chromatic-value diagram.

Exhaustive trials, making use of an unpublished set of specifications of equally spaced hues of equal saturation, selected by the OSA Committee on Uniform Color Scales (D. B. Judd, Chairman) indicated that the differences $(\rho - \gamma)$ and $(\iota - \beta)$ are not unrelated subjectively. After application of the factor 3 to the differences $(\rho - \gamma)$, it was found that it was necessary in effect, to plot them at 70 degrees to the $(\iota - \beta)$ differences, in order to fit a circle as closely as possible through the supposedly equally saturated and approximately equally spaced hues. Specifically, saturation was computed as

$$\psi = \{[3.2\ (\rho - \gamma) + \cot 70^{\circ}\ (\iota - \beta)]^2 + [\iota - \beta]^2\}^{1/2},$$

where 3.2 is approximately $3/\sin 70^{\circ}$. The hue angle was computed as

$$\phi = \tan^{-1} \{[3.2\ (\rho - \gamma) + \cot 70^{\circ}\ (\iota - \beta)]/([\iota - \beta]\}.$$

The results for the twenty colours selected by the OSA Committee are shown in *figs. 8* and *9*. The nearly circular distribution of the twenty colours, on the diagram in which $3.2(\rho - \gamma) + \cot 70^{\circ}\ (\iota - \beta)$, $(\iota - \beta)$ are used as co-ordinates, is shown in *fig. 10*. On this diagram are also shown the curved loci of constant C.I.E. chromaticity co-ordinates, x and y.

It is to be noted that the formulas for ψ, ϕ, and the colour-discrimination ellipses shown in *fig. 4* are all based on the assumption that equal colour differences are represented by equal distances in this flat diagram.

I have previously published data which indicate that equal colour differences cannot be represented by equal distances in *any* flat diagram *(ref. 37)*. That conclusion applied to diagrams in which the C.I.E. (x, y) co-ordinate network is either curvilinear or straight. The inadequacy of the present assumption of a flat diagram is indicated by the ovoid appearance of the locus of the twenty equally saturated colours, shown in *fig. 10*. The same inadequacy was indicated by the rather large disagreements between the ellipses in *fig. 4* and the corresponding experimental ellipses, and also between these computed loci of colour metric coefficients shown in *figs. 11, 12* and *13* and those derived from errors of colour-matching *(ref. 38)*. Evidently, even the curvilinear co-ordinate system cannot be flat if it is to represent equal colour differences by equal distances. Therefore, this is as good a place as any at which to state that I regard the present investigation and results as preliminary, tentative, and subject

to important modifications. The ovoid shape of the locus in *fig. 10* seems consistent with a suggestion by von Schelling that any successful diagram should have negative curvature *(ref. 39)*. The effects of applying von Schelling's suggestion to the present hypothesis, specifically on the constant-hue and saturation loci, and on discrimination ellipses, have yet to be computed.

To the same extent that I was not competent to suggest the "beat-frequency" hypothesis, I am not competent to criticize it. The best I can do is to quote from a letter that I received from H. K. Hartline, in response to a copy of my first contribution to this symposium. After a very kind first paragraph, Dr. Hartline wrote:

> "It is in the speculations about the detailed mechanism of these interactions that I find myself less willing to go along with your ideas. I do not look upon a neurone as a device that responds specifically to each individual impulse fed into it, with effects sometimes reinforcing, sometimes cancelling, impulse for impulse. A neurone does not emit or fail to emit an impulse as the fate of each incoming impulse is decided. Rather, incoming impulses produce effects (excitatory and/or inhibitory) that far outlast their own transient presence at the fiber terminations. As trains of impulses, arriving asynchronously over converging pathways, impinge upon a neurone, a state of excitation is built up (or is torn down, when antagonistic inhibitory influences prevail), and the neurone responds at its own rate of firing. This rate is determined by the net excess of excitation over inhibition, averaged over times that may well comprise many impulse-intervals for most levels of activity. Such a picture leaves little opportunity for "beat frequencies" to develop. The notion of the nervous system as a sort of digital computer has, I believe, no basis in fact. I believe that most *experimental* neurophysiologists would favor the interpretations that I have just given."

Although the remainder of Dr. Hartline's letter is somewhat more favourable to the beat-frequency hypothesis, I am ready to abandon that hypothesis, while pointing out that it has been highly suggestive and fruitful, and therefore successful in the best sense that any hypothesis can be said to be successful.

How can we hold our gains, despite the apparent collapse of their foundation? The first thing to note is that the mathematical model did not make any use of the features by which the "beat-frequency" hypothesis got its name. The accomplishments of the mathematical model would devolve upon any concept of colour perception that postulates:

1. Three kinds of photosensitive receptors.
2. Nonlinear (and not strictly logarithmic) responses to photostimulations, including a fourth "yellow" response dependent on some "pseudolinear" combination of red and green stimulations.

3. Subtraction of two pairs of such nonlinear responses, e.g., red from green, and blue from yellow.
4. Constant hue determined by constant ratio of those net responses.
5. Saturation determined by some quadratic combination of the net responses.
6. Perceptible colour differences determined by a threshold value of some quadratic combination of increments of the two net responses.
7. Adaptation according to a "coefficient law" applied to the pseudo-logarithmic responses, such that the four responses are all equal for the stimulus to which the retina is adapted. Incidentally, this adaptation hypothesis (7) fully accounts for the linear distributions

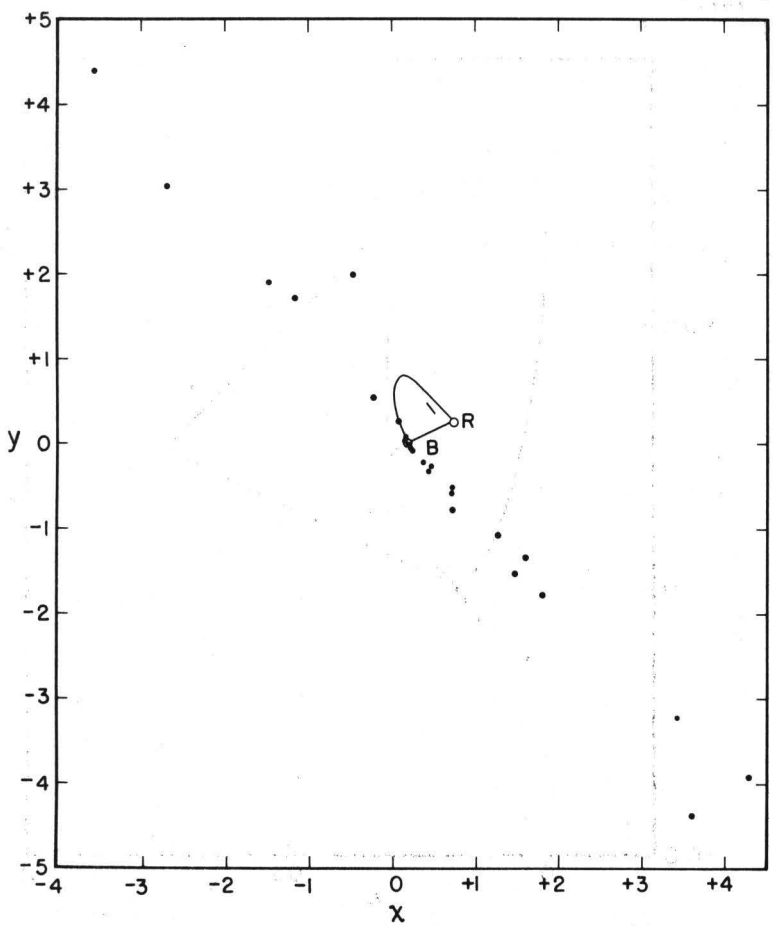


Fig. 14. Discrepancies of von Kries predictions from corresponding colours computed for adaptations to pink and green.

in the chromaticity diagram of discrepancies between predictions of the von Kries coefficient law and the results of adaptation experiments *(ref. 24)*. One example is shown in *fig. 3*. *Figs. 14* and *15* show two others, one for the corresponding colours observed with pink and green adaptations, and the other for green and white adaptations. *Fig. 16* shows constant-hue and constant-saturation loci for adaptation to C.I.E. illuminant *A*, computed by use of the new adaptation hypothesis. The success of this hypothesis, the general idea of which I owe to Dr. Hunt *(ref. 23)*, enables me to abandon my earlier hypothesis of five or six receptor processes, independently subject to the von Kries type of adaptation *(ref. 24)*. This abandonment eliminates also my question concerning the invariance of metameric colour matches *(ref. 24)*.

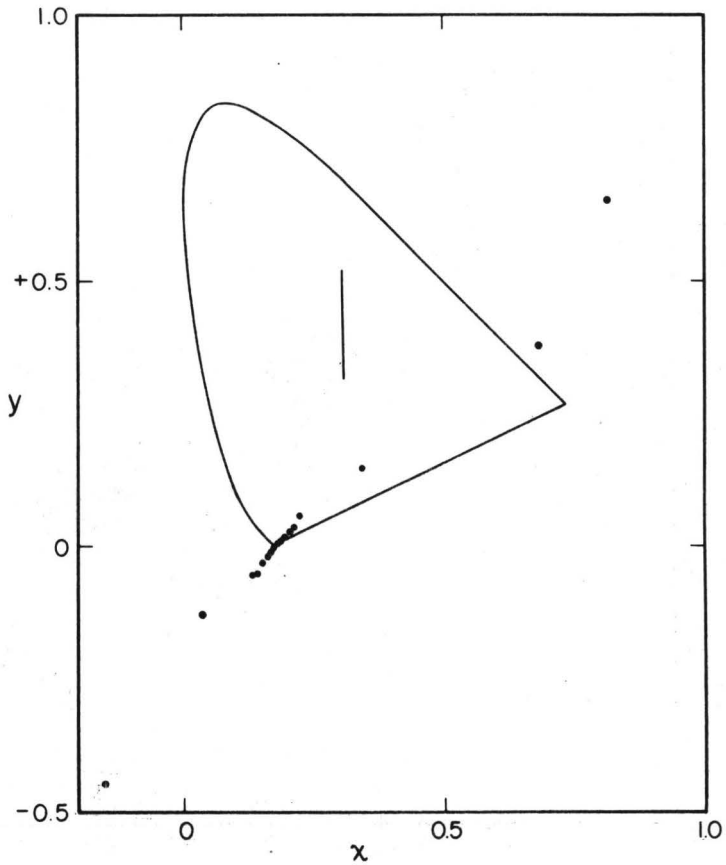


Fig. 15. Discrepancies of von Kries predictions from corresponding colours computed for adaptations to green and white.

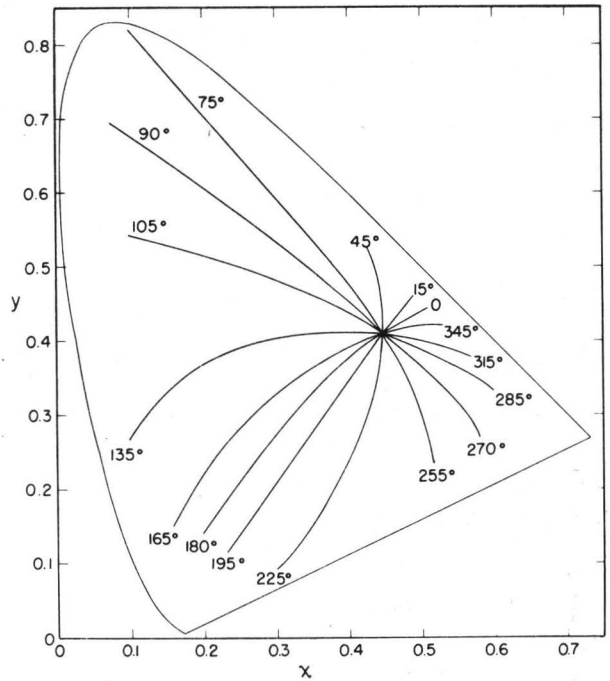


Fig.16. Constant hue loci for adaptation to tungsten light.

Is there any evidence that colour vision works in the ways I have postulated? Recent publications by Svaetichin *(refs. 40,41)*, on electroretinograms obtained by use of microelectrodes in contact with individual cones, indicate that in the eyes of some fish the components of electrical potential are:

1. Differently dependent on the spectral distribution of the stimulating light.
2. Nonlinearly related to the intensity of the stimulus.
3. Subtracted before further transmission.

Svaetichin suggests that human colour vision is similarly mediated. This hypothesis is consistent with the mathematical model I have described. If Svaetichin's hypothesis is tenable, it could inherit some of the gains won by the defunct "beat-frequency" hypothesis and would not be inconsistent with the others.

Even more recent publications by Hartline *(ref. 42)* report that in the eye of Limulus (horseshoe crab), the impulse frequency caused by stimulation of one visual cell is *reduced* as a function of the impulse frequency arising from stimulation of a nearby cell. Hartline proved that this reduction is not directly dependent upon the stimulation of the other cell, but upon its

impulse frequency. He did not report whether or not the reduction was proportional to the "inhibiting" frequency. But, as Willmer confided when he told me of Hartline's disclosure of his discovery, "I have been hopping about with joy ever since."

REFERENCES

1. HARTLINE, H. K., *J. opt. Soc. Amer.*, 1940, **30**, 239-247.
2. POLYAK, S., The Retina, Univ. of Chicago Press, Chicago, Ill., 1941.
3. GOLDMARK, P. C. and HOLLYWOOD, J. M., *Proc. IRE*, 1951, **39**, 1314-1322.
4. DI FRANCIA, G. TORALDO, *Atti Fond Ronchi.*, 1952, **7**, 3-15.
5. DITCHBURN, R. W. and GINSBORG, B. L., *Nature*, 1952, **170** (4314), 36-37.
6. RIGGS, L. A., RATLIFF, F., CORNSWEET, J. C. and CORNSWEET, T. N., *J. opt. Soc. Amer.*, 1953, **43**, 495-501.
7. MACADAM, D. L., *J. opt. Soc. Amer.*, 1956, **46**, 381A.
8. MACADAM, D. L., *Rev. d'Optique*, 1949, **28**, 161-173; *Documenta Ophth.*, 1949, **3**, 214-233.
9. MACADAM, D. L., *J. opt. Soc. Amer.*, 1950, **40**, 589-595.
10. CHAPANIS, A. and HALSEY, R. M., *J. opt. Soc. Amer.*, 1955, **45**, 1-6.
11. WILLMER, E. N., *Documenta Ophth.*, 1955, **9**, 235-313.
12. HARTLINE, H. K., *Amer. J. Physiol.*, 1940, **130**, 690-711.
13. BARLOW, H. B., *J. Physiol.*, 1953, **119**, 69-88.
14. GRANIT, R., Sensory mechanisms of the retina, Oxford Univ. Press, Oxford, 1947.
15. BOYNTON, R. M., *J. opt. Soc. Amer.*, 1956, **46**, 172-179.
16. MACADAM, D. L., *Die Farbe*, 1955, **4**, 133-143; *J. opt. Soc. Amer.*, 1956, **46**, 500-513; *J. Soc. Mot. Pict. Telev. Engrs.*, 1956, **65**, 455-469.
17. JUDD, D. B., *J. opt. Soc. Amer.*, 1945, **35**, 805.
18. JAMESON, D. and HURVICH, L. M., *J. opt. Soc. Amer.*, 1955, **45**, 546-552, 602-616; *J. opt. Soc. Amer.*, 1956, **46**, 405-421.
19. ADAMS, E. Q., *J. opt. Soc. Amer.*, 1942, **32**, 168-173.
20. STILES, W. S., *Proc. phys. Soc.*, 1946, **58**, 41-65.
21. LE GRAND, Y., *Rev. d'Optique*, 1949, **28**, 261-278.
22. NEWHALL, S. M., NICKERSON, D., and JUDD, D. B., *J. opt. Soc. Amer.*, 1943, **33**, 385-418.
23. HUNT, R. W. G., Paper 24 of this Symposium.
24. MACADAM, D. L., *J. Soc. Mot. Pict. Telev. Engrs.*, 1956, **65**, 455-469.
25. HELSON, H., JUDD, D. B. and WARREN, M. H., *Illum. Engng.*, 1952, **47**, 221-233.
26. WALTERS, H. V., *Proc. roy. Soc.*, B, 1942, **131**, 27-50.
27. WRIGHT, W. D., Researches on Normal and Defective Colour Vision C. V. Mosby, St. Louis, 1947, 271-272.

28. SÉGAL, J., Le mécanisme de la vision des couleurs, G. Doin, Paris, 1953.
29. HUNT, R. W. G., *Nature*, 1957, **179**, 1026.
30. DELBOEUF, J., Etude psychophysique, Paris, 1873, 50-51.
31. LADD, J. H. and PINNEY, J. E., *Proc. Inst. Radio Engrs., N.Y.*, 1955, **43**, 1137.
32. SMITH, T., Phys. and Opt. Soc. Discussion on Vision, Cambridge University Press, Cambridge, 1932, 212-226.
33. FARNSWORTH, D., *J. opt. Soc. Amer.*, 1957, **47**, 336.
34. MACADAM, D. L., *J. opt. Soc. Amer.*, 1942, **32**, 247-274.
35. GLASSER, L. G., REILLY, C. D., SCHNELLE, P. D. and MCKINNEY, A. H., *J. opt. Soc. Amer.*, 1957, **47**, 339.
36. TAGUTI, R. and SATO, M., *Comptes Rendus*, 1956, **243**, 654-656; also Reports 2 and 3, 1956 and 1957, of Taguti Institute of Psychophysics, 3, Kamihuzimae-Tyô, Bunkyô-Ku, Tokyo, Japan.
37. SILBERSTEIN, L., *J. opt. Soc. Amer.*, 1943, **33**, 1-9.
38. MACADAM, D. L., *J. opt. Soc. Amer.*, 1943, **33**, 18-26.
39. VON SCHELLING, H., *J. opt. Soc. Amer.*, 1955, **45**, 1072-1079; *J. opt. Soc. Amer.*, 1956, **46**, 309-316.
40. SVAETICHIN, G., *Acta physiol. scand.* 1956, **39**, Supplement 17-46, 57-112.
41. MACNICHOL, JR., E. F., MACPHERSON, L., and SVAETICHIN, G., Paper 39 of this Symposium.
42. HARTLINE, H. K., WAGNER, H. G. and RATLIFF, F., *J. gen. Physiol.*, 1956, **39**, 651-673;
HARTLINE, H. K. and RATLIFF, F., *J. gen. Physiol.*, 1957, **40**, 357-376.

PAPER 35

THE EQUICONTRAST COLORIMETRIC SYSTEM

By D. A. SHKLOVER

D. A. Shklover was born in 1915 and graduated in 1939 from the Moscow Power Institute as a specialist in electrotechnics and industrial lighting. Since 1945, he has been the chief of a Colorimetric Laboratory of the All-Union Scientific-Research Lighting Institute. He works in the field of photoelectric methods and apparatus for colour measurement and colour reproduction. He is concerned at present with the problems of higher colour metrics.

35. THE EQUICONTRAST COLORIMETRIC SYSTEM *

By D. A. SHKLOVER

SUMMARY

THE principles of a colorimetric system, using the reactions of the three receptors as the main co-ordinates, are expounded. The system takes into consideration the non-linear dependence of receptor reactions on radiation intensity, and establishes the connexion between the receptor reactions and the sensations of hue and saturation. It is shown that the new colorimetric system conforms to requirements of equicontrast, and helps to explain Bezold-Brücke's phenomenon and Abney's effect. In the particular case of high intensity and colours of low saturation, the chromaticity diagram of the new system is connected with the standard chromaticity diagram *XY* by projective transformation.

1. The standard colorimetric system C.I.E. (1931) allows the solution of problems of colour classification and colour mixture, and the calculation of the colour of radiation according to spectrum data. However, the colour space of the C.I.E. colorimetric system has only affine properties, not metric ones. In the *XYZ* colour space and in the chromaticity diagram *XY*, the distance between points corresponding to given colours is not proportional to the degree of the difference (colour contrast) between the colours.

On the other hand, a great number of facts of colour vision, e.g. the dependence of chromaticity on luminance (Bezold-Brücke's phenomenon), the change of hue by dilution of spectrum colours with white light (Abney's effect) etc., cannot be explained by this system.

A great number of experimental and theoretical works *(refs. 1,2)* have been devoted to the problem of the metrics of colour space in the C.I.E. system and to the development of a new equicontrast colorimetric system. Nevertheless this problem is not yet completely solved.

The principles of development of a colorimetric system based upon modern conceptions of the colour vision mechanism and free of the deficiencies of the C.I.E. system, just mentioned, are given below.

2. In the C.I.E. system the colour of radiation is defined by tristimulus values, giving the amounts of the three primaries or matching stimuli required to give a colour match with the measured radiation. In contrast with the C.I.E. system the suggested system uses the reaction values of the three receptors as initial co-ordinates. Of course, it is impossible to consider all the variety of the three colour receptor properties while developing such a colorimetric system.

* First communicated at the Fourth Conference on Physiological Optics in Leningrad, October 1955.

We consider that the following data of colour vision should be taken as the basis of the rational colour system:

(a) spectral response curves of the three receptors $(\bar{r}, \bar{g}, \bar{b})$;

(b) a certain non-linear dependence of receptor reactions on radiation intensity;

(c) a certain hypothesis on the mechanism of the second transformation in the process of colour vision, which should explain how a single colour sensation, characterized by hue, saturation, and brightness, is formed out of three receptor reactions.

None of the colour vision characteristics mentioned above can be considered at present as completely clear. However it is worth while trying to develop a metric system based upon the most probable suppositions, having in mind the possibility of its later revision.

It is known that the fundamental response curves should be connected with distribution coefficients of the standard C.I.E. colorimetric observer by linear relationships. For determination of the relation coefficients mentioned above the results of the study of dichromatic colour vision *(refs. 4,5,6)* experiments on colour adaptation *(ref. 1)*, colour contrasts *(ref. 8)* and others are used. The results obtained by these methods give non-coincident curves. We consider that the possibility of development of the most simple metric system on the basis of such curves is the criterion of the correctness of these curves.

The question of the dependence of receptor reactions on radiation intensity has been studied in detail only as applied to brightness sensation. This dependence for the three receptors was studied only in Rautian's work *(ref. 7)*. He showed, for a particular case, an approximation to the Weber-Fechner law for one receptor and some deviations from this law for two others.

S. O. Maisel *(ref. 3)* developed a theory founded upon Granit's experiments showing that receptor reactions are the electrical impulses, the frequencies of which depend on the intensity of radiation reaching the eye.

In the first approximation in conformity with the Weber-Fechner law, a logarithmic dependence of impulse frequencies (V_R, V_G, V_B) on the intensity of stimulation can be assumed as:

$$V_R = \lg (R + C); \quad R = \int I_\lambda \bar{r} d\lambda \tag{1}$$

$$V_G = \lg (G + C); \quad G = \int I_\lambda \bar{g} d\lambda \tag{2}$$

$$V_B = \lg (B + C); \quad B = \int I_\lambda \bar{b} d\lambda \tag{3}$$

where I_λ is the spectral intensity distribution of the perceived radiation.

The constant C in equations (1), (2) and (3) can be considered as a "dark-current" the value of which is the same for all three receptors. In the case of high intensity, when $R, G, B \gg C$, it can be neglected, and then we have a simple logarithmic dependence.

The colour space metrics, expressed in co-ordinates analogous to V_R, V_G, V_B were first presented by Helmholtz *(ref. 9)* and were then carefully studied in a new way by Stiles *(ref. 10)*.

The question of the connexion of chromaticity and brightness sensation with the receptor reactions mentioned above is very important for an explanation of the colour vision mechanism as well as for the development of a colour reaction metric.

The chromaticity sensation is usually considered to be unchanged when the intensity changes within certain limits while the relative spectral composition of the radiation remains unchanged. In this connexion the chromaticity sensation is often defined by certain ratios of receptor reactions. However this is true only in case of linear (or power) dependence of receptor reactions on intensity.

It is easy to show that if there is a logarithmic dependence the signals characterising the chromaticity of radiation, [V_α and V_β] can be obtained by a subtraction of the eye receptor signals (reactions):

$$V_\alpha = K_1 (V_R - V_G) = K_1 \lg (R + C) - K_1 \lg (G + C) = K_1 \lg \frac{R + C}{G + C} \qquad (4)$$

$$V_\beta = K_2 (V_B - V_G) = K_2 \lg (B + C) - K_2 \lg (G + C) = K_2 \lg \frac{B + C}{G + C} \qquad (5)$$

When the impulse frequencies V_R, V_G and V_B are close together, the formation of difference frequencies can be explained by the emergence of beat frequencies as a result of a simple summation of oscillations.

It should be noted that the differences of receptor reactions were used for an explanation of the colour vision mechanism in Hering and Adams' theories *(ref.11)*.

Equations (4) and (5) show that when stimulation is great enough (R, G, $B \gg C$) the signal values V_α and V_β are proportional to the logarithms of the tristimulus value ratios and consequently do not depend on the intensity of stimulation:

$$V_\alpha \longrightarrow K_1 \lg R/G \qquad (6)$$

$$V_\beta \longrightarrow K_2 \lg B/G \qquad (7)$$

3. In accordance with the theory discussed the chromaticity of radiation can be represented as a point on the chromaticity diagram in the co-ordinate system V_α, V_β *(fig.1)*. The achromatic light (the standard colorimetric source E) for which $R = G = B$ and $V_\alpha = V_\beta = 0$ will correspond to the point at the zero. Negative values of V_α and V_β for some regions of the chromaticity diagram have only a conditional meaning and show that the order of subtraction of reactions should be changed in these regions.

Constant hue lines will be represented in the diagram as straight lines originating in the zero. Thus constant hue sensation (K = const.) corresponds to an appropriate value of the chromaticity signal ratio, V_α to V_β:

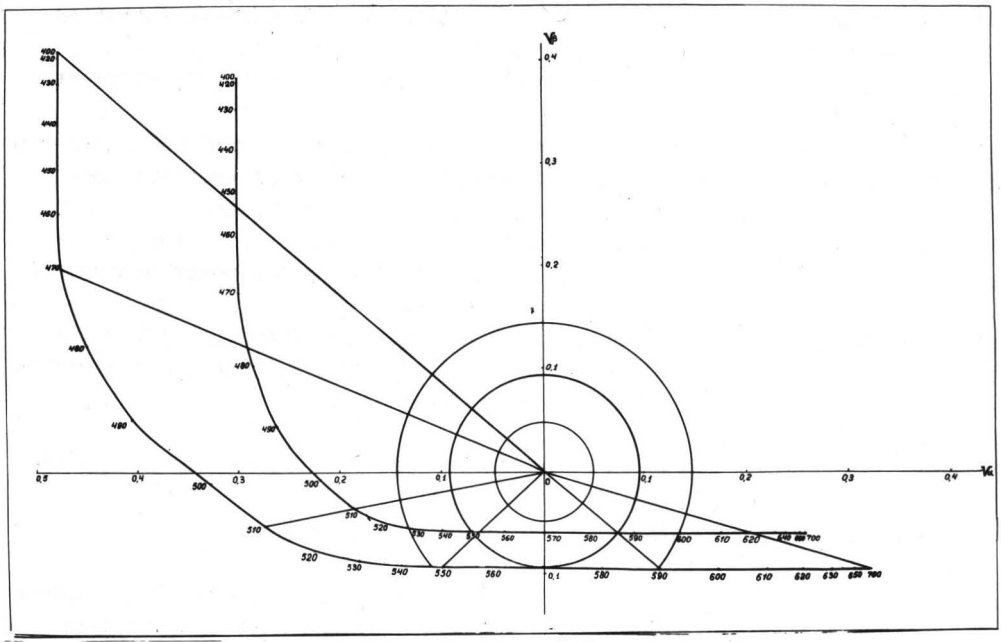


Fig. 1. The chromaticity diagram (V_α, V_β)

$$K = \frac{V_\beta}{V_\alpha} = \frac{K_1 \lg \frac{B + C}{G + C}}{K_2 \lg \frac{R + C}{G + C}} \tag{8}$$

The value of the colour saturation *(H)* in the adopted co-ordinate system is proportional to the root mean square of the chromaticity signal values:

$$H = \sqrt{V_\alpha^2 + V_\beta^2} = \sqrt{(K_1 \lg \frac{R + C}{G + C})^2 + (K_2 \lg \frac{B + C}{G + C})^2} \tag{9}$$

Lines of constant saturation will then be represented in the diagram (V_α, V_β) as concentric circles with centre at the origin. So this diagram is to be a uniform chromaticity one.

To any point of the new chromaticity diagram corresponds a quite distinct chromaticity sensation characterized by a certain hue *(K)* and saturation *(H)*.

In contrast with the standard chromaticity diagram the new diagram explains Bezold-Brücke's phenomenon and Abney's effect. Let us transform equations (8) and (9) using component ratio values α and β:

$$K = \frac{K_1 \lg \dfrac{\beta + C/G}{1 + C/G}}{K_2 \lg \dfrac{\alpha + C/G}{1 + C/G}} \tag{10}$$

$$H = \sqrt{\left(K_1 \lg \frac{\alpha + C/G}{1 + C/G}\right)^2 + \left(K_2 \lg \frac{\beta + C/G}{1 + C/G}\right)^2} \tag{11}$$

where $\alpha = \frac{R}{G}$ and $\beta = \frac{B}{G}$.

Equations (10) and (11) show that when the absolute intensity of the radiation changes, while the relative spectral composition remains unchanged (α = const, and β = const.), the sensations of hue and saturation will change.

There are only three directions in the chromaticity diagram for which the hue does not depend upon the intensity of radiation:

$$\alpha = 1; \quad K = \infty; \quad R = G;$$

$$\beta = 1; \quad K = 0; \quad B = G;$$

$$\alpha = \beta; \quad K = \frac{K_1}{K_2}; \quad R = B.$$

It is not difficult to see that these directions correspond to those wavelengths of the spectrum where the fundamental response curves of the receptors ($\bar{r}, \bar{g}$ and $\bar{b}$) intersect.

For all other points of the chromaticity diagram, the hue sensation changes with increase of intensity so that it approximates to the three points of the spectrum mentioned above. When the intensity rises, the colour saturation rises simultaneously with the change of the dominant wavelength.

For colours of low saturation, when the levels of the intensity are high ($\alpha, \beta \gg C/G$), there are no changes of the chromaticity sensation of the kind mentioned above. It is obvious that the straight lines in the diagram (x,y) passing through the white point, will be represented in the diagram (V_α, V_β) in general as curved lines. Consequently the hue sensation will change by dilution of the given spectrum colour with achromatic light.

Thus the present system of colour evaluation gives qualitatively Bezold-Brücke's phenomenon and Abney's effect.

A specification of the colour sensation must include besides the signals of chromaticity V_α and V_β, the signals of brightness:

$$V_y = K_3 \lg (y + C); \quad y = \int I_\lambda V_\lambda \, d\lambda \tag{12}$$

where V_λ is a visibility curve.

Thus the value of the colour contrast in the colour space is defined by the equation:

$$d\delta = \sqrt{(dV_\alpha)^2 + (dV_\beta)^2 + (dV_y)^2} \qquad (13)$$

4. In order to correlate the above mentioned metric relations with the results of experiments on colour discrimination it is first necessary to adopt appropriate fundamental response curves.

We will show the results of calculations for the case of the spectral curves which we used for photoelectrical colorimeters *(ref. 12)*.

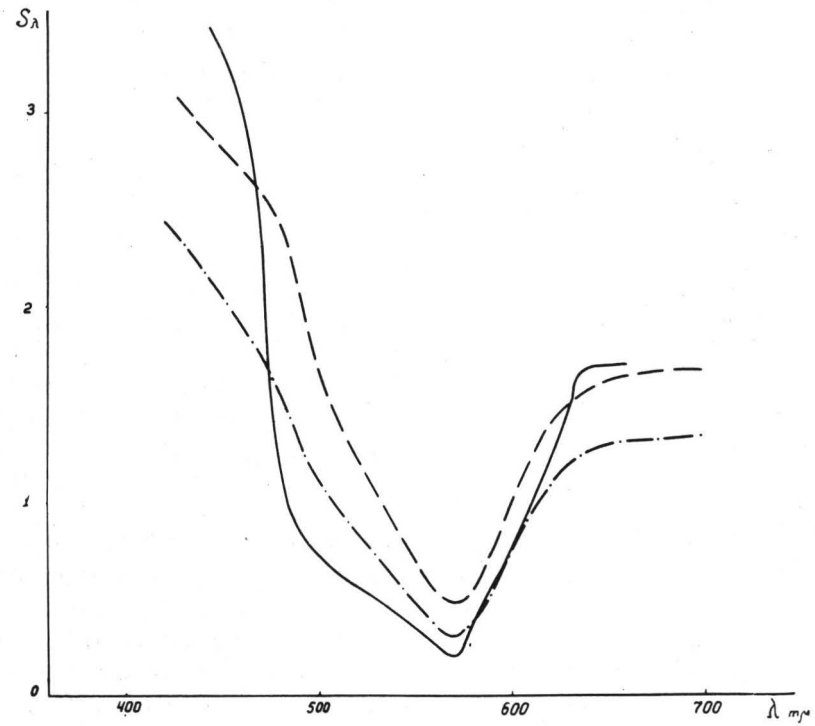


Fig. 2. The saturation of spectrum colours

— — — according to the diagram (V_α, V_β) when $C/y = 0.5$

—·—·— according to the diagram (V_α, V_β) when $C/y = 1.0$

——————— according to Priest, Brickwedde and Purdy's data

$$\bar{r} = \bar{x}_n = 0.833\bar{x} + 0.5\bar{y} - 0.167\bar{z} \quad (14)$$

$$\bar{g} = \bar{y} \quad (15)$$

$$\bar{b} = \bar{z} \quad (16)$$

The peculiarity of these curves as well as of the curves accepted by Judd *(ref. 4)* is that curve $\bar{g}$ coincides with the average visibility curve $\bar{y}$.

Substituting the values $\bar{r}, \bar{g}$ and $\bar{b}$ into equations (4) and (5) and assuming $K_1 = 1$ and $K_2 = 0.2$ we have:

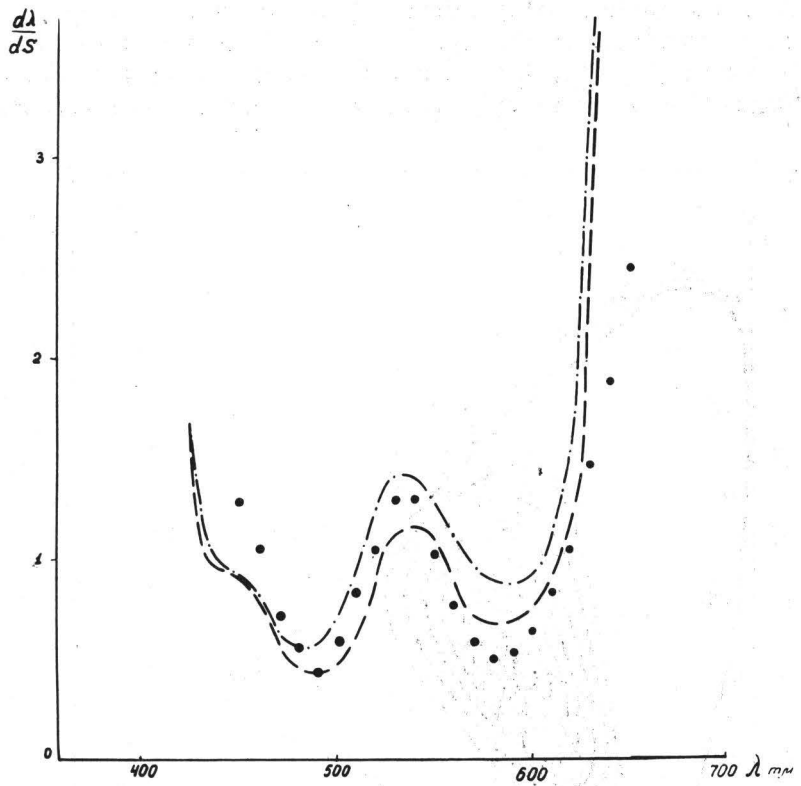


Fig. 3. The sensitivity of the eye to a change of hue
— — — according to the diagram (V_α, V_β) when $C/y = 0.5$
— · — · — according to the diagram (V_α, V_β) when $C/y = 1.0$
. . . . . according to Tyndall, Koenig and others, average data

$$V_\alpha = K_1 \lg \frac{x_n + C}{y + C} = \lg \frac{\alpha + C/y}{1 + C/y} \qquad (17)$$

$$V_\beta = K_2 \lg \frac{z + C}{y + C} = 0.2 \lg \frac{\beta + C/y}{1 + C/y} \qquad (18)$$

Spectrum colour curves on the diagram (V_α, V_β) at two luminance levels are shown in *fig.1*. *Figs.2* and *3* show the saturation curves of spectrum colours and the curves representing the eye sensitivity to a change of hue of spectrum colours. These curves are derived on the supposition that the colour contrast value in the diagram (V_α, V_β) is proportional to the distance between the corresponding points of the diagram. It is interesting to plot on the chromaticity diagram (x,y) the lines of constant hue and saturation of the diagram (V_α, V_β). *Figs.4* and *5* show the appropriate lines for two luminance levels. It is very convenient to use for such constructions

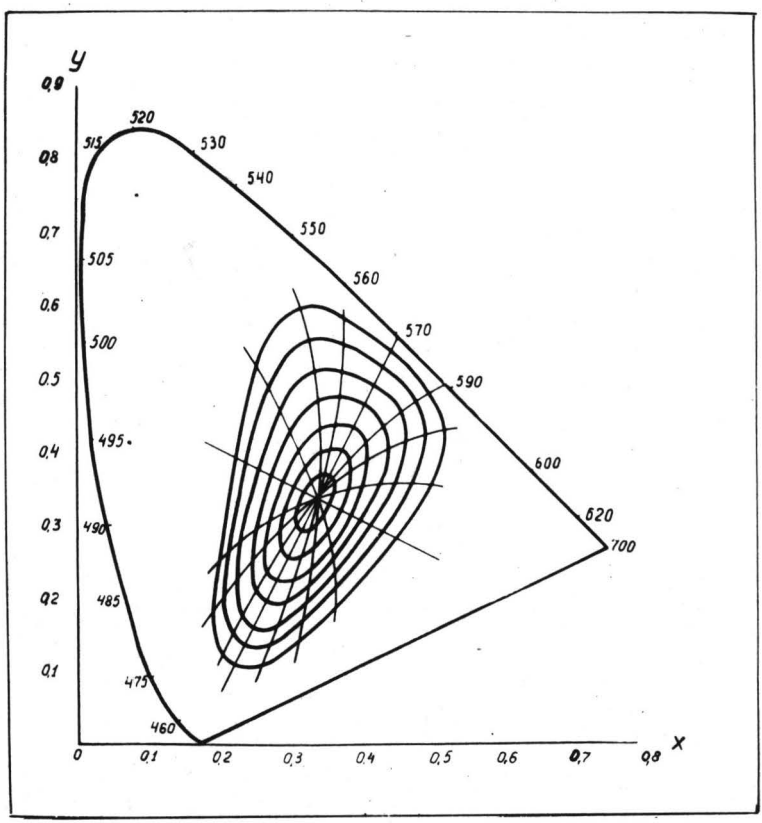


Fig.4. The lines of constant hue and saturation, when $C/y = 0.5$

the set of lines of constant values of α and β plotted on the chromaticity diagram *(x,y) (ref.12)* or to plot the lines x = const. and y = const. on the diagram (V_α, V_β).

An examination of the curves obtained shows that they are in qualitative correlation with the results of colour threshold investigations as well as with determinations of the lines of constant hue and saturation *(refs.13,14)*. It is not worth carrying out a more detailed correlation of these data as we have no standard fundamental response curves, and because of a considerable difference between the experimental data of different investigators.

5. Let us examine the metrics of the chromaticity diagram (V_α, V_β) for the particular case of colours of low saturation (α, $\beta \longrightarrow 1$) at high brightness levels where α, $\beta \gg C/y$. Expanding the logarithms in series we have for the first approximation:

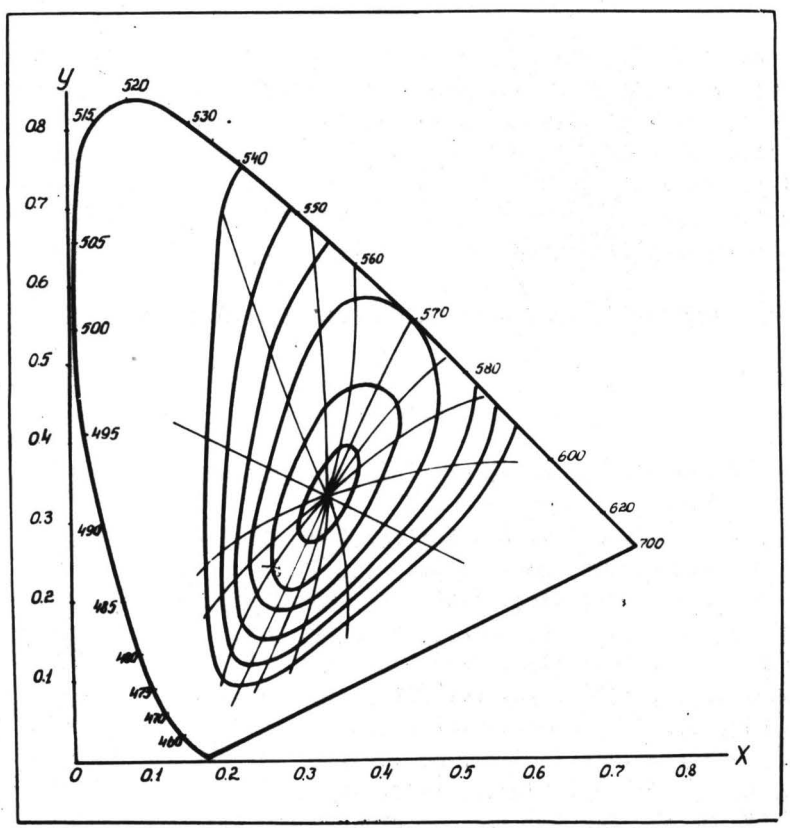


Fig.5. The lines of constant hue and saturation when C/y = 1.0

$$V_\alpha \cong \lg \alpha \cong \alpha - 1 = \frac{x + 0.5y - 0.167}{y} - 1$$

$$V_\beta \cong 0.2 \lg \beta \cong 0.2(\beta - 1) = 0.2\left(\frac{1 - x - y}{y} - 1\right)$$

$$V_\alpha = \frac{x - 0.5y - 0.167}{y} \tag{19}$$

$$V_\beta = 0.2\left(\frac{1 - x - 2y}{y}\right) \tag{20}$$

Equations (19) and (20) show that the chromaticity diagram (V_α, V_β) can be obtained by a projective transformation of the standard chromaticity diagram (x,y) when the alychne is transformed into an infinitely remote straight line. Thus the projective transformations of the chromaticity diagram (x,y) obtained by Judd and other investigators are but a particular case of a more general relationship and can be used only in a limited region of chromaticities at high luminance levels.

Note. In all equations, lg denotes exponential logarithm.

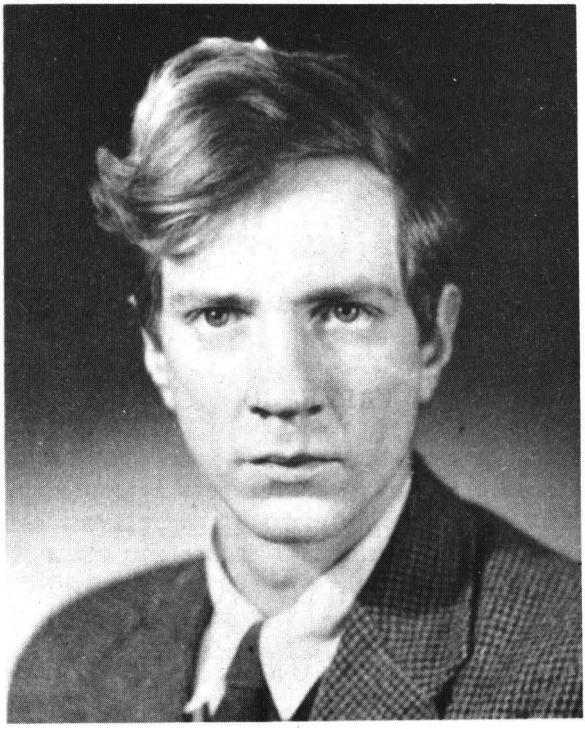
REFERENCES

1. International discussion of problems in colour metrics, Heidelberg, 1955.
2. SHKLOVER, D. A., "Svetotechnika" N I, 1956.
3. MAISEL, S. O., *Proc. C.I.E.*, Zurich, 1955, RM.
4. JUDD, D., *J.opt. Soc. Amer.*, 1945, **35**, 199.
5. YUSTOVA, E. N., *Dokl.Akad. Nauk SSSR*, 1950, **74**, 1069.
6. WRIGHT, W., *J. opt. Soc. Amer.*, 1952, **42**, 509.
7. RAUTIAN, G. N., *Dokl.Akad. Nauk SSSR*, 1951, **79**, 65.
8. FEDOROV, N. T., *Probl. physiol.Opt.*, 1953, **8**, 99.
9. HELMHOLTZ, H., *Z. Sinnesphysiol.*, 1891, **3**, 517.
10. STILES, W., *Proc. phys. Soc.*, Lond., 1946, **58**, 41.
11. ADAMS, Q., *J.opt. Soc. Amer.*, 1942, **32**, 168
12. SHKLOVER, D. A., *Proc. C.I.E.*, Zurich, 1955, R.S.
13. MACADAM, D., *J. opt. Soc. Amer.*, 1950, **40**, 589
14. NEWHALL, S., NICKERSON, D., JUDD, D., *J. opt. Soc. Amer.*, 1943, **33**, 385
15. JOFFE, R. S., SHKLOVER, D. A., "Svetotechnika" N 2, 1955, Dtsch. Electrotechnik II, N I (1957).

PAPER 28

INTRINSIC NOISE OF CONES

By H. B. BARLOW



HORACE BARLOW, Physiological Laboratory, King's College, Cambridge. Age 35. Studied Physiology at Cambridge and Medicine at Harvard and London (Univ. College Hosp.). Has worked on various aspects of vision, including eye-movements; spatial properties of receptive fields in the frog's retina; changes in temporal and spatial summation with level of adaptation; and thresholds as signal/noise discriminations. Worked for a year with S. W. Kuffler at Johns Hopkins on changes in retinal organisation in the cat's retina during dark adaptation. Interested mainly in the nervous organization of the visual pathways.

28. INTRINSIC NOISE OF CONES

By H. B. BARLOW

SUMMARY

1. A theoretical explanation is sought for the shape of the curves relating incremental threshold and adapting field intensity.
2. The simplest physical model which approximates to the behaviour of the eye is a photocell with constant quantum efficiency of photo-emission, and a dark current.
3. The eye follows the model quite accurately when its increment threshold is measured with a short duration, small area test stimulus; this is shown to be true under conditions where the red (π_5) and the green (π_4) mechanisms are operative.
4. When long duration, large area stimuli are used, the eye gives a performance closer to that predicted by Weber's law, with the addition of dark light to account for the levelling off at low background intensities.
5. The value of the dark light (analogous to the dark current of the model) of four of Stiles' mechanisms is derived from his results, and is compared with that of rods; they all have dark lights about 10^4 times that of the rods.
6. Quantum efficiencies are calculated from Stiles' data; cones have lower overall quantum efficiencies than rods, and that of the blue mechanisms is much lower than that of the red and green mechanisms.

INTRODUCTION

STILES *(refs. 1,2,3)* has shown that the increment threshold of the eye depends upon one out of six almost independent mechanisms. The threshold of the whole eye is that of the most sensitive mechanism, and which this is under any particular conditions depends upon; (i) the spectral sensitivity curves and (ii) the threshold versus intensity (t.v.i.) curves of the mechanisms in the retinal location being used. The importance of the spectral sensitivity curves for colour vision is obvious, and Stiles' analysis has mainly been concerned with their determination. The possible importance of the t.v.i. curves is less clear because one does not know what makes them the shape they are. The first part of this paper is an attempt to answer this question by finding the simplest physical model which would give curves of a similar shape. In the second part of the paper it is shown that t.v.i. curves can be obtained under certain conditions which match the performance of this model, though under other conditions the eye is considerably less efficient than the model predicts. In the third section I have

derived values of the "dark lights" of the cone mechanisms from Stiles' results, and have tried to relate these values to the thermal stability and photosensitivity of the photochemical substances of the receptors. In the final section I have made estimates of the quantum efficiencies of the different mechanisms from Stiles' results.

I. THE PHYSICAL MODEL

(a) Photocell with zero dark current.

Rose *(ref. 4)* and de Vries *(ref. 5)* suggested that the eye should be compared with an ideal detector, and their model was a photocell without any dark current. Suppose that light from a field of intensity I and area a (degrees^2) falls on the cathode and causes a current i. It is convenient here and subsequently to measure currents in electronic charges/sec, and the light intensity, I, in quanta/(sec. degree^2) reaching the cathode. Then

$$i = FIa$$

where F is the fraction of incident quanta which cause the emission of an electron. Because of the shot effect the current will fluctuate, and the least increment, δi, that can be detected in t secs is given approximately by

$$\delta i = k(i/t)^{\frac{1}{2}} \tag{1}$$

where k is a constant depending on the number of false positive responses allowed. If the increase in current is caused by an increase in I, then the smallest such increase that can be detected is given by

$$\Delta I = k(I/Fat)^{\frac{1}{2}} \tag{2}$$

Making the plausible assumptions that k, F, a, and t stay constant, this would not look at all like the relation between increment threshold and field intensity for the eye; on the usual double logarithmic plot it is simply a straight line which continues to go down when I is decreased, whereas the threshold of the eye levels off at the value of the absolute threshold. It might be suggested that the similarity would be increased if the approximations involved in equation (1) were improved or eliminated. The basic idea is that, to be detected, the current must be higher than a certain value which is set at a level which will rarely be exceeded in the absence of the incremental light; if the current is low its values in successive sampling periods will be distributed according to the Poisson, not the Gaussian, distribution, and the exact performance can be found from tables of the cumulative Poisson function (see *ref. 6)* by looking up, for a given mean rate (cathode current), first the number of events which is exceeded with the desired rarity, and then the mean rate which will exceed this number on 50% of occasions: the difference between the mean rates is then the required increment. In *fig. 1* the approximate formula (1) is compared

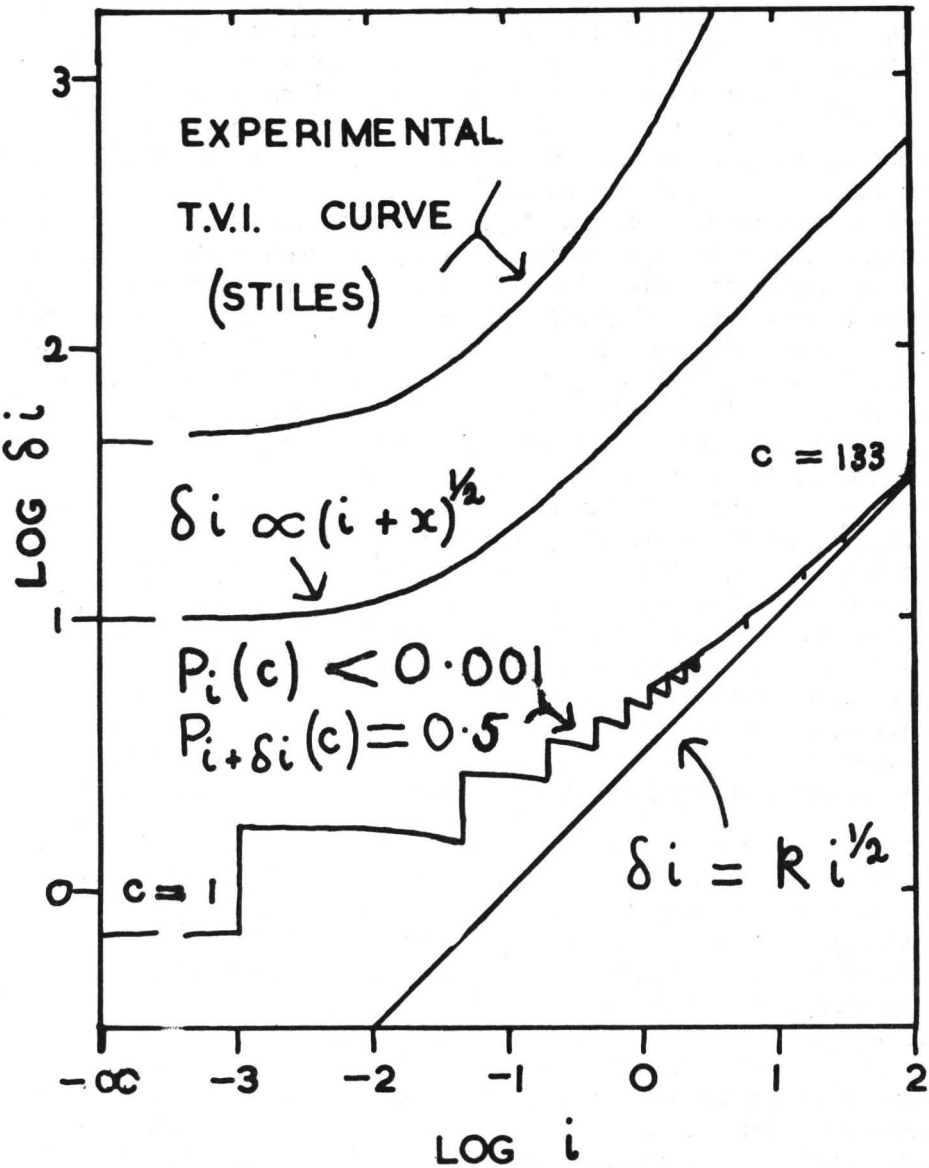


Fig. 1. Double logarithmic plot of four relations between least detectable increment (δi) and average intensity (i). From the bottom upwards: (a) approximate formula for photocell without dark current; $k = 3.3$: (b) exact relation when less than one false positive allowed in 1000 trials; $P_i(c) < 0.001$, and the value of c increases in steps from 1 to 133: (c) approximate formula for photocell with dark current; arbitrarily placed: (d) Stiles' experimental curve of increment threshold versus background intensity; arbitrarily placed.

with the exact result obtained in this way for a degree of reliability allowing 0.1% of false positive responses, which is equivalent to a value of $k = 3.3$. Using a double logarithmic plot, the mean increment required to raise the mean rate on 50% of trials to a value which it would have exceeded on less than 0.1% of trials if the mean rate had been unchanged (no increment in light intensity), are plotted for various values of the initial mean rate. Steps occur as the value of photocurrent which must be exceeded increases in steps from that corresponding to 1 electron to 2 electrons, then 3 electrons, and so on. Below this is shown the straight line corresponding to equation (1), whilst the uppermost curved line shows one of Stiles' experimental curves relating increment threshold and background illumination. It is true that the exact theory deviates from the approximate theory in the right direction, and the deviations would be even greater if the reliability demanded had been higher (corresponding to a larger value of k), but there is still a considerable difference between it and the experimental curve, which levels off much more suddenly. In addition, it should be observed that the theoretical curve can only become completely level when the threshold has come down to one quantum, and the threshold of the eye is not as low as this.

For these reasons the noiseless detector has been rejected as a model, and a source of noise has been introduced. In the following treatment the approximation which was involved in equation (1) has been relied upon, but it may be noted at this point that replacing 0.5 by 0.4 in the exponent of this equation would improve the approximation if the condition for seeing a stimulus corresponds to the absorption of between 6 and 100 quanta, and if the degree of reliability allows 0.1% of false positive responses; and that if the threshold number lay below 6, a further reduction would be needed.

(b) Effect of intrinsic noise or dark current.

Since the eye does not behave like a detector with no intrinsic noise, it seems reasonable to introduce this complication. It would certainly be encountered in any physical system which had a sensitivity of the same order as that of the eye, and arguments have been given elsewhere for the view that an intrinsic source of noise limits the sensitivity of the rod mechanism *(ref. 7)*. Many of these arguments would also apply to the cone mechanisms. Intrinsic noise of this sort could be introduced into the model in a number of ways, and that followed here is not an inevitable choice. It is assumed that the receptors are acted on by the intrinsic source of noise in a manner indistinguishable from the way they would be acted on by a constant, even, retinal illumination, which will be called the 'dark light'. This assumption has three *a priori* advantages: (1) there is a simple physical interpretation for it - thermal decomposition of the photosensitive molecules; (2) there is a simple method of estimating the intensity of the dark light from psychophysical measurements; and (3) it is conceptually simple because it is so closely analogous to the dark current of a photocell.

Proceeding from the ideal detector, equation (1) can be modified by supposing that there is a dark current x, so that the total current is $i' = i + x$, and the least detectable increment, δi, detectable in t secs, is approximately

$$\delta i = k(i + x)^{\frac{1}{2}}/t^{\frac{1}{2}} \qquad (3)$$

This relation is shown on the double logarithmic plot of *fig. 1*, and is appreciably closer in shape to the experimental curve, though there are still important differences which are considered in the next section.

Since we want to apply this theory to a detector, the output of which cannot be measured directly, it would be more convenient to write the equation for the model in units applicable to the eye, i.e. light intensities. This is easily done, taking $i = F\,I$ and $\delta i = F.\Delta I$, and gives

$$F.\Delta I = k(FI + x)^{\frac{1}{2}}/(at)^{\frac{1}{2}}.$$

Only x remains as a current, and this can be converted to light units by supposing a dark light X, which is related to the dark current, x, in exactly the same way as the real light intensity, I, is related to the photocurrent, i. Then the equation for the model becomes:-

$$\Delta I = k(I + X)^{\frac{1}{2}}/(atF)^{\frac{1}{2}} \qquad (4)$$

It will first be shown that this equation does describe the changes of increment threshold when background intensity is varied under certain experimental conditions, and if it is assumed that k, X, a, t, and F stay constant. Values of X and F will then be derived from Stiles' results.

II. INCREMENT THRESHOLD OF THE EYE

Fig. 1 shows that there is still a big difference between the theoretical curve of equation (4) and Stiles' experimental curves, and this is probably the factor which has discouraged people from pursuing the idea, put forward by Rose *(ref. 4)* and de Vries *(ref. 5)*, that visual thresholds are limited by signal/noise considerations. The difference is that the sloping parts of the experimental curves tend to show close agreement with Weber's law ($\Delta I \propto I$), whereas the theory predicts a square root law ($\Delta I \propto I^{\frac{1}{2}}$), and this divergence between the model's behaviour and that of the eye needs to be accounted for.

In the case of the rod mechanism it has been shown *(ref. 8)* that Weber's law holds for long duration, large area, stimuli, whereas the square root law holds for short duration, small area stimuli. It is true that the reasons for these differences are not well understood, but an agreement with the model's predictions is sufficient to encourage one to pursue it, and it is here shown that the same conditions of stimulation that were previously reported to give such an agreement for the rod mechanism in the periphery of the retina also give agreement in the case of the red (π_5) and green (π_4) cone mechanisms at the fovea.

Method.

Thresholds were taken by a self-setting technique in an apparatus similar in essentials to that described previously *(ref. 8)*. This allowed a test stimulus of variable area and duration to be superimposed in the middle of a uniform background field subtending 13^0. The required colours of background and test stimulus were obtained with Ilford 'Spectral' filters 608 and 604. The points of *figs. 2* and *3* are the means of four settings, and the usual precautions were taken in deciding the order of taking the readings, in avoiding any but visual cues as to the settings of the wedges, and in allowing time for the eye to adapt to each field intensity so that the thresholds were stable. Foveal fixation was obtained with an incomplete cross, the test stimuli appearing in the missing part at the intersection of the arms. The cross appeared black at high background intensities and was dimly illuminated at low intensities. The writer was the subject for both of the experiments reported here.

Results.

(a) The Red mechanism (π_5).

Fig. 2 shows an experiment in which the increment threshold for a red light added to a green background was determined at the fovea for two types of stimulus. The upper set of points was obtained with a test stimulus of duration 7.3 ms and area 0.0058 degrees^2 (diam. 5.16 minutes): the lower set with a stimulus duration of 1 second and area 4.83 degrees^2 (2.48^0 diameter). Each point is the mean of four settings, and this mean was estimated to have a standard error of 0.05 log units. It is immediately obvious that, as the background intensity is raised, the lower set of points rise more rapidly than the upper set, so that the sets of points approach each other and the threshold intensities for the two types of stimulus are less widely separated; there is apparently less temporal summation, or less spatial summation, or less of both, at high than at low background intensities. This behaviour is similar to that of the rod mechanism.

The equation of the curve drawn through the upper set of points (short duration, small area stimulus) is that of the suggested model, equation (4). It is only a moderately good fit, since two of the points lie more than two standard errors from the line, but this curve certainly fits the points better than either of the other two curves which will be considered. The curve through the lower set of points is $\Delta I \propto (I + X)$, which is a formula suggested by Fechner to explain the deviations from Weber's law at low background intensities. It will be noticed that the value of X required to give a good fit in this formula is the same as that used in fitting formula (4) to the upper points; these values of X are the values of I at the intersection of the two asymptotes of each curve, and these points are indicated thus +. The middle line is Stiles' averaged t.v.i. curve for the red (π_5) mechanism determined with a stimulus of 0.2 sec duration and 0.79 degrees^2

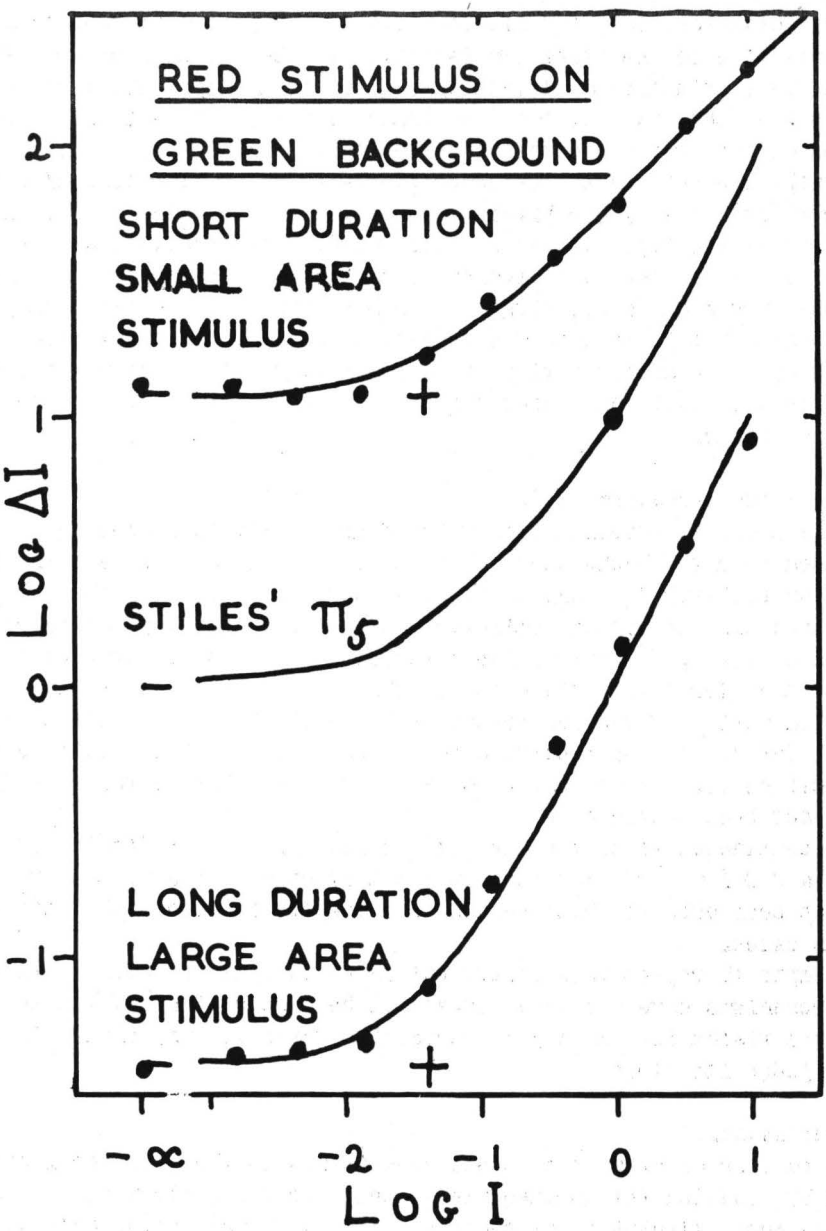


Fig.2. Threshold versus intensity curves for the red mechanism isolated by using a red stimulus on a green background. Bottom curve - stimulus 1 sec duration and 4.83 degrees^2 area. Middle curve - Stiles' average curve for π_5, stimulus 0.2 sec duration and 0.79 degrees^2 area. Top curve - stimulus 7 ms duration and 0.0058 degrees^2 area.

area (1^0 diameter) in a 10^0 diameter field. The positioning of this curve relative to the other two is arbitrary, but it will be seen that the intermediate stimulus conditions have given it a shape intermediate between the other two. It looks as though the shape of a t.v.i. curve depends on the area and duration of the test stimulus used, but that this shape will lie between the extremes indicated by the formulae $\Delta I \propto (I + X)$ and $\Delta I \propto (I+X)^{\frac{1}{2}}$. It seems likely, however, that the value of X is not dependent on the type of test stimulus used. These conclusions are rather tentative because there are two complicating factors involved in interpreting the curves of *fig. 2*. First, the red mechanism is possibly composed of low and high intensity components *(ref. 3)*. Second, the theoretical curve depends upon the approximation of equation (1), but a more exact curve cannot be used until one knows the order of magnitude of the number of quanta absorbed.

(b) The green mechanism (π_4).

Fig. 3 shows an experiment in which a green stimulus, observed foveally, was added to a red background. These conditions should isolate the green mechanism (Stiles' π_4), and the figure shows that, as with the rods and the red mechanism, the type of stimulus used affects the slope of the rising portion of the t.v.i. curve. The stimulus for the lower curve was rather smaller than for *fig. 2*, since it was thought desirable to reduce the danger of contamination by the rod mechanism by confining the stimuli to the central fovea. The upper curve has been shifted down 1 log unit relative to the lower curve. Stiles' curve for π_4 is very similar to that for π_5 and it has not been reproduced.

The continuous lines are the same as in *fig. 2*; $\Delta I \propto (I+X)^{\frac{1}{2}}$ for the upper, and $\Delta I \propto (I + X)$ for the lower set of points. Again, the same value of X has been used for both curves, and the fit is moderately satisfactory in both cases.

Attempts to repeat this experiment under conditions which isolate the blue mechanisms have not been successful because of the difficulty of getting a rising limb on any one mechanism which is long enough to enable one to judge its slope.

(c) Conclusions.

The conclusion drawn from these experiments is that the model represented by equation (4) is adequate to describe the performance of the eye when the test stimulus is of short duration and small area. Some other factor must be entering in the case of long duration, large area stimuli, and it is presumably this factor which is responsible for the ubiquitous tendency for Weber's law to appear. It might be possible to devise a model which would mimic the behaviour of the eye for all types of test stimulus, but it would involve a good many arbitrary features, and at the moment it

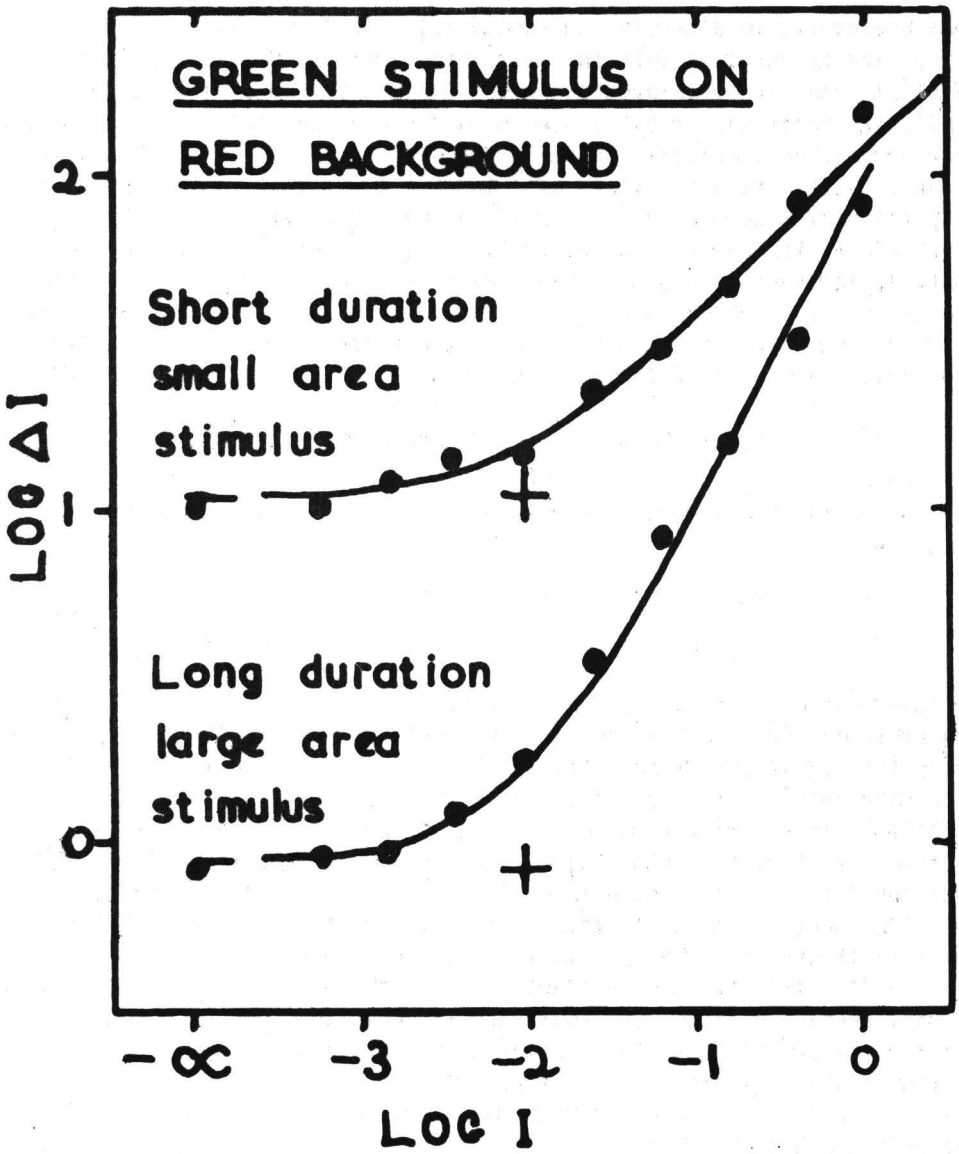


Fig.3. Threshold versus intensity curves of the green mechanism isolated by using a green stimulus on a red background. Lower curve - stimulus 0.65 degrees^2 area (55 minutes diameter) and 1 second duration. Upper curve - stimulus 0.0058 degrees^2 area (5.2 minutes diameter) and 7 ms duration: this curve has been shifted down 1 log unit relative to the lower curve. Both scales in arbitrary intensity units.

seems preferable to stick to the "photocell with dark current" model represented by equation (4), adding the proviso that the eye is less efficient than the model predicts when the stimulus is of long duration. or of large area, and probably also when the background intensity is high. These deviations complicate the estimation of F, for the values obtained by substituting measured values of I and ΔI in equation (4) depend upon the particular values of a and t used in the experimental determinations of threshold. It is, however, possible to obtain unique values of the dark light, X, for each mechanism, since the same value seems to be required both in the photocell model, and the "Weber's law with dark light" model ($\Delta I \propto (I + X)$) which was used to fit the lower curves of *figs. 2* and *3*. These values are derived from Stiles' results in the next section.

III. INTRINSIC NOISE OR DARK LIGHT OF CONES

(a) Values.

Equation (4) plotted on double logarithmic co-ordinates has two asymptotes:

$$\text{when } I >> X, \quad \Delta I \longrightarrow k(I/atF)^{\frac{1}{2}}$$

$$\text{and when } I << X, \quad \Delta I \longrightarrow k(X/atF)^{\frac{1}{2}}$$

The intersection of these asymptotes occurs at $I = X$. This point is marked by a cross on *figs. 2* and *3*, and the value of the dark light could be read off as the ordinate at this point. Rather than relying on these results, which were obtained from a single subject, it seemed preferable to make use of Stiles' curves *(ref. 3)* which are based on extensive measurements on four subjects. He gives the intensity of background required to raise ΔI to ten times the value of the absolute threshold for the mechanism under consideration. Some uncertainty is introduced in deriving the value of the dark light from this figure; if $\Delta I \propto (I + X)$, it would be 1/10 this intensity, whereas if $\Delta I \propto (I + X)^{\frac{1}{2}}$ it would be 1/100. In fact the slope of his curves in the relevant region seems to lie about half way between these (see *fig. 2*), and I have therefore taken the dark light to be 1/31.6 of the intensities of background given by Stiles. This figure cannot be out by more than $\pm$ 0.5 log units. These figures, together with those previously reported for rods *(ref. 8)* are shown in *Table I.*

(b) Interpretations.

It will be seen first that all the cone mechanisms have a dark light about 10^3 to 10^5 times as high as the rods; the "high intensity" mechanisms would presumably have even higher dark lights. This is, of course, just another way of saying that cones are less sensitive than rods, but it is rather more specific to say that they have a higher dark light, just as it might be more specific to speak of one photocell having a higher dark

TABLE I

Dark lights of rods and cones, together with wavelengths of maximum sensitivity (λ max.), calculated dark lights (see text for method), and approximate overall quantum efficiencies

Mechanism involved	λ max.	Dark lights in quanta (λ max)/sec. degrees^2		Approximate Overall quantum Efficiency
		Measured	Calculated	
Rods	507	2×10^2 to 3×10^3 (b)	1×10^3	5×10^{-2} (a)
Photopic Sensitivity Curve	555	---	3×10^6	5×10^{-3} (a)
Stiles π_1	445	1.05×10^7	2.9×10^{-3}	5×10^{-5}
Stiles π_3	440	4.5×10^7	7.2×10^{-4}	1.4×10^{-5}
Stiles π_4	542	3.1×10^6	2.6×10^5	3.8×10^{-3}
Stiles π_5	573	3.6×10^6	2.8×10^7	3.7×10^{-3}

All the figures are derived from Stiles *(ref. 3)* except
(a) Rose *(ref. 14)* and
(b) Barlow *(ref. 8)*.

current than another. Furthermore, since the value of the dark light does not depend on the type of test stimulus used, this measure of sensitivity avoids the paradoxical conclusion, reached by Arden and Weale *(ref. 9)* as a result of measurements using a small area, short duration, stimulus, that cones are as sensitive as rods. According to the present view, their finding results from central cones having an advantage over peripheral rods in detecting small *quantities* of light because the nervous pathways to which they are connected do not summate over such a large area or time, and therefore collect a smaller quantity of retinal noise.

It has been suggested *(ref. 10)* that dark light results from the thermal instability of the photosensitive substances in the receptors, that the rate of thermal breakdown depends upon the energy required to activate the molecules, and that this energy controls the position of the peak of the spectral sensitivity curves. It was hoped that a knowledge of the dark lights of the different cone mechanisms, together with knowledge of their spectral sensitivity curves, might be used to test the validity of this conjecture. In the fourth column of the table are given dark lights for the various mechanisms calculated on the following basis:

1. Rods have a dark light of 1000 hν(507 mμ)/s. degrees^2.
2. Each species of cone contains a substance similar to rhodopsin except for its activation energy, E, which is such as to cause maximum absorption at the wavelength shown in column II.
3. All the substances, *in situ* in the retina, have the same photosensitivity.

The calculations were made from the expression *(ref.11)*

$$f = \exp(-E/kT)$$

where k is Boltzmann's constant, T the absolute temperature, and f the fraction of molecules with energy greater than the activation energy. It is obvious that the dark lights calculated on this basis are very different from those observed. The individual sensitivity curves and dark lights do not, therefore, support the suggested relation between the two; but it will be noticed that the dark lights of all the cones are close to that expected from the overall photopic sensitivity curve (max. sensitivity 560 mμ, calculated dark light 3 x 10^6 hν/s. degrees^2). It is almost certainly wrong to assume that all the substances have the same photosensitivity *in situ* in the retina; for example, Brindley *(ref.12)* found evidence that the red mechanism had a photosensitivity 18 times that of rhodopsin. A tricolour system in which the three components had very different dark lights might give rise to curious illusions at light intensities which were insufficient to bring in all components, and it is possible that a light concentrating mechanism has been evolved to increase the photosensitivity of the red mechanism, and a screening pigment to decrease the photosensitivity of the blue mechanism, thus bringing their dark lights closer together. Quantum efficiency might be expected to vary with photosensitivity, so the low values for the blue mechanism shown in the final column of the table appear to support this suggestion, but very much greater differences would actually be needed. The idea that there is only a single photopic pigment whose spectral sensitivity was varied by coloured screens might fit in with the observed dark lights, and so might a system in which contributions from different receptors were combined at a low level in the optic pathways.

IV. QUANTUM EFFICIENCIES OF CONES

F in the equations for the model was defined as the fraction of quanta incident on the photocathode which caused emission of an electron. The corresponding quantity for the eye would be the fraction of quanta sent through the pupil which are "effectively absorbed" by the photosensitive materials subserving the mechanism under consideration, but a difficulty arises in deciding what to understand by the words "effectively absorbed". In the case of rhodopsin a quantum can be absorbed without bleaching the molecule, and even if bleaching occurs it is by no means certain that the

rod is always activated. Further, if the rod is activated, it is still not certain that this information is successfully transmitted to the place where the threshold decision is made. It therefore seems desirable to accept as "effectively absorbed" only the minimum number of quanta required to account for the performance actually achieved by the eye. F is then the *overall quantum efficiency*; that is, the smallest fraction of the quanta sent into the eye which would enable it to perform the task which it does perform. This quantity will, of course, always be smaller than the fraction of quanta actually absorbed, but it might approximate to it in the case of a task to which the eye is well adapted. One might hope to subdivide the overall quantum efficiency into the efficiencies of the various steps - absorption, excitation of receptors, transmission to the central nervous system, etc., - but this is clearly not possible until information becomes available about the stages intermediate between the light entering the eye and the subject giving his responses.

The overall quantum efficiencies shown in *Table I* were calculated from Stiles' results in the following way. Equation (2) was used rather than (4) because it was thought better not to make any allowance for the dark light in the first place; k was assumed to have a value of 3.3, which corresponds to a degree of reliability which allows the subject to give 1/1000 positive responses to zero stimuli; a and t were the area and duration of the test stimuli (0.79 degrees^2 and 0.2 sec); and the values of ΔI and I were taken from the t.v.i. curves at the point where F is greatest, which is the point where the curve (plotted on double logarithmic coordinates) touches a line of slope $\frac{1}{2}$.

The overall quantum efficiencies are low compared with that of rods (e.g. 0.07 derived from Hecht *et al's* figures *(ref. 13)*, and 0.05 from Rose *(ref. 14)*); allowance for the dark light would increase the figures by a factor of less than 2, and they might be further increased by the use of more favourable areas and durations of stimulus. The fact which emerges quite clearly is that the blue mechanisms have very low quantum efficiencies compared with the red and green mechanisms.

GENERAL CONCLUSION

THE photocell with dark current provides a fairly satisfactory physical model which mimics the principle features of the performance of the eye in detecting incremental stimuli. It is suggested that each of the mechanisms separated by Stiles has a characteristic dark light, analogous to the dark current of a photocell, and a characteristic quantum efficiency, in addition to its characteristic spectral sensitivity curve. These would account for the shape and position of the t.v.i. curves under some conditions, but a feature of the performance of the eye which is not mimicked by the model is the decrease in quantum efficiency that occurs when the test stimulus is made larger and longer, and when the background is made brighter. This

feature leads to the appearance of Weber's law when long duration, large area, test stimuli are used, and causes reduced temporal and spatial summation at higher background intensities.

ACKNOWLEDGEMENT

I am very grateful to Dr. W. S. Stiles for the help he has given in deriving figures for dark lights and quantum efficiencies from his results.

REFERENCES

1. STILES, W. S. The directional sensitivity of the retina and the spectral sensitivities of the rods and cones. *Proc. roy. Soc.*B, 1939, **127**, 64-105.
2. STILES, W. S. Increment thresholds and the mechanisms of colour vision. *Docum. Ophthal.*, 1949, **3**, 138-165.
3. STILES, W. S. Further studies of visual mechanisms by the two colour threshold method. *Union Internationale de Physique pure et appliquée: Coloquio-sobre Problemos Opticos de la Vision. Madrid*, 1953.
4. ROSE, A. The relative sensitivities of television pick-up tubes, photographic film, and the human eye. *Proc. Inst. Radio Engrs. N.Y.*, 1942, **30**, 293-300.
5. DE VRIES, Hl. The quantum character of light and its bearing upon the threshold of vision, the differential sensitivity and acuity of the eye. *Physica*, 1943, **10**, 553-564.
6. MOLINA, F. C. Poisson's Exponential Binomial Limit. D. Van Nostrand Co. Inc., New York, 1942.
7. BARLOW, H. B. Retinal noise and absolute threshold. *J. opt. Soc. Amer.*, 1956, **46**, 634-639.
8. BARLOW, H. B. Increment thresholds at low intensities considered as signal/noise discriminations. *J. Physiol.*, 1957, (in the press).
9. ARDEN, G. B. and WEALE, R. A. Nervous mechanisms and dark adaptation. *J. Physiol.*, 1954, **125**, 417-426.
10. BARLOW, H. B. Purkinje shift and retinal noise. *Nature*, 1957, **179**, 255-256.
11. STILES, W. S. The physical interpretation of the spectral sensitivity curve of the eye. *Worshipful Company of Spectacle Makers Convention*, Nov. 1948.
12. BRINDLEY, G. S. A photochemical reaction in the human retina. *Proc. phys. Soc.* B., 1955, **68**, 862-870.
13. HECHT, S., SHLAER, S. and PIRENNE, M. H. Energy, quanta and vision. *J. gen. Physiol.*, 1942, **25**, 819-840.
14. ROSE, A. The sensitivity performance of the human eye on an absolute scale. *J. opt. Soc. Amer.*, 1948, **38**, 196-208.

PROFESSOR Y. LE GRAND presented his paper (21). DR. W. A. H. RUSHTON said that as it had been established that the deuteranope, like the normal, had two pigments it would seem to him that deuteranopy arose from a loss of organisation. Professor Le Grand had mentioned an alternative view on which the normal had a random distribution of two pigments. In that case, the deuteranope would have increased the organisation and in such a way as exactly to eliminate the possibility of colour discrimination.

DR. M. H. PIRENNE referred to the cone connexion scheme with which Professor Le Grand had illustrated the possibility of colour integration at the retinal rather than the cortical stage. As a basis for discussion he presented a lantern slide, showing retinal connexions, from Polyak's contribution to the 1947 Conference on Colour Vision held at Cambridge.

MR. J. GUILD also referred to Professor Le Grand's suggestion that each cone might contain different concentrations of three light-sensitive pigments. Twenty-five years ago, he (Mr. Guild) had suggested* that one possible way in which the three-dimensional behaviour of vision in matching experiments could arise might be the following. The individual receptors (of which many were involved in the perception of colour) might differ among themselves in spectral sensitivity, the differences being, possibly, a mere random variation from a norm, and there might be three cortical centres (or three types of cortical centre) whose relative excitation determined the colour sensation evoked in the cognitive element of the observer. If the probability of any retinal receptor being coupled to one or other of these cortical centres was determined in some way by the position in the spectrum of its maximum sensitivity, the whole collection of receptors in operation at any one time would operate as three independent receiving systems with distinctive spectral sensitivities. In that paper, he was not concerned with physiological or biochemical implications; his analysis was wholly schematic. If Professor Le Grand's hypothesis were correct, the random variation of the concentrations of the three photosensitive substances in each cone would provide the kind of variation of individual receptors from a norm which he (Mr. Guild) had mentioned, and the relative concentrations in any given receptor might quite possibly determine the probability of the receptor being coupled to a cortical element of one or other of the three types involved in colour cognizance.

THE CHAIRMAN (DR. W. S. STILES) remarked that he had found the conception of lability of the brain in the development of colour vision, mentioned by Professor Le Grand, most useful at least as a simple model in

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*"Some problems of visual reception" contribution by J. Guild to "Joint Discussion on Vision", Physical and Optical Societies, June 1932, Cambridge University Press.

trying to understand the colour-naming properties of persons with normal colour-vision in one eye and defective colour-vision in the other. The name applied to a stimulus to the defective eye would be the one that had the greatest probability of agreeing with the name applied by the more discriminating eye, and this association of names and stimuli would be acquired when the colour "learning" of the child was in a very early stage.

In introducing his paper together with the supplement, (25), DR. D. L. MACADAM said that its title should perhaps be changed to "A Non-Linear Hypothesis": it had features in common with several other contributions to the Symposium including that of Prof. Shklover.

THE CHAIRMAN asked whether the non-linearity introduced had got rid of the original discrepancies which Dr. MacAdam had found in his colour adaptation results *(ref. 16,* Paper 25).

DR. MACADAM said that the computers were working on this but had not yet provided the answer.

THE CHAIRMAN then asked Professor S. G. Yurov to read the paper by Prof. D. A. Shklover (Paper 35) together with the latter's comments on Dr. MacAdam's contribution.

PROFESSOR YUROV explained that Prof. Shklover had returned to Moscow only recently and had immediately mailed him the following comments:

"The problem of the mechanism of formation of hue, saturation and brightness sensation and the adjacent problem of the development of an equicontrast colorimetric system are very important for present-day colorimetry.

Of all the papers presented at the Symposium which we have had the opportunity to get acquainted with, only Dr. MacAdam's paper (especially the supplementary material) and my own are devoted to these problems. An equicontrast colorimetric system cited in my paper was first communicated at the Fourth Conference on Physiological Optics, Leningrad, October 1955, and was published in the form of theses. We were very pleased to learn that Dr. MacAdam had recently arrived at a solution of this problem which was in principle very close to ours.

In Dr. MacAdam's first paper sent at the same time as ours, there was proposed a very interesting attempt to explain the great majority of the facts of visual processes with the help of the "beat-frequency" hypothesis.

In the supplement to his paper sent in July this year Dr. MacAdam reflects this hypothesis previously proposed by him and develops a purely mathematical model of the colour vision process, the principles of which are expounded by him in the form of seven main statements of the theory. It is of interest to point out that the "beat-frequency" hypothesis and all the main statements of Dr. MacAdam's theory (with the exception of the point 7, relating to the problems of adaptation which we did not touch upon) are also formulated in my paper.

But though the main statements are very similar yet the theories differ in the concrete forms of the solutions of the problems proposed. That is why we consider that it would be worth while comparing the results obtained by the two authors:

1. In both works definite spectral response curves of the three receptors are taken as the basis for further development.

We used the curves $\bar{x}$, $\bar{y}$ and $\bar{z}$.

In Dr. MacAdam's work the curves $\bar{r}$, $\bar{g}$, $\bar{b}$, obtained as a result of his experiments on colour adaptation were used.

Our calculations lately have shown that the best coincidence of the theory with the results of experiments is obtained when the spectral characteristics of the receptors found by E. N. Yustova are used as the main curves. These curves were obtained on the basis of the investigation of the colour vision of dichromats carried out in accordance with a new method suggested by N. D. Nuberg.

As our formulae state, the intersection points of the spectral response curves of the receptors correspond to those wavelengths for which the constant hue loci in the colour diagram are straight lines. That is why not only the form of the spectral response curves of the receptors, but a correlation of their scales is important for the results of our calculations. In this connexion we consider the curves, $\bar{r}$, $\bar{g}$, $\bar{b}$, used in Dr. MacAdam's report, which for the white radiation ("E" or "C") give reactions differing to a large extent from each other, to be unacceptable.

2. The second main thesis of both theories is the acceptance of a certain non-linear dependence between receptor reactions and the intensity of the perceived radiation.

In our work there is used the logarithmic dependence:

$$V_R = \log (R + C).$$

Dr. MacAdam in his report uses the power dependence:

$$V_R = a + bR^P, \text{ where } P = 0.3 - 0.42.$$

With suitable assignments of the coefficients in the equations, these formulae can give very similar dependences. Nevertheless we consider the logarithmic dependence to be preferable as it: (a) agrees with the Weber-Fechner law and was used by Helmholtz and Stiles in their works on the metrics of colour space, (b) enables one to explain the non-dependence of chromaticity sensation on brightness in a certain range of intensities

$$(R \gg C;\ \log R - \log G = \log {}^{R}/_{G}),$$

(c) leads, in the case of colours of low saturation and sufficiently high brightness to an equicontrast chromaticity diagram connected with the standard chromaticity diagram by linear equations.

Dr. MacAdam states in his report that in the case of a strict logarithmic dependence, loci of constant hue must be straight lines, but in practice it is not so.

3. Both theories under consideration hypothecate the formation of two new signals (V_α, V_β), characterising the colour of the perceived radiation from three non-linear primary receptor responses.

These signals, according to our theory, are formed by subtraction of three primary signals:

$$V_\alpha = 5\ (V_R - V_G);\ V_\beta = (V_B - V_G).$$

In MacAdam's work the formation of signals of chromaticity is also connected with the formation of differences of receptor responses. However in contrast with our work, MacAdam, besides the difference of "red" and "green" responses, uses in his theory the difference of some fourth "yellow" (dependent on some "pseudolinear" combination of red and green stimulations) and "blue" responses.

Chromaticity signals are connected with these differences by the following complex equations:

$$V_\alpha = 3.2\ (V_R - V_G) + \mathrm{Cot}\ 70^0\ (i - V_3)$$

$$V_\beta = i - V_B$$

where - $i = G + R\ (V_R - V_G) - 0.0282\ (V_P - V_G)$.

It is of interest to note that the principle of the formation of chromaticity signals proposed by us very closely recalls the well-known equation proposed by Adams in 1942 which is widely used at present in the practice of colorimetry. A substantial difference of our formulae and Adams' equations consists, however, in the fact that instead of C.I.E. tristimulus values, we use the spectral sensitivity curves of the three receptors and that empirical correlation between responses and components we replace by logarithmic dependence.

Already in 1955 we had proposed a hypothesis on the possible mechanism of formation of differences of receptor responses. This hypothesis considered a new differential frequency as a beat-frequency which is formed as a result of a simple addition of two series of corresponding impulses. We think that notwithstanding the fact that the first MacAdam report, widely using the beat hypothesis, raised objections, the use of the beat hypothesis in connexion with the problem of formation of chromaticity signals is very penetrating. One of the difficulties connected with this hypothesis is that in such a case we don't deal with the sinusoidal oscillations considered in the usual theory of beat-frequencies but with trains of pulses. However, it is easy to prove that in the case of

summation of two trains of pulses, the difference frequencies are also formed.

These difference frequencies in that case may be interpreted as periodical "condensation" of impulses or as their periodical superposition, resulting in the doubling of their amplitudes.

We built an electronic model of the colour vision process which is based on the theory propounded and which provides a colour diagram of the new colorimetric system directly on the screen of a cathode-ray tube. *Fig. 1* gives some oscillograms which were obtained with this model

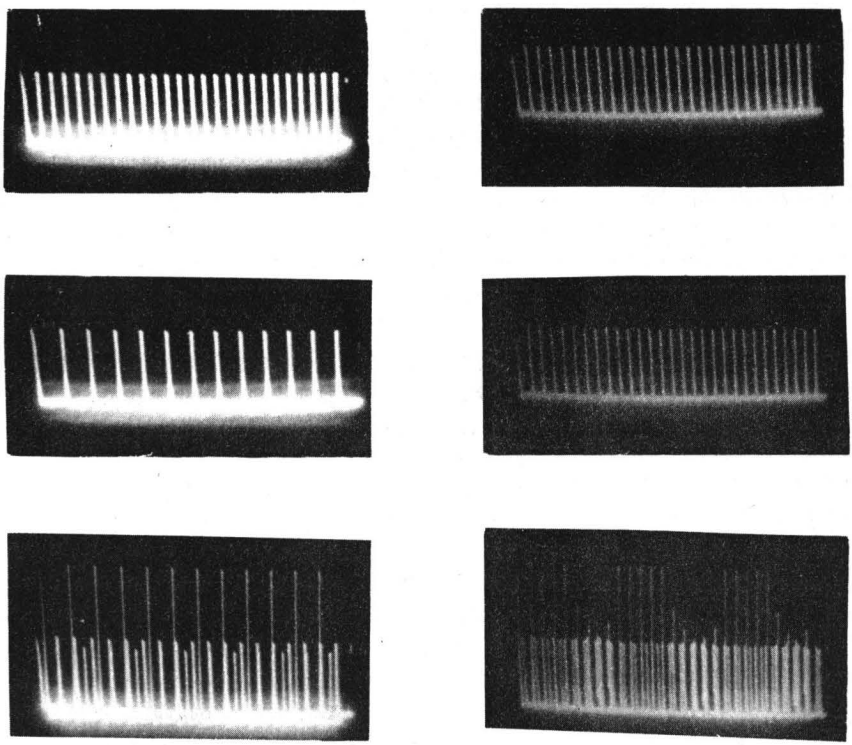

Fig. 1a $V_1 = 25$; $V_2 = 13$; $V = V_1 - V_2 = 12$.

Fig. 1b $V_1 = 27$; $V_2 = 30$; $V = V_2 - V_1 = 3$.

Fig. 1. - Oscillograms, obtained on the electronic model, illustrating the process of formation of beat-frequencies by the summation of two trains of pulses of different frequencies.

showing the result of summation of two trains of pulses of different frequencies. In these oscillograms we can clearly see the process of formation of beat-frequencies. However, it should be pointed out that in the case of great differences between frequencies of summed impulses there are some difficulties both in obtaining and in the further separation of beat-frequencies.

4. In both Dr. MacAdam's and our theories the forms of the relations between colour hue, colour saturation and colour contrast sensations and the signals, characterising the chromaticity of perceived light, are completely identical:

(a) The colour hue is determined by the ratio of the chromaticity signal values.

(b) The saturation of colours is determined by the root mean square of the chromaticity signal values.

(c) Colour contrast between two colours is determined by the root mean square of chromaticity signal differences.

The comparison of final equations for colour hue, saturation and colour contrast sensations, obtained by Dr. MacAdam and by us, shows that our equations are simpler and therefore the physiological interpretations are easier. On the other hand MacAdam's equations including more constants might give a closer fit to the experimental results.

However, owing to the inaccuracy of the data of the standard C.I.E. observer on which all the calculations are based and also owing to the uncertainty of experimental results, it is not now expedient to build complicated empirical equations which have to reproduce experimental data with great precision.

Though we agree with Dr. Hartline's opinion, expressed in his letter to Dr. MacAdam, that the nervous system is not a sort of digital computer, we must take into account experimental facts showing that the human visual apparatus is able to discriminate radiation according to colour hue and saturation. Consequently the visual apparatus must solve in an unknown way the mathematical equations mentioned above.

In this connexion the task of colorimetrists is to formulate the simplest equations, describing, at least qualitatively, the experimental facts, while physiologists must find the corresponding mechanism in the visual system and investigate its action.

For just this purpose the new equicontrast colorimetric system is proposed. It is undoubtedly preliminary and subject to further modifications."

DR. D. B. JUDD asked whether Dr. MacAdam's theory could be applied to heterochromatic brightness matching. In reply, DR. MACADAM said he had not so far developed its possibilities in that direction but the simplest

procedure for bringing in brightness-matching would lead to non-additivity in the reverse sense to the Kohlrausch effect, i.e., mixed (desaturated) stimuli would come out too bright.

DR. H. B. BARLOW presented his paper (28). He concluded by speculating whether the Purkinje shift could be attributed to the large increase in noise to be expected from thermal dissociation at longer wavelengths. By using the "dark light" of the threshold-versus-intensity curves for rods and cones, quite good agreement with the peak shift of 560-505 mμ was obtained. On the other hand the blue cone mechanism was just as noisy as the red mechanism and one might have to assume that noise could spill in neurally to the blue from the red mechanism or that a system of overlying pigments might be involved.

PROFESSOR G. WALD said that noise was certainly fundamental to the visual process; it could be generated thermally and added to the signal at any stage of its journey to the cortex, and the possibility of more central origin should always be remembered.

With regard to the Purkinje shift, he thought there were two factors worth considering. Firstly the possible kinds of chromophore pigments had absorptions in the ultra-violet and it was difficult to obtain from them a visual pigment with a maximum even in the blue. On the other hand, the reduction of chromatic aberration made it worth while to move to the red.

DR. H. J. A. DARTNALL said that cold-blooded animals, for whom thermal noise would be much less important, were found to supply considerably more visual pigments to the retina; on the other hand the birds, who had the highest body temperatures, had abandoned a variety of pigments in favour of coloured oil globules.

DR. E. BAUMGARDT favoured the theory that two quanta in a double hit were needed to excite a nerve fibre. The number two was implied by the laws of Piper for areal summation and Piéron for temporal summation. Frequency-of-seeing curves suggested that the minimum number of quanta required was more like four, five, six or seven. It had been shown that the double hit theory with the assumption of several double hits for threshold stimulation involved no contradiction and predicted a toe for the threshold-versus-intensity curves even if noise were absent. He himself would not wish to deny that noise was present, and he agreed with Professor Wald's suggestion of cortical origin.

He had recently recomputed the equivalent number of dark quanta required to explain the noise level, using the figures given by Graham and Margaria, and found that he could not agree with Dr. Barlow's calculation. He had consulted Dr. Graham on the interpretation of these figures, and was sure that he had used them correctly. The number of available noise quanta was too small to explain the results.

THE CHAIRMAN said that further discussion on Dr. Barlow's paper would be reserved until the remaining papers had been read.

PAPER 24

ADAPTATION AND THE TRICHROMATIC THEORY

By R. W. G. HUNT

Dr. R. W. G. Hunt graduated at Imperial College, London, and carried out research on adaptation under Professor W. D. Wright. Since 1947 he has been with the Kodak Research Laboratories at Harrow and is now leader of a group working on colour photography. He has been engaged in research and development work on the theory and practice of colour reproduction, and has carried out research on adaptation, and its effects on colour vision theory. He was secretary of the Physical Society Colour Group from 1952 to 1954.

24. ADAPTATION AND THE TRICHROMATIC THEORY*

By R. W. G. HUNT

SUMMARY

THE trichromatic theory is examined with particular regard to its ability to account for certain phenomena connected with adaptation, such as the constancy of metameric matches, the non-linearity of corresponding tristimulus values, and the variation of saturation with adaptation.

It is concluded that the trichromacy of colour matching is best accounted for by the theory that there are only three basic photochemical substances operating in photopic vision, and that they are present only in low concentrations. It is also concluded that there must be an adaptation-dependent non-linearity in the visual system, and it is suggested that it occurs in the compounding of two "colour difference" signals from the photochemical absorptions. It is suggested that a luminosity signal is compounded from the photochemical absorptions on a linear basis. It is concluded that the existence of a logarithmic signal-stimulus relationship cannot be properly deduced from discrimination data, and, for luminosity, theoretical considerations suggest a power relationship which also has some experimental support.

INTRODUCTION

IT is becoming more and more appreciated that the visual process consists of many stages, each linked to the other in complex fashion. As Thomson *(ref. 1)* so ably put it: "Each mechanism is activated by the one before it not as a line of goods trucks being pushed by an engine, ... but as a number of philosophers following each other in history. The wise men differ from the trucks because they choose and transmit to their juniors according to complicated, but nevertheless definite, laws only certain facts from the knowledge received from their predecessors". In one sense this trend in outlook is a departure from the trichromatic theory, which in fact some workers have abandoned altogether in favour of some form of polychromatic theory. The present paper is an attempt to show that the trichromatic theory is still the foundation of colour vision, but can no longer claim to be the entire edifice.

The directions from which the trichromatic theory has come under fire include the following:

(1) the absence of any anatomical or photochemical basis for the three colour mechanisms of the theory;

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* Communication No. 1897H from the Kodak Research Laboratories.

(2) the existence of five, rather than three, distinctly different colour sensations; red, yellow, green, blue, and white;
(3) the failure of the theory to account for certain colour changes induced by varying adaptation; and
(4) the failure of the theory to account for the various forms of colour deficiency.

Evidence can of course be marshalled from many quarters to defend the theory on all these counts, but it is the purpose of this paper to examine chiefly the testimony of adaptation and to attempt to build up a picture of the visual process which does justice at least to this aspect.

THE CONSTANCY OF METAMERIC MATCHES

IT is convenient to start with one of the most remarkable of all visual phenomena, the constancy of metameric matches. By this is meant that if a colour match is made when the two halves of the field are seen under the same adaptation condition, the match will remain a match when that adaptation condition is varied. Thus, for example, with the eye dark-adapted, a spectral orange may be matched by a mixture of spectral red and green; if the eye is then adapted to red light, the spectral orange may no longer look orange at all, but green, for instance; nevertheless the same red and green mixture also changes in appearance in exactly the same way and by exactly the same amount, so that the two halves of the field still match one another. From the point of view of visual theory this phenomenon is crucial; it is also vital for the application of colorimetry, for most colour matching experiments are carried out under conditions of dark adaptation, but the mixture curves thus derived are used to predict metamers (pairs of physically different but visually matching stimuli) for a wide range of adaptation conditions. It is curious, therefore, to find that the recent literature seems to have as much, or more, to say about the breakdown of metameric colour matches than about their constancy *(refs. 2, 3)*.

The same is true, however, of another basic phenomenon of colorimetry, namely additivity. By additivity is meant that if two physically different stimuli, A and B, match one another, and are additively mixed with another pair of physically different, but visually matching, stimuli, C and D, then the mixture of A and C will match the mixture of B and D. This phenomenon also has far-reaching consequences for colorimetry and, as we shall see, for visual theory also; but, again, recent literature deals mostly with the breakdown, or alleged breakdown of this conception *(refs. 4, 5)*. One reason for this state of affairs, both with respect to metameric constancy and additivity, is that when these phenomena occur there is nothing new to report, the original concepts having been published years ago. It is only when there is a discrepancy that pen is put to paper. In the case of additivity, however, Miss Trezona has recently re-examined the concept in some detail *(ref. 5)* and found that large deviations from additivity only

occurred under conditions of poor discrimination and that they were generally within the just-discriminable colour step for the particular conditions obtaining in the observation. A comparable modern vindication of the constancy of metameric matches does not seem to be available at present and the evidence for breakdowns at very high intensities seems incontrovertible; but the concept is still generally accepted *(ref. 6)* as being valid for most adaptation conditions. In this paper metameric matches will be assumed to be constant with adaptation, and the conclusions therefore will not apply to those conditions, such as adaptation at very high intensities, where these matches break down.

What conclusions can be drawn from the phenomenon of metameric constancy? There seems no escape from the conclusion that each basic spectral sensitivity curve of the retina must remain constant in shape (apart from changes made by multiplying all the ordinates by a factor independent of wavelength) *(ref. 7)*. From this deduction it follows that either the concentrations of the photochemical substances (upon which these spectral sensitivities depend) are always very low, or that the concentrations do not vary. For if the concentration of the photochemical substances were such that, for the wavelength of maximum absorption, more than about 20% of the light were absorbed, the spectral absorption curve, and hence the spectral sensitivity curve, would show marked variations in shape as the concentration was varied. A fixed photochemical concentration seems unlikely in view of the large changes in spectral sensitivity which can be induced by adaptation; and hence we conclude that the photochemical substances are present in the retina in such a way that they absorb only a small fraction of the incident light. This is, in part, an answer to the first of the criticisms of the trichromatic theory mentioned above: that a photochemical basis for the theory is lacking. If the photochemical substances are only present in small amounts, they will clearly be very difficult to detect.

Brindley *(ref. 8)* has suggested that the breakdown of red-green matches at very high adapting intensities is due to the "red" photochemical substance changing in concentration from that giving a peak absorption of about 70% at normal intensities to something appreciably lower at very high intensities. A difficulty with this approach is that the shape of the spectral sensitivity curve should change most at intensities near normal, and least as the intensities become higher, whereas the reverse seems to be the case: over a large range of medium intensities metameric matches hold, but as very high adapting intensities are approached, the matches break down, a little at first and then considerably. It seems therefore more satisfactory to attribute the constancy of metameric matches at normal intensities to a low but variable concentration of photochemical substance, and to seek an explanation for the breakdown of the matches at very high intensities elsewhere. For example, it has been suggested that the "red" substance is composed of a mixture of two component substances whose

concentrations retain the same ratio, except at very high intensities where one is perhaps rendered ineffective before the other. The hump in the luminosity curve at 0.60 μ reported by Wright might be construed as evidence for the red substance having a composite nature *(ref. 9)*.

THE NUMBER OF RETINAL MECHANISMS

DOES the constancy of metameric matches throw any light on the question of the number of independent retinal mechanisms? At first sight it may seem that since colour matching can always be performed with only three matching stimuli, there can be only three retinal mechanisms. But this does not follow. Suppose for the sake of argument that there were five retinal mechanisms, each dependent on a different photochemical substance. Suppose two stimuli, S_1 and S_2, resulted in photochemical absorptions equal to r_1, g_1, b_1, y_1, w_1, and r_2, g_2, b_2, y_2, w_2, respectively. If the conditions for a match were that each of these photochemical absorptions had to be equal, then five matching stimuli would be required. If, however, the conditions for a match were, for example:

$$r_1 - g_1 = r_2 - g_2 \quad \ldots \quad (1)$$

$$b_1 - y_1 = b_2 - y_2 \quad \ldots \quad (2)$$

$$w_1 = w_2 \quad \ldots \quad (3)$$

then only three matching stimuli would be required since the system, as far as matching is concerned, would be one of only three conditions. Thus the five mechanisms might give rise to sensations of redness (r), greenness (g), blueness (b), yellowness (y), and whiteness (w), a colour match being attained when the whiteness signals were equal, when the differences between the redness and greenness signals were equal, and when the differences between the blueness and yellowness signals were equal. It is the constancy of metameric matches, and additivity, which make the above type of system untenable for the following reasons.

We have seen that changes in adaptation can only result in overall changes in the heights of the spectral sensitivity curves, the shapes remaining constant. It therefore follows that if the two stimuli S_1 and S_2 are now viewed under different adaptation conditions, the same fractional change, say l, must occur in both r_1 and r_2. Similarly, let m, n, p, and q be the fractional changes occurring in the other four absorptions so that the two stimuli will continue to match if:

$$lr_1 - mg_1 = lr_2 - mg_2 \quad \ldots \quad (4)$$

$$nb_1 - py_1 = nb_2 - py_2 \quad \ldots \quad (5)$$

$$qw_1 = qw_2 \quad \ldots \quad (6)$$

The constancy of metameric matches with adaptation means that these equations should hold independently of l, m, n, p and q. Clearly this is not the case, except for q.

If however the conditions for a match were as follows:

$$r_1/g_1 = r_2/g_2 \quad \ldots \quad (7)$$

$$b_1/y_1 = b_2/y_2 \quad \ldots \quad (8)$$

$$w_1 = w_2 , \quad \ldots \quad (9)$$

then changes of adaptation would not upset the match, for

$$lr_1/mg_1 = lr_2/mg_2 \quad \ldots \quad (10)$$

$$nb_1/py_1 = nb_2/py_2 \quad \ldots \quad (11)$$

$$qw_1 = qw_2 \quad \ldots \quad (12)$$

clearly are independent of l, m, n, p, and q. This system, however, denies the concept of additivity. For if, in addition to S_1 and S_2, we have another pair of stimuli S_3 and S_4 which also match one another, then additivity experiments show that the mixtures $S_1 + S_3$ and $S_2 + S_4$ should also match one another. This implies that given:

$$r_1/g_1 = r_2/g_2 \text{ and } r_3/g_3 = r_4/g_4, \quad \ldots \quad (13)$$

it ought to follow that:

$$(r_1 + r_3)/(g_1 + g_3) = (r_2 + r_4)/(g_2 + g_4), \quad \ldots \quad (14)$$

and this is certainly not generally true.

It is thus clear that the constancy of metameric matches and additivity are crucial facts in visual theory, and over the range of conditions where they hold, there seems no alternative to the conclusion that there are only three *spectrally independent* retinal mechanisms operating. It is natural to identify these with three photochemical substances present at low concentrations.

This conclusion does not, however, necessarily limit the number of possible retinal mechanisms to three. For supposing a fourth receptor had a spectral absorption curve whose shape could be exactly matched by adding together certain proportions d, e, f, (which might vary with adaptation) of the three basic spectral absorption curves. The absorption, w, say, of such a receptor would clearly be given by:

$$w = dr + eg + fb \quad \ldots \quad (15)$$

It would therefore follow that any two stimuli S_1 and S_2, for which $r_1 = r_2$, $g_1 = g_2$, and $b_1 = b_2$, would give rise to absorptions w_1 and w_2,

which would be equal. If the response from this fourth mechanism were added to those from the three other mechanisms the conditions for a match might then be, for example:

$$lr_1 + \tfrac{1}{3}pw_1 = lr_2 + \tfrac{1}{3}pw_2 \quad \ldots \quad (16)$$

$$mg_1 + \tfrac{1}{3}pw_1 = mg_2 + \tfrac{1}{3}pw_2 \quad \ldots \quad (17)$$

$$nb_1 + \tfrac{1}{3}pw_1 = nb_2 + \tfrac{1}{3}pw_2 \quad \ldots \quad (18)$$

These equations would be independent of l, m, n, and p whenever $w_1 = w_2$, and this would occur whenever $r_1 = r_2$, $g_1 = g_2$, and $b_1 = b_2$. Thus, in these circumstances there are only three conditions for a match, the matches are independent of adaptation, and additivity holds; and yet there are four different types of receptor operating. This can only happen, however, if the fourth receptor has a spectral sensitivity curve which can be synthesized from those of the other three receptors. The same arguments can be applied to a fifth and sixth receptor or in fact to any number of receptors. The general formulation of the position is as follows: the constancy of metameric matches and the additivity of colour matches require that the spectral sensitivity curves of all retinal receptors be any linear combination of three basic sensitivity curves, and that as the adaptation is varied these curves either remain constant or change in such a way that the new curves are always linear transformations of the old curves.

It now, therefore, becomes possible to postulate an answer to the second criticism of the trichromatic theory, that there exist five, rather than three, distinctly different colour sensations. By regarding the trichromatic theory simply as a restriction on the variety of spectral sensitivity curves permissible in the receptors, no limitations are placed on the number of mechanisms or sensations. For instance, it is not incompatible with this form of the trichromatic theory for there to be five different types of receptor, having different spectral sensitivity curves, sending messages by five different routes to five different centres in the brain resulting in five different types of sensation, such as red, green, blue, yellow and white. It is only required that it be possible to synthesize linearly the spectral sensitivity curves of the five receptors from three basic curves. It must be admitted, however, that the transmission of five different types of signal from the retina to the brain contrasts a little strangely with the economy usually found in Nature.

MATCHING COLOURS SEEN UNDER DIFFERENT ADAPTATIONS

So far, although adaptation has been considered as a variable, we have restricted our attention to the case where the two halves of a matching field have always been seen under the same adaptation conditions. Colour

matches can, however, be made when the two halves of the matching field are seen under different adaptation conditions, either by the binocular matching technique or by local adaptation of different areas of the retina. The basic experiment usually consists of first matching a stimulus with a red, green, and blue mixture in the ordinary way with both halves of the field seen under the same adaptation conditions, and then repeating the match when either the test stimulus or the mixture is viewed under a different state of adaptation.

Suppose that under the first adaptation conditions the amounts of red, green and blue light needed to match a series of stimuli S, are represented by R, G, B, and that under the second adaptation conditions the amounts are R', G', B'. Because of the additivity of colour matches the photochemical absorptions corresponding to each of these sets of tristimulus values must be linearly related to them. Thus for any three of the photochemical absorptions:

$$\begin{pmatrix} r \\ g \\ b \end{pmatrix} = A \begin{pmatrix} R \\ G \\ B \end{pmatrix}, \quad \begin{pmatrix} r' \\ g' \\ b' \end{pmatrix} = A' \begin{pmatrix} R' \\ G' \\ B' \end{pmatrix} \quad \ldots \quad (19)$$

where r, g, b are the photochemical absorptions in the first state of adaptation, r', g', b', those in the second, and A and A' are nine-element square matrices.

Now if the conditions for a colour match are that the photochemical absorptions for the two halves of the field must be equal, then

$$\begin{pmatrix} r \\ g \\ b \end{pmatrix} = \begin{pmatrix} r' \\ g' \\ b' \end{pmatrix} \quad \ldots \quad (20)$$

Hence, from equation (19):

$$A \begin{pmatrix} R \\ G \\ B \end{pmatrix} = A' \begin{pmatrix} R' \\ G' \\ B' \end{pmatrix} \quad \ldots \quad (21)$$

which implies that the corresponding tristimulus values R, G, B, and R', G', B', are linearly related.

Now it has been shown *(refs. 10, 11, 12)* that in fact the tristimulus values R, G, B, and R', G', B', obtained under different adaptation conditions are not exactly linearly related. A linear transformation represents a useful

approximation to the results, but significant discrepancies not attributable to experimental error do occur. MacAdam has sought to explain this state of affairs by assuming more than three (actually six) basic spectral sensitivity curves. In order to explain the non-linearity of the tristimulus values, these spectral sensitivity curves must not be linear combinations of three basic curves, and, as MacAdam admits, this denies the constancy of metameric matches. It is important, therefore, to see whether there is a way of avoiding this position.

When the two halves of a matching field are viewed under the same adaptation conditions it seems entirely logical to believe that the condition for a match is equality of the photochemical absorptions; for equality of adaptation implies identical conditions, in which it is hard to see how identical absorptions could give rise to different sensations. But when the two halves of the matching field are viewed under different adaptation conditions, it seems quite possible that identical photochemical absorptions might give rise to different sensations because the signals initiated by them might be differently processed in the two instances. That this is, at least in theory, an adequate way out of the difficulty can be seen by the following.

Suppose that the photochemical absorptions give rise to signals in the optic nerve of magnitudes l, c_1, c_2, in the first adaptation condition, and l', c_1', c_2', in the second. The condition for a match would presumably be equality of signal magnitudes, that is: $l = l'$, $c_1 = c_1'$, and $c_2 = c_2'$. If these signal magnitudes were linearly related to the photochemical absorptions, we should have:

$$\begin{pmatrix} l \\ c_1 \\ c_2 \end{pmatrix} = B \begin{pmatrix} r \\ g \\ b \end{pmatrix}, \quad \begin{pmatrix} l' \\ c_1' \\ c_2' \end{pmatrix} = B' \begin{pmatrix} r' \\ g' \\ b' \end{pmatrix}; \quad \ldots \quad (22)$$

where B and B' are nine-element square matrices. Hence, using equation (19), the conditions for a match become:

$$BA \begin{pmatrix} R \\ G \\ B \end{pmatrix} = B'A' \begin{pmatrix} R' \\ G' \\ B' \end{pmatrix}, \quad \ldots \quad (23)$$

which again implies that R, G, B, and R', G', B', are linearly related. As we have seen, experiment shows that this is not exactly true and hence one or more of the matrices B, A, B', A' must be non-linear.

We have already seen that additivity necessitates the linearity of the matrices A and A', therefore the non-linearity must be confined to the B and B' matrices. Moreover these matrices must clearly not be equal to one another, otherwise they would cancel from the above equation, and R, G, B and R', G', B', would again be linearly related. It is clear, therefore,

that what is required is an adaptation-dependent non-linear relationship between the photochemical absorptions and the signals. It may be asked whether such a non-linear relationship can be reconciled with the linear chromaticity discrepancies found by MacAdam. There is no easy answer to this question, but the linearities found by MacAdam might be consequences of suitably formulated non-linear relationships, or they might represent approximations to limited portions of relationships which in their entirety were non-linear.

The data considered thus far give no clue as to what these relationships might be, but it is perhaps as well to remember that luminances are additive irrespective of chromaticity, at least approximately, and hence, as Willmer has recently remarked *(ref. 13)*, luminosity must presumably be established on an additive basis. Furthermore, Wright *(ref. 14)* has shown that, at least in some conditions, when colours seen under different adaptations match one another, the match is not upset by altering the intensities of the two colours by the same percentage. Facts such as these impose certain limitations on the form which the adaptation-dependent non-linear relationship can take. But suppose a luminance signal l, and two colour difference signals, c_1 and c_2, were compounded from the photochemical absorptions, thus:

$$l = f(a_1 r + a_2 g + a_3 b) \quad \ldots \quad (24)$$

$$c_1 = f_1(r/g) \quad \ldots \quad (25)$$

$$c_2 = f_2(g/b) \quad \ldots \quad (26)$$

f, f_1 and f_2 being unknown functions. Suppose, further, that changing the adaptation could be represented by:

$$l' = f(a_1' r' + a_2' g' + a_3' b') \quad \ldots \quad (27)$$

$$c_1' = f_1'(r'/g') \quad \ldots \quad (28)$$

$$c_2' = f_2'(g'/b') \quad \ldots \quad (29)$$

f_1' and f_2' being unknown functions. It is clear that luminosity is established on an additive basis as required. It is also clear that if $l = l'$, $c_1 = c_1'$, and $c_2 = c_2'$, the multiplication of r, g, b, and r', g', b', by the same factor k will not upset the equalities, because f does not change with adaptation and the other two signals depend on ratios; hence the match will not be upset by changing the intensities of the two matching fields by equal factors. The required non-linearity between R, G, B and R', G', B', is assured if either f_1 and f_1' or f_2 and f_2' (or perhaps both pairs) are unequal and non-linear.

In so far as luminances are not perfectly additive, and matches are sometimes disturbed by varying the intensity of both colours *(refs. 15, 16)*, the permissible forms of the above equations may be extended.

The above arguments are not affected if further photochemical absorptions w and y, for instance, are present, provided always, of course, that their spectral absorption curves are already related to the other three.

In *equation 27* the coefficients a_1', a_2', a_3' are not necessarily the same as a_1, a_2, a_3 of *equation 24*. If they were the same then changes in chromatic adaptation would be fully reflected in the spectral luminosity function. If, on the other hand, a_1', a_2', a_3' and a_1, a_2, a_3 were so related that $a_1 r/a_1' r' = a_2 g/a_2' g' = a_3 b/a_3' b'$, then the shape of the spectral luminosity function would be unchanged by changes in chromatic function. Hurvich and Jameson *(ref. 17)* have shown that the spectral luminosity function is affected by changes in chromatic adaptation, but it is not at present clear whether the effects are as great as would be expected if these changes were fully reflected. It seems better for the moment, therefore, to retain the different coefficients a_1', a_2', a_3' in *equation 27*, bearing in mind that it may subsequently be shown that they are in fact equal to a_1, a_2, a_3 of equation 24.

THE VARIATION OF SATURATION WITH ADAPTATION

THE marked variation of colour saturation with adaptation intensity *(refs. 16, 18)* is another phenomenon which requires relating to the trichromatic theory. At first sight it might seem that the progressive lowering of colour saturation as the adaptation intensity level drops, as shown in *fig.1*, should be expected as a result of the participation of the rods. But the previous arguments make it clear that activity of a fourth receptor can only be envisaged if its spectral absorption curve is a linear combination of the three basic curves. The visual purple curve, however, which so closely resembles the scotopic luminosity curve, cannot be synthesized even approximately from a linear combination of any set of colour mixture curves, as can be seen from *fig.2*, where an attempt at such a synthesis has been made. Dartnall, however, has suggested *(ref.19)* that owing to the production of indicator yellow when visual purple is bleached the visual purple absorption curve moves to longer wavelengths when the eye is light-adapted and closely resembles the photopic luminosity curve, which, of course, can be synthesized from a linear combination of colour mixture curves. The above explanation, however, would imply that when small field-sizes are used, there being no rods in the central fovea, the variation of saturation with adaptation should be eliminated, or at least greatly reduced. This, however, does not occur, as can be seen from *fig.3*, where results for a 1° field are shown *(ref.20)*; it is clear that the desaturation effect for a 1° field is at least as great, if not greater, than that for a 20° field.

One explanation of this variation of saturation with adaptation requires very little departure from the traditional trichromatic theory. It is well known that as dark adaptation proceeds, the luminosity of the adapting field decreases *(ref.21)*, so that even when the eye is fully adapted a dimly lit

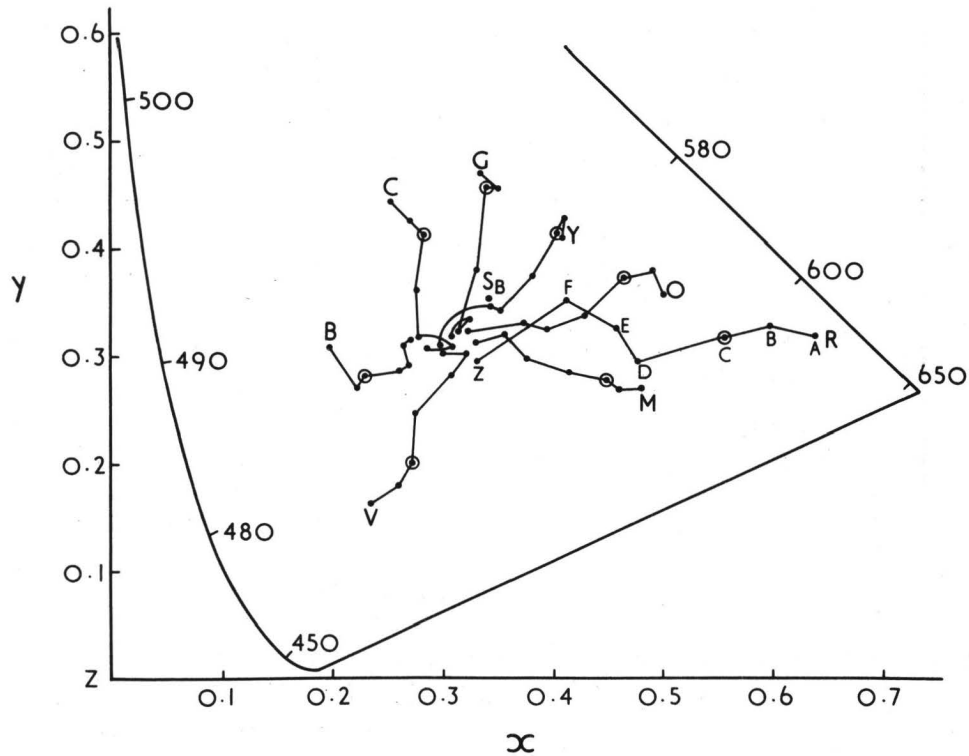

Fig. 1. By means of a binocular matching technique, eight colours, having the chromaticities shown by the ringed points, were matched at seven different adapting luminances ranging from 100 candles/ft^2, (A), to zero (Z). The changes in appearance were recorded in terms of a red, green, and blue mixture seen at adaptation level C, 0.75 candles/ft^2. The luminances of the eight colours were varied with the adapting luminance, so that they were always equal to it. The field size was 2°. The colour of the adapting light was standard illuminant B throughout.

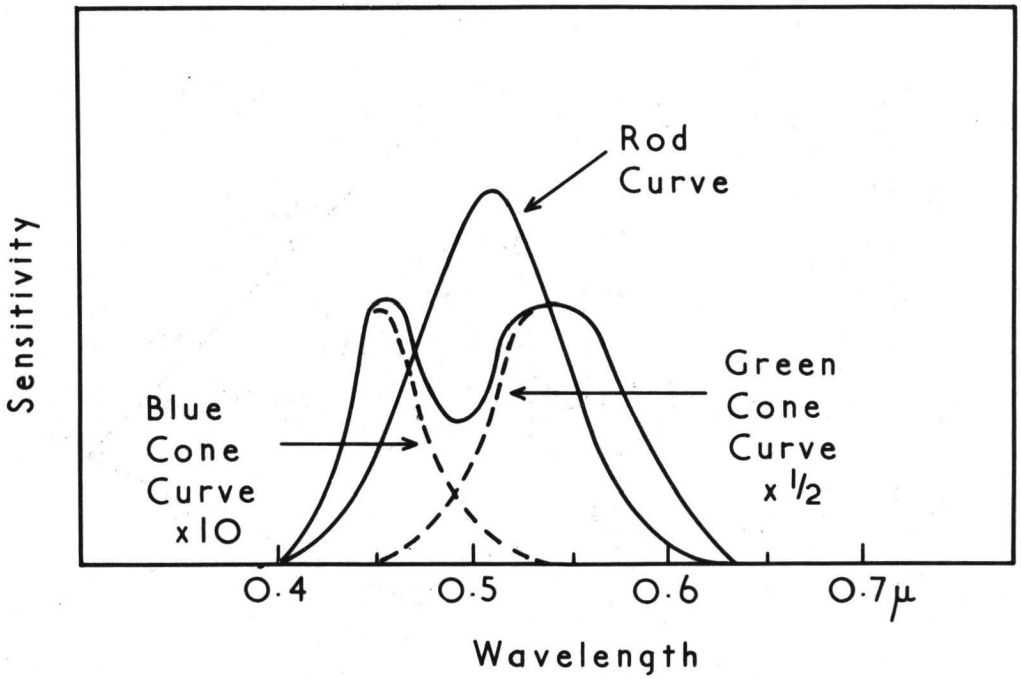

Fig. 2. An attempt to synthesize the scotopic luminosity curve with a mixture of likely "green-cone" and "blue-cone" curves. No mixture of these curves, or of any possible colour-mixture curves, gives even an approximate synthesis.

scene appears less bright than a brightly lit one. Similarly, it could be argued that the saturation of the sensations produced by the signals in three colour channels decreases as the intensity decreases. Thus a red light, stimulating only the red mechanism, might look saturated when its luminosity was high and desaturated when its luminosity was low, simply because that might be the way in which the brain interprets variation in the strength of the signal in the red channel. A re-examination of the data, however, renders the above explanation untenable. In *figs. 1* and *3* the luminances of the test colours were in all cases equal to those of the adapting field, so that the luminosity would have decreased as the adapting intensity was lowered. But in *fig. 4*, results are shown for the 20^{0} field when test colours were used having luminances such that the luminosity remained approximately constant throughout. It is seen that saturation still decreases with adaptation intensity.

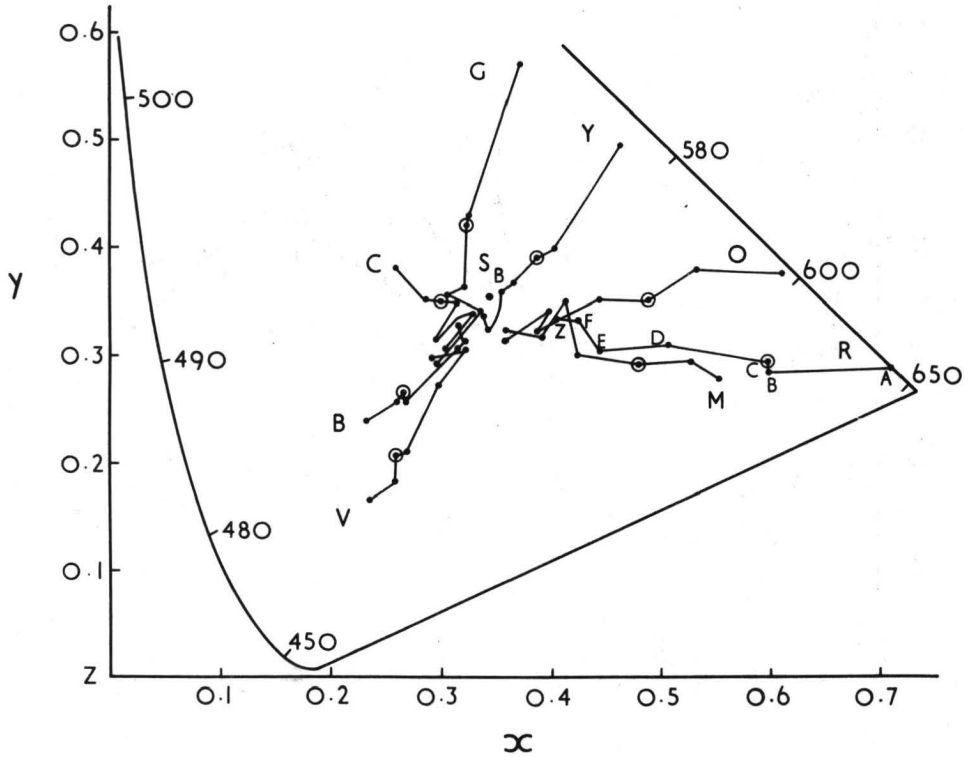

Fig. 3. Results similar to those shown in Fig. 1 but for a 1^{0}, instead of a 20^{0}, field size.

What explanations, then, of this saturation effect are compatible with the facts? We have seen that provided only three basic sensitivity curves are involved we are not limited to only three retinal mechanisms. One permissible, and quite attractive explanation, is therefore to postulate the existence of a fourth "white" mechanism in addition to the three colour mechanisms of the trichromatic theory. Alternatively, as implied in the equations for l, c_1, and c_2, given in the previous section, we can regard the white mechanism as one of the three, the other two being some form of colour difference mechanism. The variation of saturation with adaptation is then explained if the white mechanism for some reason becomes more and more active relative to the colour mechanisms as dark-adaptation proceeds. The limitation of only three basic sensitivity curves could be ensured in a variety of ways, but a plausible suggestion is that the white mechanism

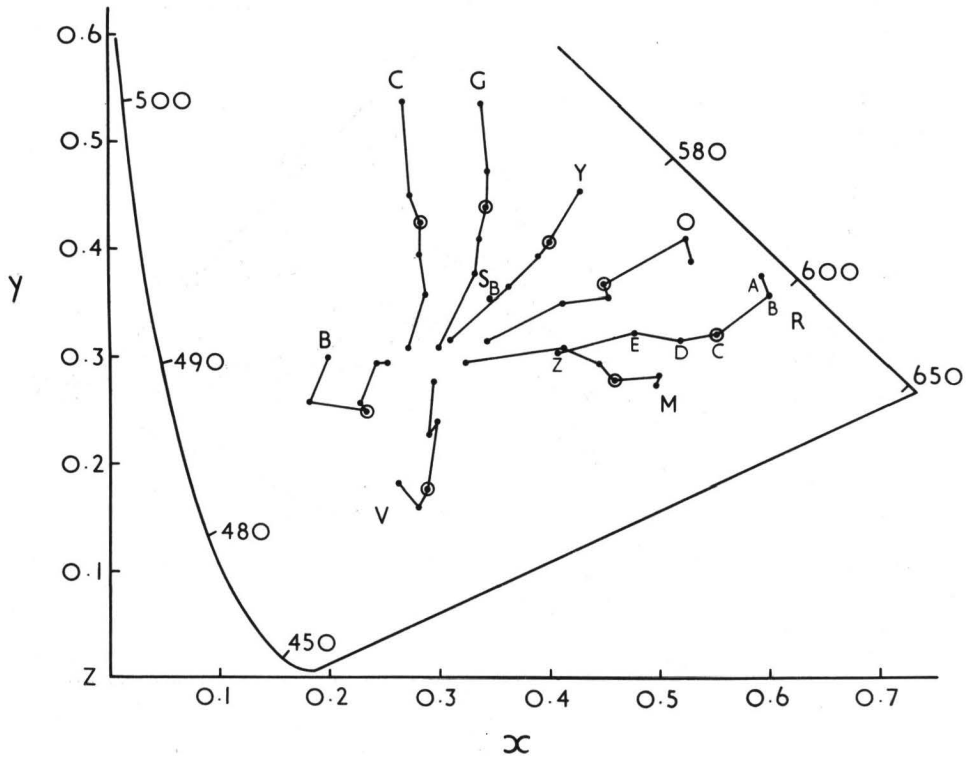

Fig. 4. Results similar to those shown in Fig. 1 but for test colours of constant luminosity, instead of for test colours of luminances equal to the adapting luminances.

contains a mixture of all three basic photochemical substances. There are obvious similarities between this picture and the Dominator-Modulator theory propounded by Granit *(ref. 22)*, so that it is not altogether without some physiological backing.

The postulation of a "white" mechanism is not, however, the only possible explanation of the variation of saturation with adaptation. In connection with an explanation for the non-linearity between tristimulus values for corresponding sensations produced under different adaptations, it has been suggested that there must be a non-linear adaptation-dependent link somewhere in the visual chain between the brain and the retina. If this consisted of a spilling over, or mixing, of the responses occurring in the channels to the brain, and this became progressively greater as dark adaptation proceeded, then a gradual desaturation of colour sensations might well result. This idea is shown diagrammatically in *fig. 5*. If this

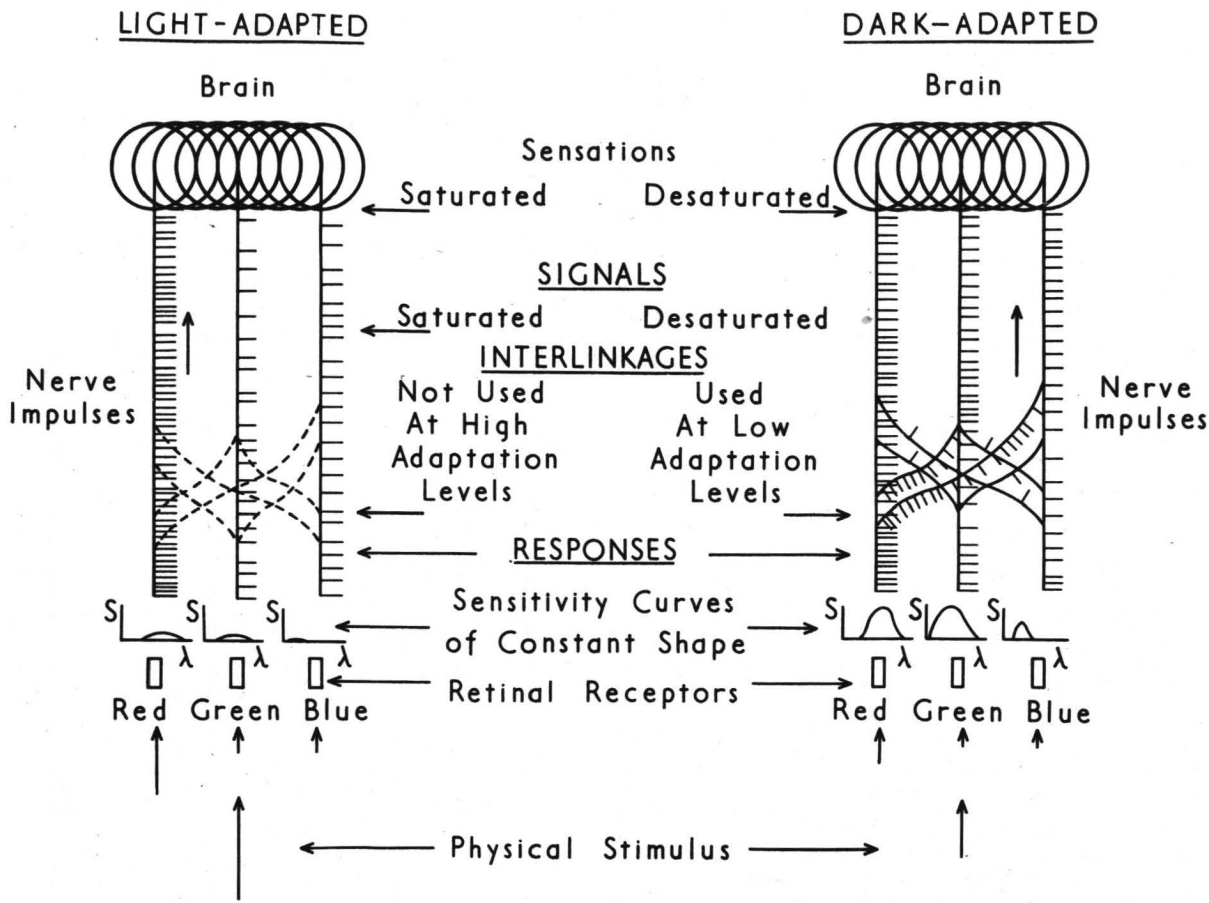

Fig. 5. Schematic diagram of process proposed to explain the decrease in the saturation of sensations produced as dark adaptation proceeds.

were the true explanation a gradual reduction of visual acuity for fine detail ought to occur as dark-adaptation proceeds and this, of course, is the case. Moreover, histological examination of the retina shows many interconnections between one receptor pathway and those of its neighbours, so that this picture can also claim some physiological backing, and has in fact been suggested by a number of workers on various grounds *(refs 23, 24)*.

Of course, it is possible that both these pictures are true; that there is a white receptor, and that spilling over of responses occurs. But it has been shown *(ref. 25)* that the changes in colour saturation with adaptation take place at much the same rates as other changes induced by adaptation (completion of the phenomena taking some three minutes or so) and this perhaps favours a photochemical explanation more on the lines of the white mechanism. However, if the degree of spilling over of responses was controlled by the concentrations of the photochemical substances, the times involved would be similar to those observed in other adaptation phenomena, even though the effect was neurally rather than chemically operated.

THE STIMULUS-SIGNAL RELATIONSHIP

IT is of interest to see whether any light can be thrown on the form of the functions relating the magnitudes of the photochemical absorptions and the neural signals to the brain. The linearity and additivity of colour matching and luminosity requires, as we have seen, that the photochemical absorptions be linearly related to the stimulus intensities. But what of the rest of the process?

It is frequently claimed that physiological studies reveal a logarithmic relationship between stimuli and physiological responses. This is an empirical observation, physiological mechanisms with exactly logarithmic characteristics not having been located. Moreover, the observations are only approximately logarithmic and other functions sometimes fit the data as well or better. Furthermore, the case for a logarithmic relationship has often been bolstered up by arguments from discrimination data, which have been severely criticized *(ref. 26)*.

The problem may be illustrated by the very interesting results recently published by Willmer *(ref. 27)*. Willmer has shown that protanopes and deuteranopes have only monochromatic vision in the central fovea, and by measuring their threshold sensitivity curves he obtained two curves, P and D, which he suggested might together be the basis of the dichromatic colour vision experienced by the normal observer for central foveal observations. He discovered that if he plotted the P and D curves on a logarithmic scale the distance between the two curves correlated in a simple fashion with both hue discrimination and saturation discrimination observations.

But can we deduce from this that there is a logarithmic step in the P and D mechanisms? All that can really be deduced is that hue and saturation

discrimination depend on the ratio of the P and D signals and not on their arithmetic difference. Now it has been argued with some force *(ref. 26)* that the reason for the finite size of the discrimination step in vision, is that the signals received by the brain are subject to both physical and physiological fluctuations. For instance, it has been shown *(ref. 28)* that the Weber fraction $\Delta I/I$ is inversely proportional to the square root of the number of receptors operating in different field sizes, as would be expected if discrimination were a statistical phenomenon *(See fig. 6)*. If the

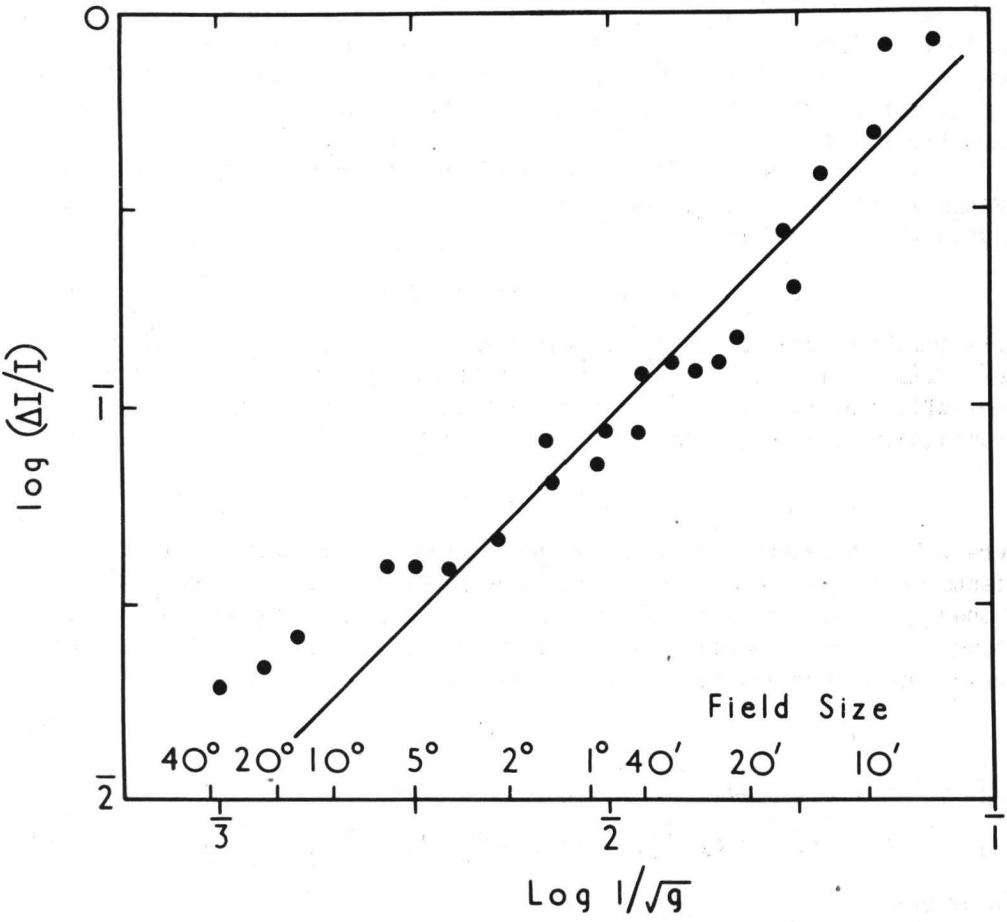

Fig.6. If luminance discrimination is a statistical phenomenon $\Delta I/I$ should be proportional to $1/\sqrt{g}$ where g is the number of receptors operating in the field of view. By plotting log $\Delta I/I$ against log $1/\sqrt{g}$ a very wide range of values is covered and it is seen that the points lie closely on a straight line at 45° as required. g was estimated from available data on the topography of cones in the retina.

magnitudes of the fluctuations were proportional to the signal magnitudes then this alone would account for discrimination depending on the ratio of, rather than on the arithmetic difference between, two signals. Thus if a signal varying from 90 to 100 units had to be compared with one varying from 100 to 110 units in order to be discriminated, then a signal varying from 900 to 1000 units would presumably have to be compared with one varying from 1000 to 1100 units in order to be discriminated. If on the other hand the 900 unit signal only varied from 900 to 910 units, then presumably it would be discriminated from a signal varying from 910 to 920 units. In the former case discrimination would rest on the ratio of the two signal magnitudes, and in the latter on the arithmetic difference between them. In the former case, discrimination data such as Willmer's do not require a logarithmic step in the process, in the latter case, they do. Can we decide between these two alternatives?

From arguments used earlier in this paper, it was suggested that a luminance signal l might be related to photochemical absorptions r, g, b by an equation of the form:

$$l = f(a_1 r + a_2 g + a_3 b), \quad \ldots \quad (30)$$

variation in adaptation only changing the values of a_1, a_2, a_3. In the case where changes of adaptation are confined to changes in intensity, the chromaticity of the adapting light remaining constant, it does not seem unreasonable to simplify the above equations to the form

$$l = a.F_1(I), \quad \ldots \quad (31)$$

where a is a parameter dependent on adaptation and represents all the effects of adaptation as far as luminance is concerned, I is the intensity of the stimulus, and F_1 is any function. If, with constant adaptation, the intensity of the stimulus I is now increased by a small increment ΔI, the corresponding increase in l will be given by:

$$\Delta l = a.F_1(I + \Delta I) - a.F_1(I). \quad \ldots \quad (32)$$

Where F_2 is some unknown function we can in principle always write:

$$\Delta I/I = F_2 \left\{ F_1(I + \Delta I) - F_1(I),\ F_1(I) \right\}. \quad \ldots \quad (33)$$

Therefore:

$$\Delta I/I = F_2 \left\{ \Delta l/a,\ l/a \right\}. \quad \ldots \quad (34)$$

But, as can be seen from *fig. 7*, Craik *(ref. 29)* has shown that over a very considerable range of intensities and adaptations, luminance discrimination is independent of adaptation. Over this range, therefore, the above equations must be independent of a, and it can be proved *(ref. 28)* that the equation may be rewritten:

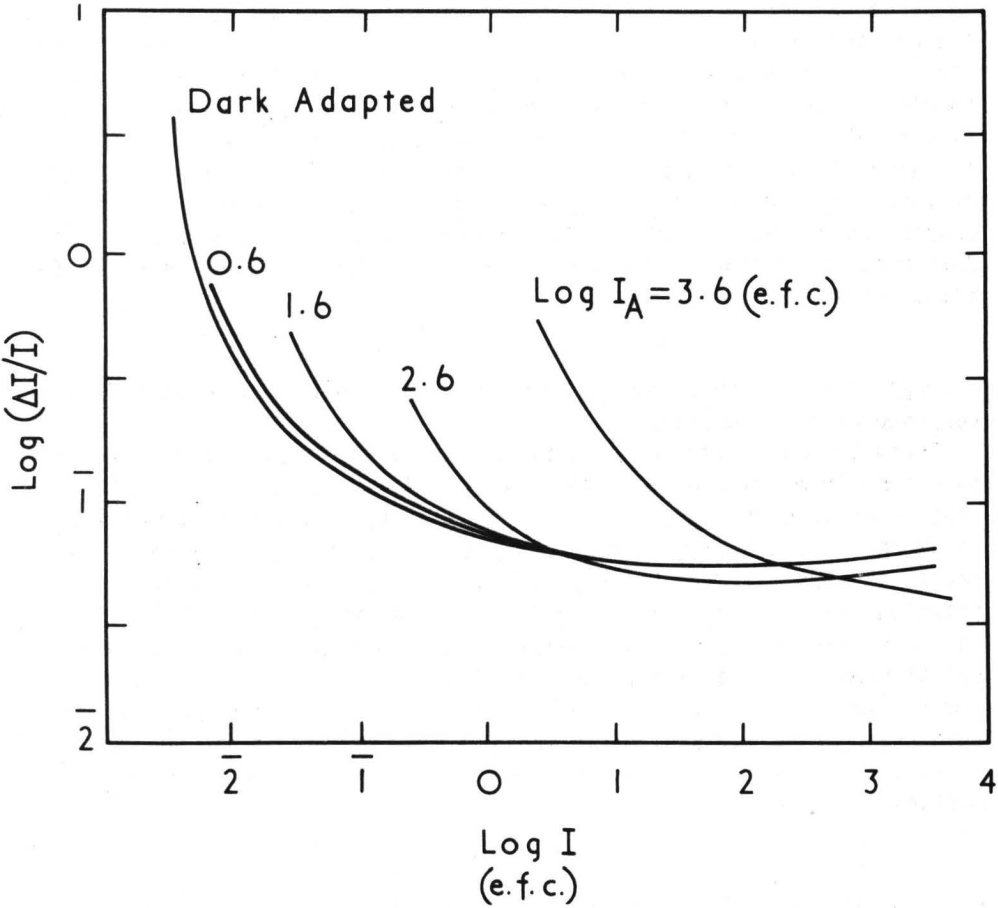

Fig. 7. Craik's results for the effect of adaptation on luminance discrimination. I is the stimulus intensity, and I_A the adapting intensity. Adaptation intensities giving log I_A values of -0.4, -1.4, -2.4 and -3.4 (log e. f. c.) were also investigated and gave curves indistinguishable from that for dark-adaptation. Thus for adaptation intensities from zero to 0.6 log e. f. c. luminance discrimination is almost independent of adaptation; at high adaptation intensities, adaptation has some effect but it is generally small provided the test stimulus intensity is not less than about 1% of that of the adapting stimulus.

$$\Delta I/I = F_3\{\Delta l/l\} \qquad (35)$$

where F_3 is some other function.

Hence we come to the conclusion that over the range of adaptations and intensities for which luminance discrimination is not affected by adaptation, it is dependent on the presence of a certain *ratio* between two physiological signals and not on a certain arithmetical difference. Hence discrimination results, at any rate for luminance, do not necessitate the stimulus-signal relationship being logarithmic. Over the range of values of intensity and adaptation for which $\Delta I/I$ is not only independent of adaptation but also constant, it follows from the above equation that $\Delta l/l$ must be constant. It can be shown *(ref. 28)* that this leads to the relationship

$$l = aI^p + l_0 \qquad \ldots \qquad (36)$$

where p is a constant, and l_0 represents any spontaneous physiological response or dark current.

There is one further experimental fact on which the stimulus-signal relationship must have a bearing. It is well known that if a series of grey cards is arranged so as to obtain a scale of greys from white to black having equal visual increments, the position of any card in the series is very far from being proportional to its reflectance. The relationship is more nearly logarithmic, and, as with discrimination data, this has been used to support belief in a logarithmic stimulus-signal relationship. A careful examination of the facts, however, reveals that a power relationship gives a much closer fit, as shown in *fig. 8*. In fact, when the Munsell scale of greys was first drawn up in 1920, the value, V, or visual position of a grey between black (zero) and white (ten), was defined simply as

$$V = 10R^{\frac{1}{2}} \qquad \ldots \qquad (37)$$

where R was the reflectance of the sample *(ref. 30)*. Subsequent investigations have shown that the exact form of the relationship varies slightly according to the luminance of the background, and for a middle grey (reflectance 0.191),

$$V = 10(1.474R - 0.474R^2)^{\frac{1}{2}} \qquad \ldots \qquad (38)$$

is a closer approximation. However, Judd *(ref. 31)*, as recently as 1952, described the simple square-root relationship (and not a logarithmic relationship) as a "convenient first approximation", and several other workers *(refs. 32, 33, 34)* have also demonstrated the superiority of power relationships.

The correspondence between this practical result and the theoretical reasoning given above is striking.

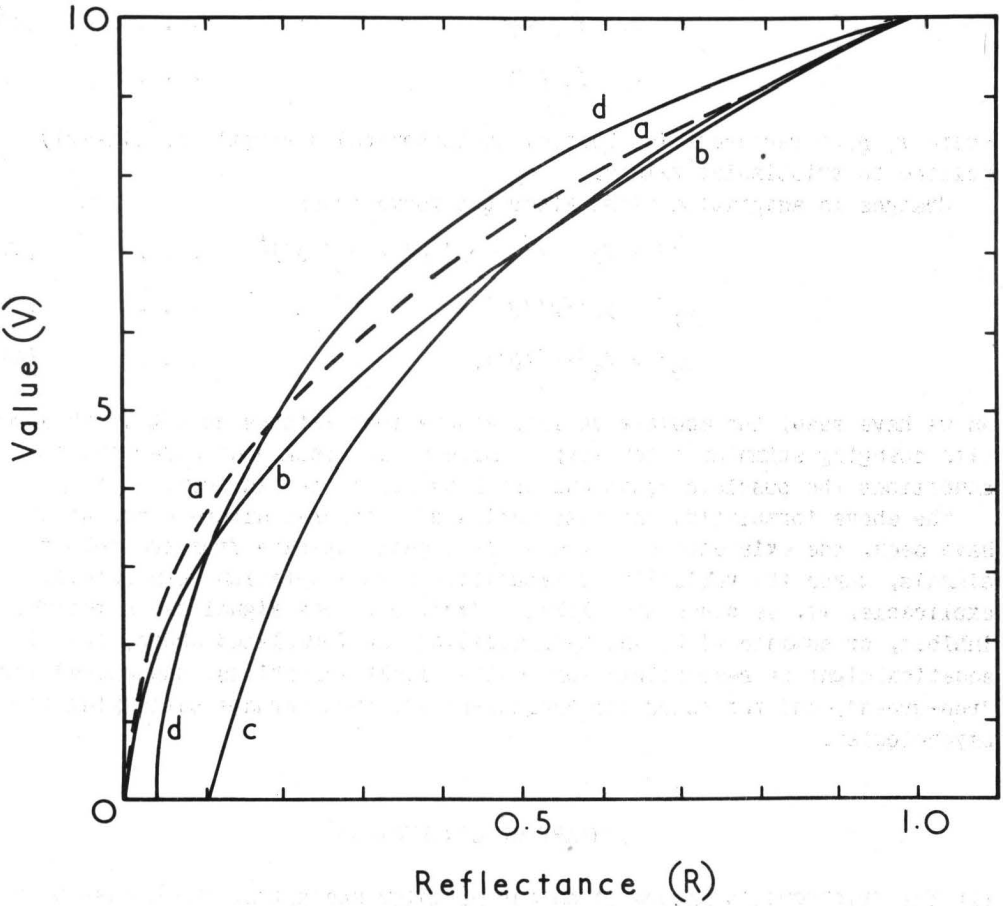

Fig. 8. Value V, (distance along a scale of uniform visual steps from zero, for black, to ten, for white) plotted against reflectance, R. (a) Munsell Renotation: (b) $V = 10R^{\frac{1}{2}}$; (c) $V = 10 \log 10R$; (d) $V = 3 + 7 \log 10R$. At low reflectances the errors in value are very much higher for curve c (logarithmic relationship), than for curve b (power relationship). The modified logarithmic relationship of curve d is similar at high and medium reflectances, but is worse than curve b at low reflectances.

One set of stimulus-signal relationships, then, which would seem to satisfy all the data reviewed is as follows:

$$l = (a_1 r + a_2 g + a_3 b)^p \quad \ldots \quad (39)$$

$$c_1 = f_1(r/g) \quad \ldots \quad (40)$$

$$c_2 = f_2(g/b) \quad \ldots \quad (41)$$

where r, g, b represent (as before) photochemical absorptions, linearly related to tristimulus values.

Changes in adaptation might alter the forms thus:

$$l' = (a_1' r' + a_2' g' + a_3' b')^p \quad \ldots \quad (42)$$

$$c_1' = f_1'(r'/g') \quad \ldots \quad (43)$$

$$c_2' = f_2'(g'/b'). \quad \ldots \quad (44)$$

As we have seen, the above equations ensure that matches do not break down with changing stimulus intensity; if matches do break down under these conditions the possible equations are less restricted in form.

The above formulation has some merits of a general nature also. As we have seen, the existence of a luminance signal separate from the colour signals, makes the variation of saturation with adaptation very readily explicable, if, as seems most likely, *(ref. 35)*, one signal can sometimes inhibit, or summate with, another. Moreover, as formulated above, the first equation might be responsible for "white-black" sensations, the second for "red-green", and the third for "yellow-blue", thus perhaps satisfying the psychologist.

SUMMARY OF CONCLUSIONS

(1) The trichromatic nature of colour matching means that there must be a triple restriction somewhere in the visual process.

(2) The additivity and constancy of metameric colour matches means that only three basic sensitivity curves can exist in the photopic retina. It is natural to associate these with three photochemical substances, and the constant shape of their absorption curves requires that they are present only in small quantities.

(3) Some adaptation results could be very satisfactorily ascribed to a white mechanism, which could be present along with two, three, or more, colour mechanisms, provided always that no more than three basic sensitivity curves were involved.

(4) The non-linearity between corresponding sets of tristimulus values for colours seen under different adaptations, requires an adaptation-dependent non-linearity somewhere in the visual system.

(5) In so far as the additivity of luminances, and the constancy of matches with variation of stimulus intensity, take place, certain restrictions are placed on the form which the adaptation-dependent non-linearity can take. (6) Although logarithmic signal-stimulus relationships have often been proposed, they cannot be properly deduced from discrimination data, and a few simple assumptions regarding adaptation lead to a power relationship. A power relationship has also been found to relate, to a good approximation, the reflectances of a visually uniform grey scale.

ACKNOWLEDGEMENTS

I am conscious of much help derived from discussions and correspondence with others. I would particularly like to name Dr. D. L. MacAdam, Dr. W. S. Stiles, Dr. W. D. Wright, and Mr. A. Marriage for the help thus given.

REFERENCES

1. THOMSON, L. C., *Ophthal.Lit.*, 1952, **6**, No.1, 33.
2. WRIGHT, W. D., "Researches on Normal and Defective Colour Vision", Kimpton, 1946, 229.
3. HARTRIDGE, H., *Nature*, 1947, **160**, 538.
4. BLOTTIAU, F., *Rev.Opt. (théor.instrum.)*, 1947, **26**, 193.
5. TREZONA, P. W., *Proc.phys.Soc.B*, 1953, **66**, 547, and *Proc.phys.Soc.B*, 1954, **67**, 513.
6. WRIGHT, W. D., "Researches on Normal and Defective Colour Vision", Kimpton, 1946, 146.
7. WRIGHT, W. D., "Researches on Normal and Defective Colour Vision", Kimpton, 1946, 148 and 367.
8. BRINDLEY, G. S., *J.Physiol.*, 1953, **122**, 332.
9. WRIGHT, W. D. "Researches on Normal and Defective Colour Vision", Kimpton, 1956, 91.
10. WRIGHT, W. D. "Researches on Normal and Defective Colour Vision", Kimpton, 1956, 263.
11. MACADAM, D. L., *J.opt.Soc.Amer.*, 1956, **46**, 500, and *J.Soc.Mot.Pic. Tel.Engrs.*, 1956, **65**, 455.
12. BREWER, W. L., *J.opt.Soc.Amer.*, 1954, **44**, 207.
13. WILLMER, E. N., *Docum.ophthal.*, 1955, **9**, 295.
14. WRIGHT, W. D. "Researches on Normal and Defective Colour Vision", Kimpton, 1956, 262,
15. WALTERS, H. V., *Proc.Roy.Soc., B*, 1942, **131**, 27.
16. HUNT, R. W. G., *J.opt.Soc.Amer.*, 1952, **42**, 190.
17. HURVICH, L. M., and JAMESON, D., *J.opt.Soc.Amer.*, 1954, **44**, 213.

18. HUNT, R. W. G., *J. opt. Soc. Amer.*, 1950, **40**, 362.
19. DARTNALL, H. J. A., *Brit. J. Ophthal.*, 1948, **42**, 793.
20. HUNT, R. W. G., *J. opt. Soc. Amer.*, 1953, **43**, 479.
21. CRAIK, K. J. W., *Proc. roy. Soc. B*, 1940, **128**, 232.
22. GRANIT, R., "Sensory Mechanisms of the Retina", Oxford 1947.
23. LYTHGOE, R., *Medical Res. Council Spec. Rep. Ser.*, 1932, No. 173, London.
24. PIRENNE, M. H., *Nature*, 1952, **170**, 1039.
25. HUNT, R. W. G., *J. opt. Soc. Amer.*, 1952, **42**, 367.
26. WRIGHT, W. D., "Researches on Normal and Defective Colour Vision", Kimpton, 1956, 190-198.
27. WILLMER, E. N., *Docum. ophthal.*, 1955, **9**, 235.
28. HUNT, R. W. G., *J. photogr. Soc.*, 1953, **1**, 152.
29. CRAIK, K. J. W., *J. Physiol.*, 1938, **92**, 406.
30. PRIEST, I. G., GIBSON, K. S., and McNICHOLAS, H. J., *Nat. Bur. Standards Tech. Paper*, 1920, 167.
31. JUDD, D. B., "Colour in Business Science and Industry", John Wiley, New York, 1952, p. 230.
32. LADD, J. H., and PINNEY, J. E., *Proc. I.R.E.*, 1955, **43**, 1137.
33. HOPKINSON, R. G., *Nature*, 1956, **178**, 1065.
34. GLASSER, L. G., REILLY, C. D., SCHNELLE, P. D., and McKINNEY, A. H., Abstract TC 58, Optical Society of America 1957 Winter Meeting.
35. GRANIT, R., "Discussion on Vision", The Physical Society, London (1932). p. 263.

PAPER 27

CHROMATIC ADAPTATION WITH SPECIAL REFERENCE TO THE BLUE-GREEN REGION OF THE COLOUR-MIXTURE DIAGRAM

By G. A. FRY

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27. CHROMATIC ADAPTATION WITH SPECIAL REFERENCE TO THE BLUE-GREEN REGION OF THE COLOUR-MIXTURE DIAGRAM

By G. A. FRY

INTRODUCTION

SEVERAL years ago the writer *(ref. 1)* formulated a theory of colour vision similar to that proposed by Houstoun, *(ref. 2)*, in which chromaticness is subserved by independent red-green and blue-yellow mechanisms.

Each of these mechanisms involves two photosensitive substances. It is proposed that the co-ordinates of the colour mixture diagram (u and v in *fig. 1)*, if properly selected, can be defined as follows:

$$u = \frac{Y/\phi_Y}{B/\phi_B + Y/\phi_Y} \tag{1}$$

and

$$v = \frac{G/\phi_G}{R/\phi_R + G/\phi_G}, \tag{2}$$

where R, G, B and Y represent rates of decomposition of red, green, blue and yellow photosensitive substances and where the ϕ values are constant for a given state of adaptation.

According to this theory, the stimulus at each of the four corners of the colour-mixture diagram *(fig. 7A)* excites one member of each pair of substances. The stimuli on each side line of the diagram excite three substances; but one of the stimuli on each side line excites the three substances in such proportions that the two paired stimuli neutralize each other leaving the third to determine what colour is seen. These four equilibrium colours, one on each side of the diagram, must correspond to the equilibrium colours of the Bezold-Brücke effect *(ref. 3)*.

A certain whitesstimulus at the centre of the diagram excites the four substances in proportions in which the two members of each pair of substances neutralize each other. This also constitutes an equilibrium colour.

The process of chromatic adaptation involves primarily a change in the relative concentrations of the four exciting substances.

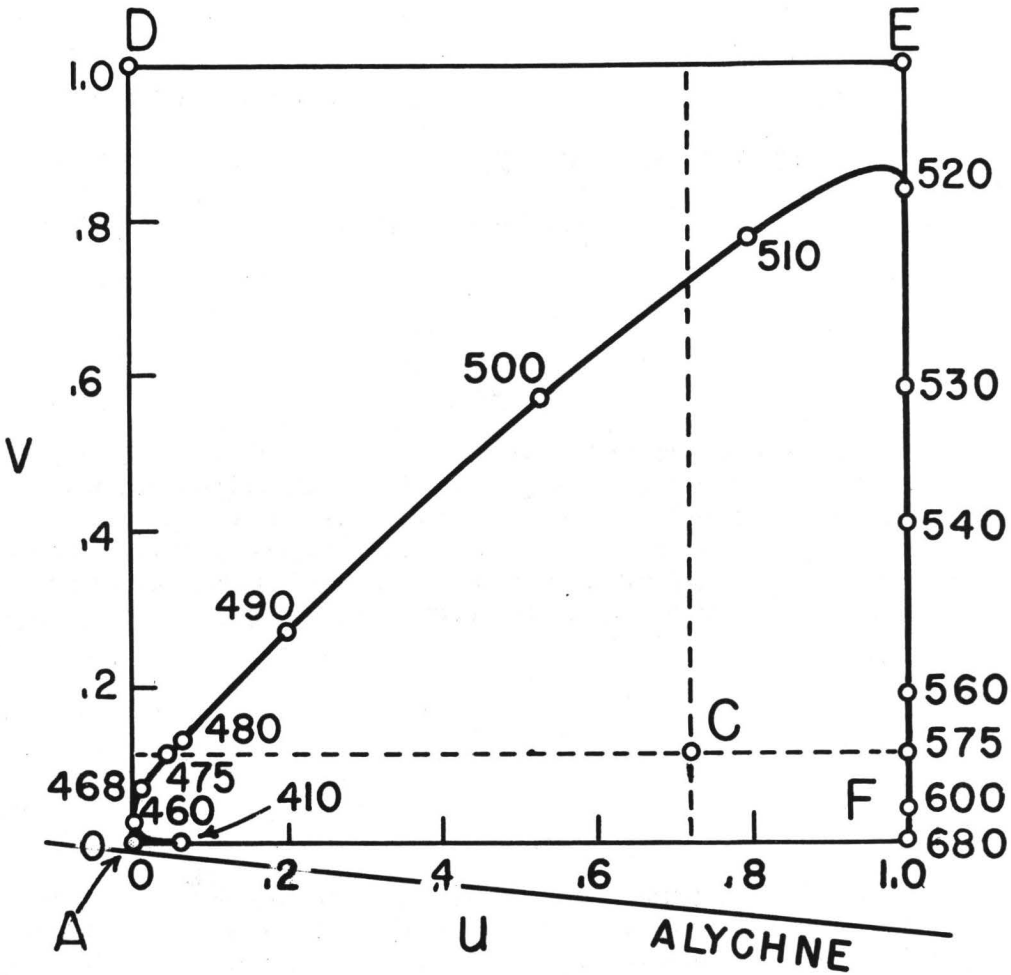


Fig.1. Colour-mixture data of G. A. F. expressed in terms of u and v co-ordinates. This represents a projective transformation of the diagram in *fig.2*. The dotted lines represent the equilibrium axes.

THE BASIC DATA

IN relating this theory to experimental data, one may begin by trying to select the proper co-ordinates for the colour-mixture diagram. The data must be expressed first in terms of working primaries and on a plot of this basic data one can locate the corner colours of the final diagram.

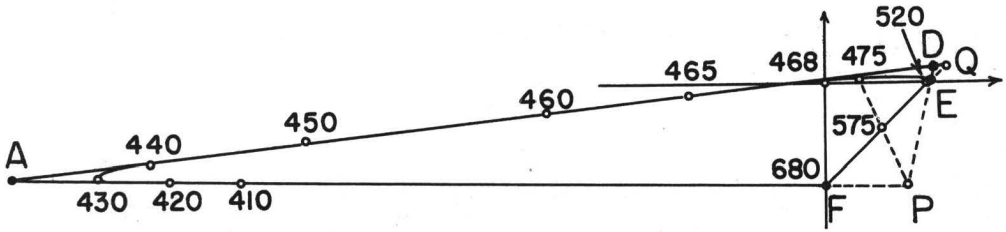


Fig. 2. Colour-mixture diagram for G. A. F. Luminance units have been used in computing the mixture coefficients. Wavelengths 680, 520 and 468 mμ represent the primaries. The co-ordinates are $B_{520}/(B_{680} + B_{520} + B_{468})$ and $-B_{680}/(B_{680} + B_{520} + B_{468})$.

Fig. 2 represents the colour-mixture data of the writer obtained with a bipartite 2^0 circular stimulus centrally fixated with a dark surround. The primaries are monochromatic stimuli having wavelengths of 468, 520 and 680 mμ. Each of the intermediate spectrally pure stimuli was depurified with one of the primaries and matched with a mixture of the other two primaries. Luminance units were used in computing the tristimulus coefficients. The retinal illuminance was kept constant at 276 trolands. The apparatus is described elsewhere *(ref. 4)*.

THE RED-GREEN AND CYAN-VIOLET SIDE LINES

THE spectrally pure colours in the range between 680 and 520 mμ and between 435 and 460 mμ lie on straight lines and on this account it is reasonable to assume that these lines constitute side lines connecting corner colours.

THE RED AND GREEN CORNER COLOURS

A method has been described in a previous paper *(ref. 5)* for locating the red and green corners (F and E) but the experiment has been repeated using a monocular method *(ref. 4)* similar to that devised by MacAdam *(ref. 6)*. The right eye was exposed to the adaptation stimulus shown in *fig. 3A* for eight seconds and then to the test and measuring stimuli shown in *fig. 3B* for three seconds. This cycle was repeated over and over and the mixtures in the two stimuli were adjusted until a match was obtained at the end of the three second exposures. It follows from the theory outlined above that the data (open circles) must be fitted as shown in *fig. 4* by a curve which conforms to the equation,

$$\frac{m' - h}{k - m'} = \phi \frac{m - h}{k - m} \qquad (3)$$

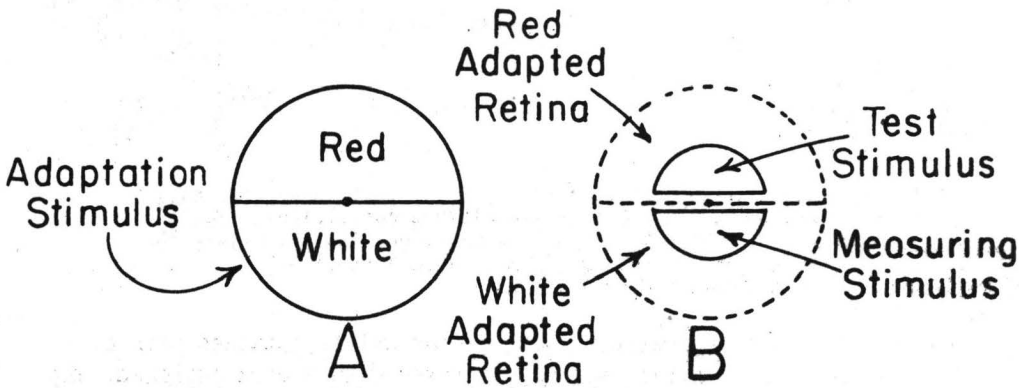


Fig.3. Stimuli used in the study of chromatic adaptation. The adaptation stimulus subtends a visual angle of 9°. The measuring and test stimuli are segments of a circle 2° in diameter and the intermediate dark segment is 34' wide.

In this equation ϕ is a constant which expresses the differential adaptation of the two patches of retina, and the lower case letters represent distances along the line FE measured from the red primary (680 mμ); h is the distance to F, k the distance to E and m and m' are the distances to two stimuli which match when applied to the two patches of retina. Distances toward the green primary are positive and those in the opposite direction are negative. The green primary is assumed to lie at a distance of one unit from the red primary.

From the data it may be assumed that the red corner (F) is located at or near the red end of the spectrum locus and that the green corner (E) has a k value of 1.02. This differs from the k value of 1.06 determined by the binocular method, and this discrepancy will require further study. In this paper the 1.02 value has been assumed to be correct.

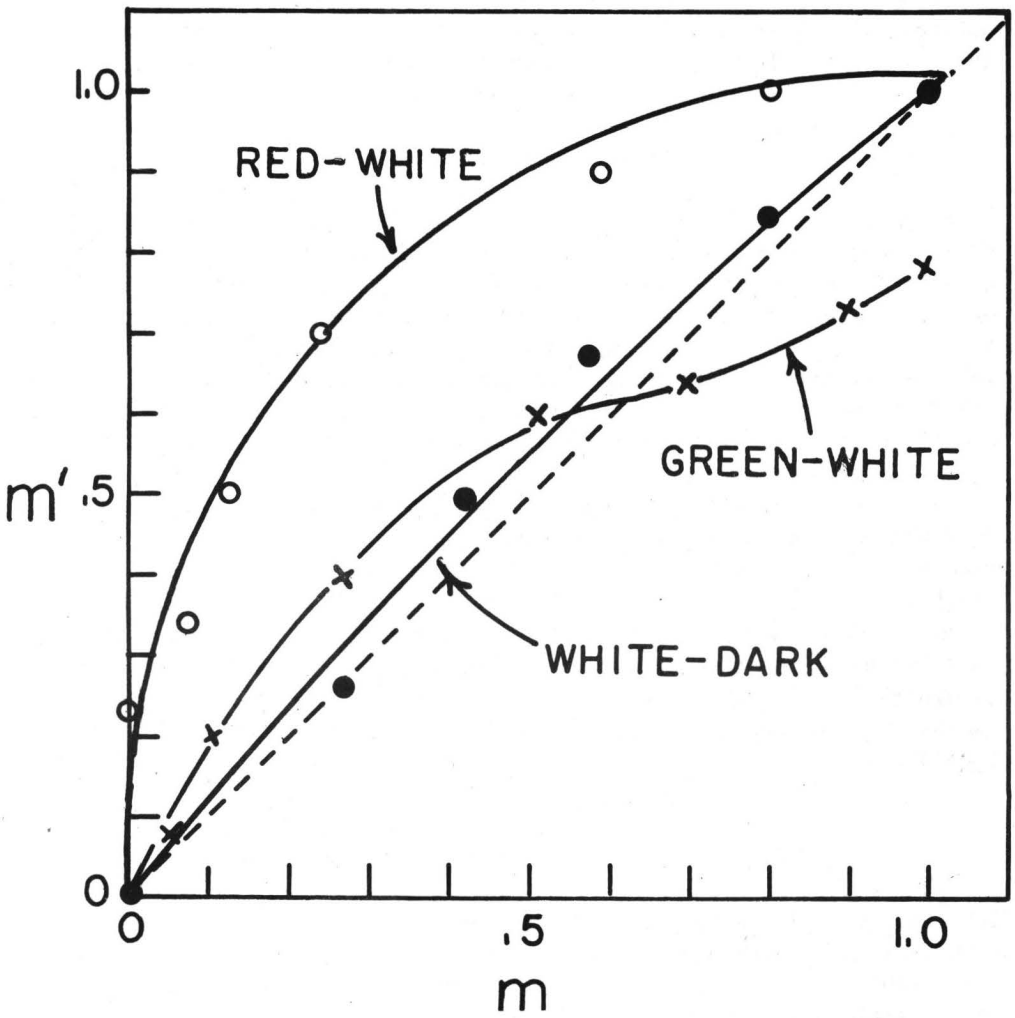


Fig. 4. Effect of differential adaptation on matches between red-green mixtures. The co-ordinates (m' and m) represent the fractions of red in the red-green mixtures used as test and measuring stimuli. The retinal illuminance produced by the measuring stimulus was kept constant at 276 trolands. The retinal illuminance produced by the adapting stimuli are as follows: red-white = 953 trolands; green-white and white-dark = 13,300 trolands. The light for the adaptation stimuli comes from a daylight incandescent bulb and is filtered through Corning filters 4010 and 4303 to obtain green light, through Corning filter 2030 to obtain red light, and through crossed polaroids to obtain white light.

THE NEED FOR A DIFFERENT METHOD FOR LOCATING THE CYAN AND VIOLET CORNERS

IT is not possible to apply the same procedure to the stimuli on the opposite side line because the stimuli between 440 and 460 mμ which lie on this line are indistinguishable from each other *(ref. 7)*.

THE VIOLET CORNER

IN spite of the fact that an observer is dichromatic in the violet corner of the mixture diagram *(ref. 7)* this does not affect the mixture data, because in gauging the blue end of the spectrum the subject compares a mixture of 680 and 468 mμ with a mixture of 520 mμ and one of the colours below 468 mμ on the wavelength scale. These mixtures fall in the region of the colour-mixture diagram where unique matches can be made, and hence one can plot the colours at the blue end of the spectrum locus at different places on the colour-mixture diagram even though they cannot be differentiated from each other.

In the case of the writer the blue end of the spectrum locus turns backward and becomes tangential to a line through the red corner and it is assumed therefore that this represents one of the side lines of the diagram.

In one subject investigated by the writer the blue end of the spectrum locus comes to an abrupt stop and the stimuli in this region lie on a straight line through 440 and 460 mμ. In this case the line connecting the two ends of the spectrum locus may be assumed to represent the violet-red side line.

THE INDIRECT METHOD FOR LOCATING THE CYAN CORNER

THERE appears at the moment to be no direct method of locating the fourth corner of the diagram and hence it is proposed to use an indirect method. This method is based upon the assumption that the cyan-green and violet-red side lines and the line through the white, blue and yellow equilibrium stimuli all converge on a common point.

THE BLUE-YELLOW EQUILIBRIUM AXIS

THE white, blue and yellow equilibrium colours have not yet been determined with anywhere near the precision that appears to be possible.

Wright *(ref. 8)* has demonstrated that a retina adapted to violet light sees a 460 mμ test stimulus shifted toward green and that a retina adapted

to green light sees a 460 mμ test stimulus shifted toward violet and finally that a retina adapted to blue light sees no shift for a 460 mμ test stimulus. It may be deduced from this that the blue equilibrium colour lies in the region of 460 mμ. Presumably Wright used low luminance levels, because at high luminance levels discrimination between stimuli in the blue region of the spectrum becomes very poor and the experiment is not possible.

The invariable blue of the Bezold-Brücke effect lies in the region of 475 mμ. This means that the stimuli on either side of 475 mμ shift toward 475 mμ as the luminance increases.

The invariable yellow of the Bezold-Brücke effect lies in the region of 575 mμ.

Although the experiment has not yet been carried out it appears possible to apply a yellow stimulus to a patch of retina adapted to yellow light of the same composition, and compare it with a mixture of red and green applied to a patch of dark adapted retina. Immediately after the adaptation to yellow light, the yellow test stimulus would appear desaturated and the subject would have to base the match on similarity in hue in the face of a difference in saturation. This difference in saturation is not a serious problem because the lines of constant hue through the yellows in the region of 575 mμ are reasonably straight and probably pass through the equilibrium white.

An alternative procedure to this would be to use as a measuring stimulus a mixture of red, green and 475 mμ or a mixture of 475 mμ and a selected yellow.

Obviously the white equilibrium colour must be one which remains achromatic at different luminance levels. Another approach to the matter is to use a white adapting stimulus and a test stimulus of the same composition and match it with a stimulus applied to a dark adapted retina. Various whites could be tried to find the white which appears the same with and without adaptation to the same white.

For the purpose of locating the yellow-blue equilibrium axis it suffices to locate points which lie on this axis without determining where they lie along the axis. This objective can be achieved by studying the effect of white adaptation upon mixtures of red and green.

The data represented by the solid circles in *fig. 4* show the effect of a white adapting stimulus on red-green mixtures. The effect of white adaptation is compared with that of dark adaptation. Mixtures applied to a white adapted retina almost match the same mixtures applied to a dark adapted retina. The data are fitted by a curve which has a small value of ϕ. Such a white may be assumed to lie near the blue-yellow equilibrium axis. The white adapting stimulus chosen for this demonstration happened to be one immediately available and which had been arbitrarily selected for use as a standard white for comparing the effects of white adaptation to those obtained with chromatic stimuli. This particular white which comes from an

incandescent daylight lamp and is filtered through a pair of crossed polaroids can be matched colorimetrically with a mixture of 750 trolands of 582 mμ and 206 trolands of 475 mμ.

A more precise approach would be to use a series of whites ranging from greenish white to purplish white and to determine by interpolation which of these has a zero value of ϕ.

THE CYAN-GREEN SIDE LINE

TO illustrate the theory I have assumed that the line through 575 and 475 mμ represents the blue-yellow equilibrium axis. This line and the red-violet side line converge at P in *fig. 2*. I have also assumed that the green-cyan side line passes through P and E.

THE FINAL DIAGRAM

THE diagram in *fig. 1* represents a projective transformation of the diagram in *fig. 2* in which the lines which converge at P and Q in *fig. 2* are parallel in *fig. 1*. The alychne is located as indicated.

PREDICTION OF CHROMATIC ADAPTATION EFFECTS

IT follows from the theory outlined above that the relative displacement on the colour-mixture diagram produced by differential adaptation should be predicted from the following equations *(refs. 5,9)*:

$$\frac{u'}{1-u'} = \psi \frac{u}{1-u} \tag{4}$$

and

$$\frac{v'}{1-v'} = \phi \frac{v}{1-v} \tag{5}$$

where a stimulus (u', v') applied to a retina under one condition of adaptation matches a stimulus (u,v) applied to a retina under a different condition of adaptation. ψ and ϕ are constants which depend upon the two states of adaptation.

A single match is sufficient to establish the values of ψ and ϕ if the proper test stimulus is selected. A white stimulus is a good one because the shifts in the red-green and blue-yellow directions are nearly maximal.

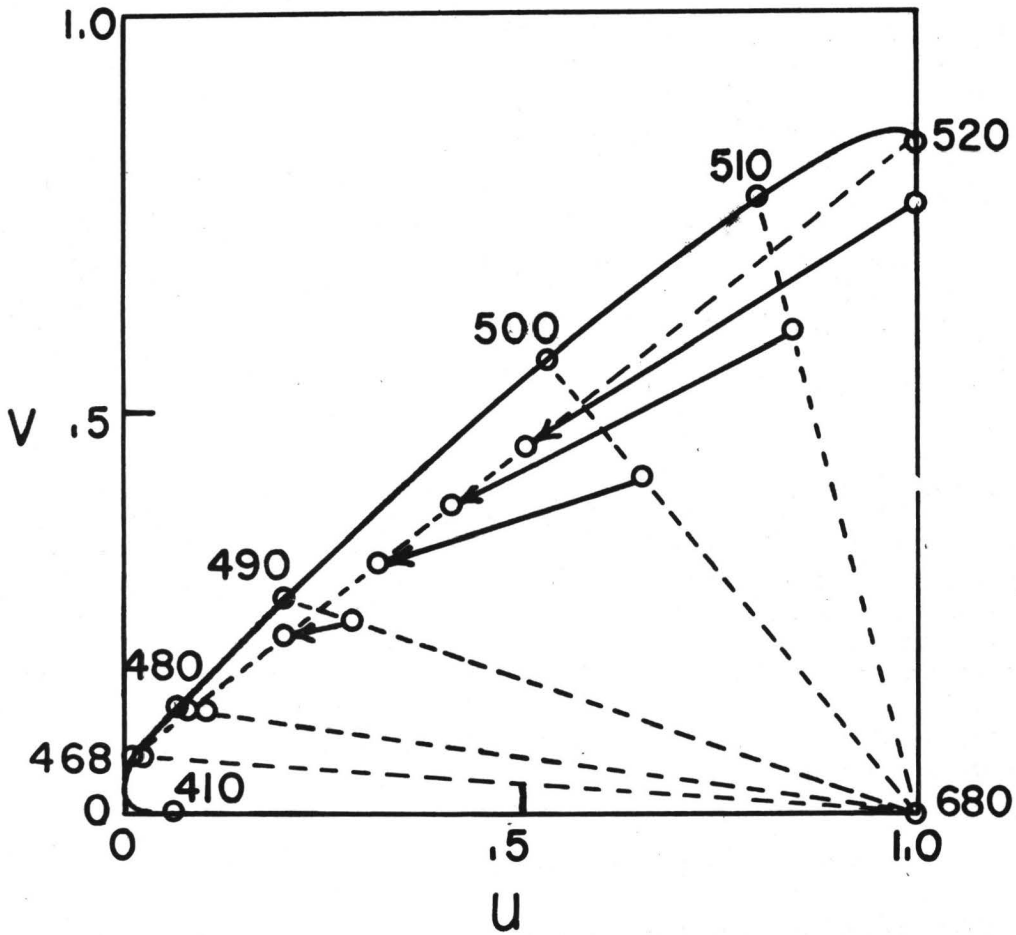


Fig. 5. Effect of red adaptation on monochromatic test stimuli in the range between 468 and 520 mμ. These test stimuli (tails of arrows) have to be depurified with 680 mμ in order to be matched with mixtures of 520 and 468 mμ (heads of arrows) applied to a white adapted patch of retina. The light for the adapting stimuli comes from a daylight incandescent lamp and is filtered through Corning filter 2030 to obtain red light and through a pair of crossed polaroids for the white light. The retinal illuminance produced by the measuring stimulus was kept constant at 276 trolands and the adapting stimuli produced a retinal illuminance of 953 trolands.

USE OF THE TIME FACTOR IN PRODUCING SHIFTS PARALLEL TO THE v-AXIS

THE adaptation changes in the blue-yellow mechanism are relatively rapid, and by allowing an interval of time between the cessation of the adapting stimuli and the time at which a match is made one can measure changes in the red-green mechanism free from contamination of changes in the yellow-blue mechanism. This is illustrated in *fig. 5* which shows matches between stimuli applied to red and to white adapted patches of retina. The matches represent those that prevail 3 seconds after the cessation of the adapting stimuli. The adaptation stimuli and test-measuring stimuli were presented alternately for periods of 8 and 3 seconds. The shifts indicated on the diagram are in general parallel to the v-axis.

SHIFTS PARALLEL TO THE u-AXIS

ACCORDING to the theory it should be possible to produce shifts parallel to the u-axis by employing the equilibrium yellow as the adaptation stimulus and adjusting the measuring stimulus so that a match is obtained between the test and measuring stimulus immediately after each exposure of the adaptation stimulus. The adaptation stimuli and test-measuring stimuli were presented alternately for periods of 8 and 2 seconds. *Fig. 6* shows matches between stimuli applied to patches of retina adapted to white and yellow light. The yellow adaptation stimulus is a colorimetric match for 584 $m\mu$, but the white adaptation stimulus is slightly purplish, and this probably accounts for the failure to obtain purely lateral shifts.

SHIFTS ALONG THE RED-GREEN AND RED-VIOLET SIDE LINES

THE effect of any adaptation stimulus on the red-green mechanism can be conveniently measured by test stimuli which lie on the red-green side line because the shifts are along this side line, especially if the precaution is taken to allow time after the cessation of the adapting stimulus to avoid yellow-blue adaptation effects.

Finally the theory predicts that the effect of any adaptation stimulus on the blue-yellow mechanism can be measured with stimuli that lie on the violet-red side line because the shifts are confined to this line. This has already been demonstrated to be the case for red and violet adaptation stimuli *(ref. 9)*.

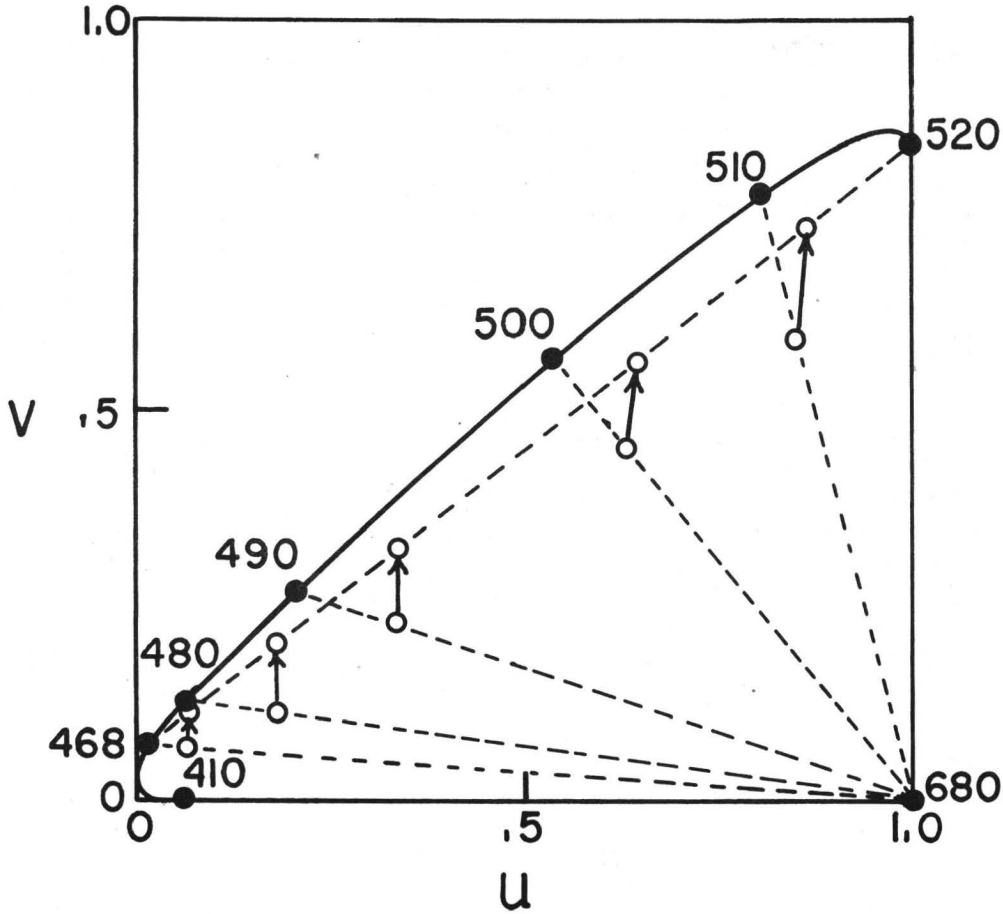


Fig.6. Effect of yellow adaptation on monochromatic test stimuli in the range between 468 and 520 mμ. These test stimuli (tails of arrows) have to be depurified with 680 mμ in order to be matched with mixtures of 520 and 468 mμ (heads of arrows) applied to a white adapted patch of retina. The light for the adaptation stimuli comes from a daylight incandescent lamp and is filtered through Corning filters 3480 and 4303 to produce yellow light and through a pair of crossed polaroids to produce white light. The retinal illuminance produced by the measuring stimulus was kept constant at 276 trolands and the adapting stimuli produced a retinal illuminance of 1,035 trolands.

SIMULTANEOUS INDUCTION

ONE of the most important findings of this study is that the results obtained with MacAdam's monocular method of studying chromatic adaptation *(ref. 6)* do not agree with the results obtained with the binocular method. The crosses in *fig. 4* show data obtained with green and white adaptation. An 8 second-3 second cycle was used, and the matches represent those that prevailed at the ends of the 3 second exposures. The data are not fitted by equation (3). The discrepancy is not the type of thing that can be attributed to possible errors in the photometric measurements. The same type of thing has been obtained repeatedly by two different observers. Furthermore, the same kind of thing has been obtained at different luminance levels and in comparing a green adapted retina with a dark adapted retina, and the only thing that remains to account for the discrepancy is the fact that the test and measuring stimuli are applied to the same retina. It appears, therefore, that the effect has to be accounted for in terms of simultaneous induction. This explanation is supported by the purely qualitative observation at the green end of the curve that it is the measuring stimulus which appears too green, and the test stimulus appears green as it ought to appear. Furthermore, if the subject is permitted to look at the test and measuring stimuli for a long time following the green adaptation stimulus, the green test stimulus appears green at the outset and remains green and the yellow-green measuring stimulus which also appears green at the outset changes to yellow-green.

It is planned therefore in future experiments to abandon MacAdam's monocular method and return to the binocular method.

POSITIVE AFTER-IMAGES

ANOTHER complication that has to be avoided in this kind of work is that the adapting stimuli, if too bright, will produce positive after-images.

DICHROMATIC CONFUSION LINES

IT is interesting to note the relation of the confusion lines of colour blind subjects to the corners and side lines of the colour-mixture diagram *(refs. 1, 10)*. The confusion lines of protanopes and deuteranopes have been found to converge at points on the extension of the red-green side line. This means that both of these kinds of colour blindness can be explained by assuming the absence of the blue-yellow mechanism. The difference between the two types can be explained on the basis of a difference in the luminosity curves and/or the luminosity coefficients.

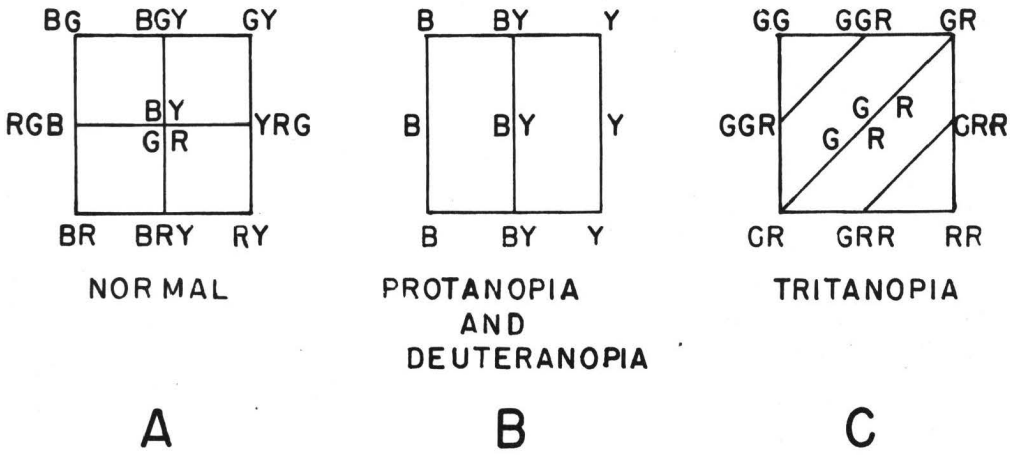


Fig. 7 Schematic colour-mixture diagrams for normal and dichromatic observers.

The relation of red-green dichromatism to normal vision is illustrated in *figs. 7A* and *7B*. The colour-mixture diagram for the normal observer indicates the photosensitive substances evoked by stimuli which lie on the boundary and at the centre of the diagram. If the blue-yellow mechanism is absent, the diagram for the red-green dichromat acquires confusion lines parallel to the v-axis.

Tritanopia appears to be best explained by assuming that Y becomes transformed to R and B to G and the resultant is a set of confusion lines parallel to the green-violet diagonal or converging at a point on this diagonal. The confusion lines of the tritanope converge at a point outside the mixture diagram and the point of convergence lies very close to the green-violet diagonal.

REFERENCES

1. FRY, G. A., *J. opt. Soc. Amer.*, 1945, **35**, 114.
2. HOUSTOUN, R. A., Vision and Colour Vision, Longmans, Green and Co., London, 1932, 223-234.
3. PURDY, D. MCL., *Amer. J. Psychol.*, 1931, **43**, 541.
4. FRY, G. A., A Device for the Study of Chromatic Adaptation (unpublished).
5. FRY, G. A., *Die Farbe*, 1955, **4**, 175.
6. MACADAM, D. L., *Die Farbe*, 1955, **4**, 133.
7. FRY, G. A., The Dichromatic Zone of the Colour-mixture Diagram, Phase 4, Final Report to the Office of Naval Research, Contract No. Nonr - 1066 (00), Project No. NR 140-061.
8. WRIGHT, W. D., Researches on Normal and Defective Colour Vision, Kimpton, London, 1946.
9. FRY, G. A., Determination of Fundamental Colours from Chromatic Adaptation Data, Phase 3, Final Report to the Office of Naval Research, Contract No. Nonr - 1066 (00), Project No. NR 140-061.
10. FRY, G. A., *Die Farbe*, 1955, **4**, 233.

PAPER 37

VARIATION OF COLOUR SENSATION DURING ADAPTATION TO THE COLOUR OBSERVED

By E. N. YUSTOVA

E. N. Yustova, born in 1910, graduated from the Faculty of Physics of Leningrad University in 1932, and is at present working at the State Optical Institute. Master of Sciences. She is mainly concerned with colorimetry and physiological optics and studies the effect on the eye of colour adaptation in connexion with the problems of colorimetry.

37. VARIATION OF COLOUR SENSATION DURING ADAPTATION TO THE COLOUR OBSERVED

By E. N. YUSTOVA

SUMMARY

THE variation of the sensation of a permanent stimulus due to the adaptation of the eye was studied colorimetrically.

For the experimental conditions used the adaptation state of one part of the retina was continuously changing while the given stimulus was being observed: the other adjacent part of the retina preserved permanent adaptation to the colour of a certain surround. Owing to this difference of adaptation, the visual equality established initially under the conditions of equal adaptation of the two parts of the retina to the colour of the surround was destroyed.

From time to time the equality of the fields was restored by changing the colour of the comparison field, that is the difference produced by adaptation was compensated by a difference of the stimuli. In these circumstances the colour of the field of comparison progressively approached the colour of the surround.

Thus, the continuing process of the adaptation of a certain part of the retina to the colour observed was determined, using another part of the retina adapted to a definite surround.

After some successive measurements the process of variation of adaptation ceased and the visual equality of fields that had been already established was not further disturbed.

The process was resumed again, the stimulus observed being replaced by the stimulus of the field of comparison previously reached, and measurements continued to a new stationary state. After several replacements the process ended just when the colour of the field of comparison coincided with the surround.

The results of measurements plotted on the uniform chromaticity diagram reveal that the adaptation process reduces the extent of the domain of the sensation of chromaticity by 15-20 thresholds and consequently the determination of colour thresholds without taking into consideration the state of adaptation is senseless.

VARIATION OF COLOUR SENSATION DURING ADAPTATION TO THE COLOUR OBSERVED

IN the practice of visual colorimetric measurement we observe a phenomenon of the relaxation of the saturation of the colour sensation (discoloration) if the observation lasts for a considerable time. Radiation affecting the eye being invariable, the cause of this relaxation lies in the variation of the adaptation state of the eye during observation. This phenomenon is of interest for the study of colours in connexion with the problem of defining colour thresholds.

We have investigated the character of the variation of the colour sensations during the observation. For this purpose a pair of neighbouring colorimetric fields of 2^{0} visual angle with a large light surround has been used. One of the fields of a constant colour has been observed continuously, the other served for comparison. The latter was shielded by a screen of a colour identical with that of the surround. The screen was removed only at the moment of measurement. Thus a part of the retina changed continuously its adaptation state, while the other part, preserving the adaptation to the colour of the surround, registered these changes.

1. The measurements were carried out as follows: firstly, both fields were approximately equalized in colour and were shut off by a screen of the colour of the surround for a period of 2-3 minutes, during which the initial adaptation to this colour was established. Then one of the fields was opened and the adaptation process began under fixation of the dividing line of the fields. After a certain time the comparison field was opened. Then the colour of the field under test seemed less saturated than that of the field of comparison. Visual equality was restored colorimetrically and after this the field of comparison was screened once more for a certain time (3-10 sec). The comparison field was opened again, visual equality re-established, and so on.

After 4-5 measurements the process of variation of the sensations stopped and the equality established remained invariable within the limits of the measuring errors; for example, the red colour did not pass the unsaturated orange, the violet did not pass the lilac, etc.

Then the colour of the comparison field taken and fixed in the last equalization was set up in the test field. After this substitution the discoloration process resumed and measurements continued up to a new stop, and so on. Usually after one, two or sometimes three stops and relative substitutions of the fields, any saturated colour became identical with the colour of the surround and any variation of the colour sensation stopped.

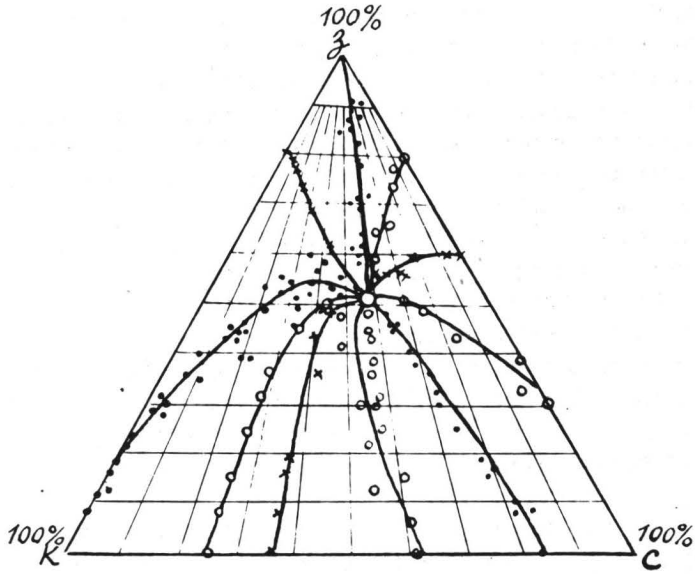


Fig. 1

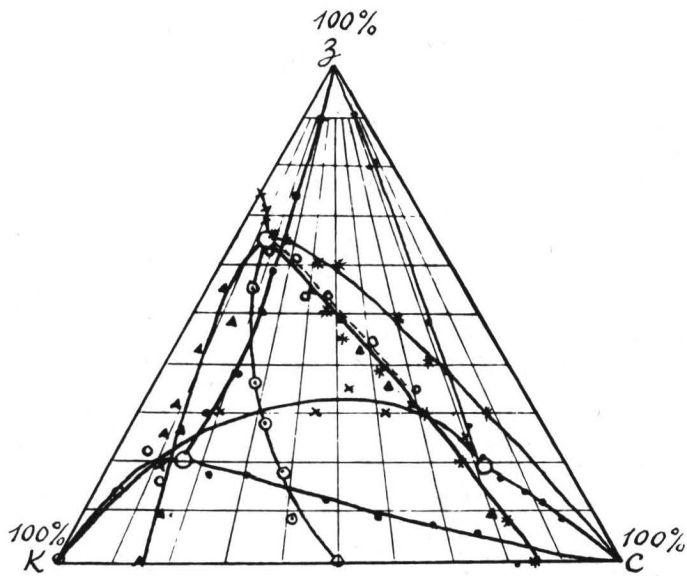


Fig. 2

As a result of these measurements we arrived at a number of colour co-ordinate values measured by the eye adapted to the colour for arbitrarily chosen and unfixed time intervals. The results obtained characterized the process of adaptation to the colour observed.

Such measurements were carried out for a number of colours with five different surrounding fields: that of daylight, of evening light colour, a rose colour and of saturated red and blue.

Co-ordinates of the colours measured were expressed in the system of the colorimeter colours.

Indices "k", "z" characterize the chromaticity, and the brightness is taken as the third co-ordinate.

The results of measurements are represented on *figs. 1-3* in the colour triangle of the colorimeter. In the diagrams the results of some measurements are given and mean curves are drawn, showing the course of the variation of colour sensations during the observation of a corresponding colour.

First of all we should note the continuity at the points of substitution of field colours of the discoloration process in the colour space.

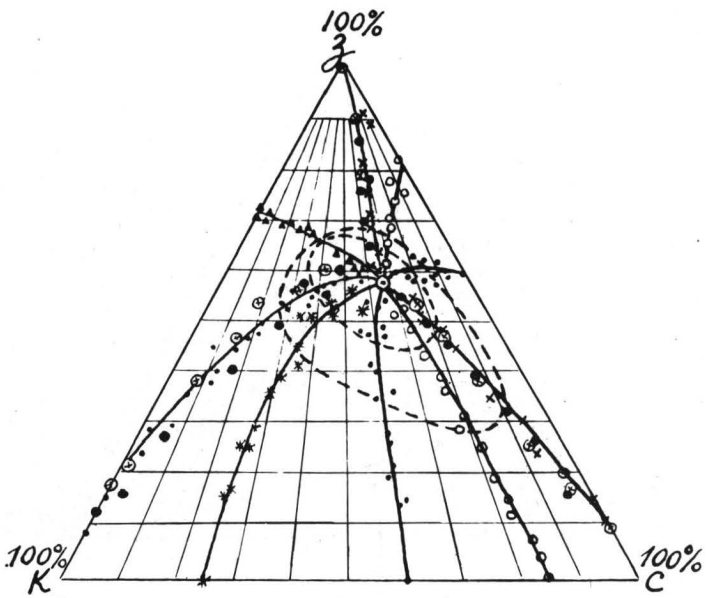


Fig.3

This continuity is confirmed by the absence of fractures on the curves at the substitution points. We also repeated the experiments substituting the colours much earlier than the moment of the stop. Nevertheless the discoloration process was obtained on the same curve (the dotted curve on *fig. 2* which corresponds to the discoloration of the violet against the evening light surround). This means that any colour of this curve can be regarded as a test colour; then all the subsequent points which characterize its discoloration will lie on the same curve.

2. Diagrams show *(fig. 2)* that during the adaptation process every colour tends to reach the surround colour as a limit.

Variation of the colours of the surround involves a corresponding displacement of the whole "spider" on the diagram. Nevertheless, it would be wrong to conclude that the variation of the colour sensation under test is determined by the colour of the surround.

Practically, as far as we can judge by our impressions and memory, the course of colour sensations always remains the same during the observation for any different, even sharply, coloured surrounds. Owing to the complete adaptation to the surround the colour sensation disappears completely in the case of the daylight, evening light and rose-coloured surrounds. For the sharply expressed red and blue ones the saturation becomes greatly relaxed. Similarly the colours under test lose their saturation without any noticeable change of a colour tone.

It is quite evident that the influence of the colour of the surrounds on the discoloration process is merely an apparent effect. Taking a certain definite surround we adapt our eye to the field of comparison and we attribute the colour changes observed to this state of adaptation.

For example, it is quite natural that the part of the retina adapted to the blue loses its sensitiveness for blue colours. That is why, while referring our measurements to the state of adaptation, insensitive for the blue, we should always increase to a great extent a portion of the blue in order to get visual equality.

Hence it becomes clear why the discoloration curve when measured with the blue surround in the course of its variation tends to the blue side.

3. Measurements have shown that the curve of the chromaticity variation is determined solely by the chromaticity and does not depend on brightness. The curves of the chromaticity variation obtained for different levels of brightness appear to be the same within the limits of measuring accuracy.

In *fig. 3*, black and white dots show the trend of the discoloration process of the red, green and blue colours for the two levels of brightness, which differ by a factor of six.

The brightness co-ordinate of the colour under test reaches the brightness of the surround. If the surround is brighter than the colour under test, then during the adaptation process the colour becomes lighter; if the surround is darker than the colour under test, then the latter gets darker.

It is characteristic that the colour under test, brighter than that of the surround, fully coincides with the surround both in brightness and in chromaticity, whereas if it is darker than that of the surround, the increase of its brightness is relatively more slow than the process of equalization in chromaticity with the surround. In the latter case, while attaining the equality in chromaticity, differences of brightness were still preserved.

Thus, when a constant stimulus affects the eye, the adapting state of the eye changes and consequently the colour sensation changes too. In its change adaptation reaches a certain limit depending on the stimulus, after which the process of the change of adaptation stops and the colour sensation remains invariable.

This process of the change of stimulus sensation measured by the eye, which is adapted to a definite surround, is represented by a part of the curve in the chromaticity diagram. The ends of this part are defined by the initial and final sensation in the process of colour variation. If we choose as the colour under test one of the colours lying on this curve the discoloration process of this new colour will develop along the same curve; but the limiting adapting state, depending on the stimulus, will be different.

The corresponding part of the curve, representing the discoloration process in the chromaticity diagram, will be a continuation of the former curve with partial superposition. Hence the limiting stimulus sensation at the complete adaptation to it depends on the stimulus.

In those cases when there is a small difference between the stimuli, their colour sensation can have one common limit at complete adaptation to them.

From the phenomena observed we can draw the following conclusions. As a result of adaptation, all the colour sensations tend to the colourless one and reach a certain limit. In *fig. 3* the dotted line connects the points of the first stops for the saturated colours of the colorimeter triangle. This closed curve characterizes the reduced region of the perception of the saturated colours of the colorimeter, (measured by the eye adapted to the daylight colour), at complete adaptation to them.

When the discoloration process develops (by means of the field substitution mentioned above) we at length reach the point corresponding to the colour of the surround, which is seen by us as neutral.

Having drawn a dotted line connecting the points of the last stops, we have represented in *fig. 3* a region of colours which cannot be discerned during adaptation to them.

Actually this region must be larger; its dimensions in our diagram have been determined by a casual choice of initial colours. By special tests the boundary of the colour regions converging to the same point during adaptation might be widened.

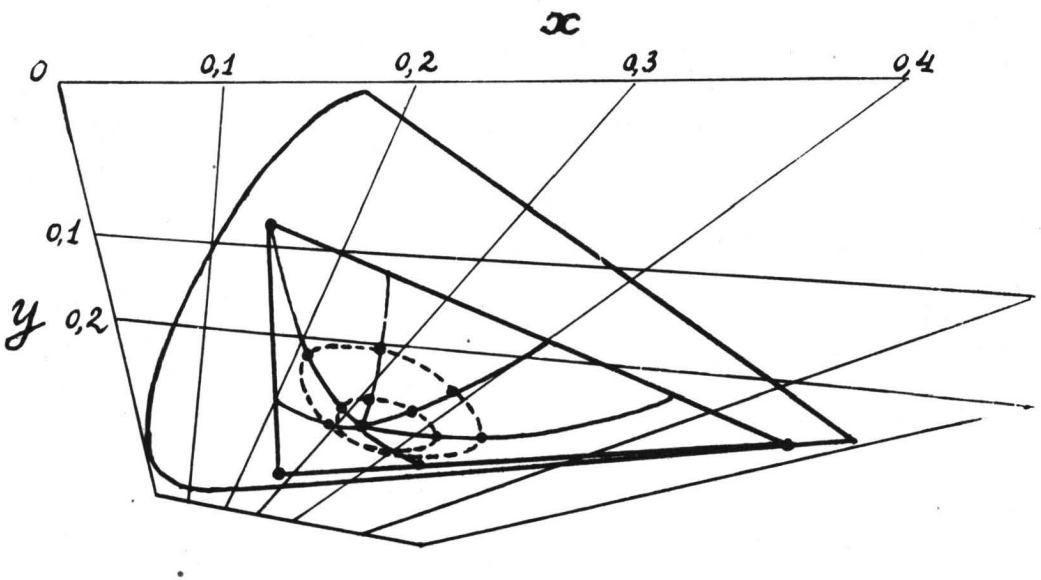


Fig. 4

In *fig. 4* discoloration processes referring to the daylight surround in the "equal distant" (uniform chromaticity) diagram, are represented, and both the region of reduction of initially chosen saturated colours, and the region of indistinguishable colours are marked.

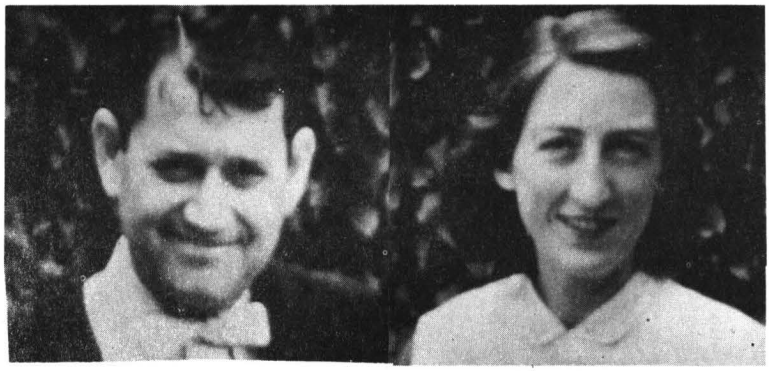
As a result, it appears that during the adaptation process every colour sensation changes by 15–20 chromaticity thresholds.

These observations once more confirm that the notion of the colour threshold belongs in the domain of eye reaction. Thus the determination of the colour threshold without taking into consideration the state of adaptation is senseless.

PAPER 22

FURTHER DEVELOPMENT OF A QUANTIFIED OPPONENT-COLOURS THEORY

By L. M. HURVICH and DOROTHEA JAMESON



Leo M. Hurvich was born in Malden, Massachusetts in 1910, and received his college and graduate training at Harvard University (BA 1932, PhD 1936). He taught Psychology at Harvard until 1940, and has since devoted full time to research in the area of sensory psychology - in the division of research of the Harvard Graduate School of Business Administration until 1947, and since that time in the Colour Technology Division of the Eastman Kodak Company. The latter years have been devoted almost exclusively to problems of colour vision. This work has been carried out jointly with his wife, Dorothea Jameson Hurvich (b. 1920, Newton Mass.), with whom he first became professionally associated at Harvard during the war years following Mrs. Hurvich's graduation from Wellesley College in 1942.

22. FURTHER DEVELOPMENT OF A QUANTIFIED OPPONENT-COLOURS THEORY

By L. M. HURVICH and DOROTHEA JAMESON

SUMMARY

THE basic postulates of the opponent-colours theory are briefly reviewed, the derivation of the hypothetical photopigment distributions is considered, and the three-variable nature of the Hering concept is discussed.

The different rates of response increase with increase in level of excitation of the paired chromatic and achromatic systems are related to the facts of small field colour distortions in all retinal regions, and experiments are reported which indicate that increased density of macular pigment rather than loss of photosensitive material is responsible for the differences in small field phenomena between the central fovea and other retinal regions.

The roles of induction effects and of changes in excitability are discussed in relation to experiments on brightness and chromatic adaptation.

Recent results in neurophysiology are reviewed and it is concluded that the physiological concepts basic to the opponent-colours theory of vision are consistent with present-day knowledge of nerve and sense physiology.

INTRODUCTION

"MORE is to be gained," wrote Selig Hecht in his discussion of colour theory, "by the rigorously quantitative treatment of a small field in a concrete manner than by the multiplication of vaguely general and obviously inadequate theories (of colour vision) of which there are already far too many" *(ref. 1)*. One can hardly take exception to this opinion in view of the large accumulation of precise psychophysical data relating to almost every aspect of colour vision. But where Hecht in his own early and stimulating quantitative formulation based himself squarely on the Young-Helmholtz three-receptor, three-primary sensation hypothesis, we have found Hering's theory of a three-variable opponent-colours mechanism to be a more satisfactory working hypothesis.

A quantitative formulation of this theory accounts systematically for the colour sensations associated with the primary stimulus variables of wavelength and luminance, for the facts of colour mixture, and for colour discrimination data whether in normal, dichromatic, or anomalous

trichromatic colour vision *(refs. 2–4)*. The theoretical analysis of the phenomena of chromatic adaptation has so far been limited to a restricted range of observational conditions *(ref. 5)*, and we shall, in the present discussion, try to indicate the direction that we think an extension of this analysis will take. We shall also discuss the way in which certain postulated properties of the paired chromatic processes relate to colour distortions in small fields, relations that were merely suggested in an earlier report *(ref. 3)*.

Before turning to these matters and to a consideration of the compatability of the opponents notion with current concepts of neuro-physiology, we should like first to clarify two aspects of the theoretical formulation that seem not to have been sufficiently emphasized in our earlier papers. One of these issues concerns the specific spectral distributions of the photochemical absorption functions assumed in the theory, and the other the number of independent variables involved.

PHOTOPIGMENT DISTRIBUTIONS IN THE THREE-VARIABLE OPPONENT-COLOURS THEORY

IN the opponent-colours theory, perceived hue, brightness and saturation are correlated with the directly measurable chromatic (yellow-blue, red-green) and achromatic (white-black) response functions. (See *fig. 1*). The physiological response activities in these three paired response systems are initiated by absorption of light in the set of three independent photosensitive materials that we have labelled α, β, and γ. (See *fig. 2*). Neither the forms nor wavelength maxima of these three functions are directly measured. They are mathematically derived functions that satisfy certain theoretical requirements. The high degree of overlap exhibited by these derived photopigment functions is disconcerting to research workers who are concerned with the direct measurement of photopigment absorptions. These physiologists and biochemists quite understandably hope to find visual photopigments with more widely spaced absorption peaks and they are just as resistant to our theoretical α, β and γ distributions today as they were to Hecht's V_0, G_0 and R_0 functions in 1932 *(ref. 6)*.

We should like to make it clear that, despite the adequacy of the α, β and γ functions as we have been using them in our quantitative treatment, we hold no brief for their ultimate correctness. The forms and wavelength maxima are what they are simply because of the specific interrelations that we assume to exist between photochemical and response events. Having assumed that excitation of the α photopigment eventuates in blue, red and white responses, excitation of the β photopigment in green, yellow and white responses, and excitation of the γ photopigment in yellow, red and white responses, mathematical transformation of the experimentally measurable chromatic and achromatic response functions leads to these specific photosensitive distributions.

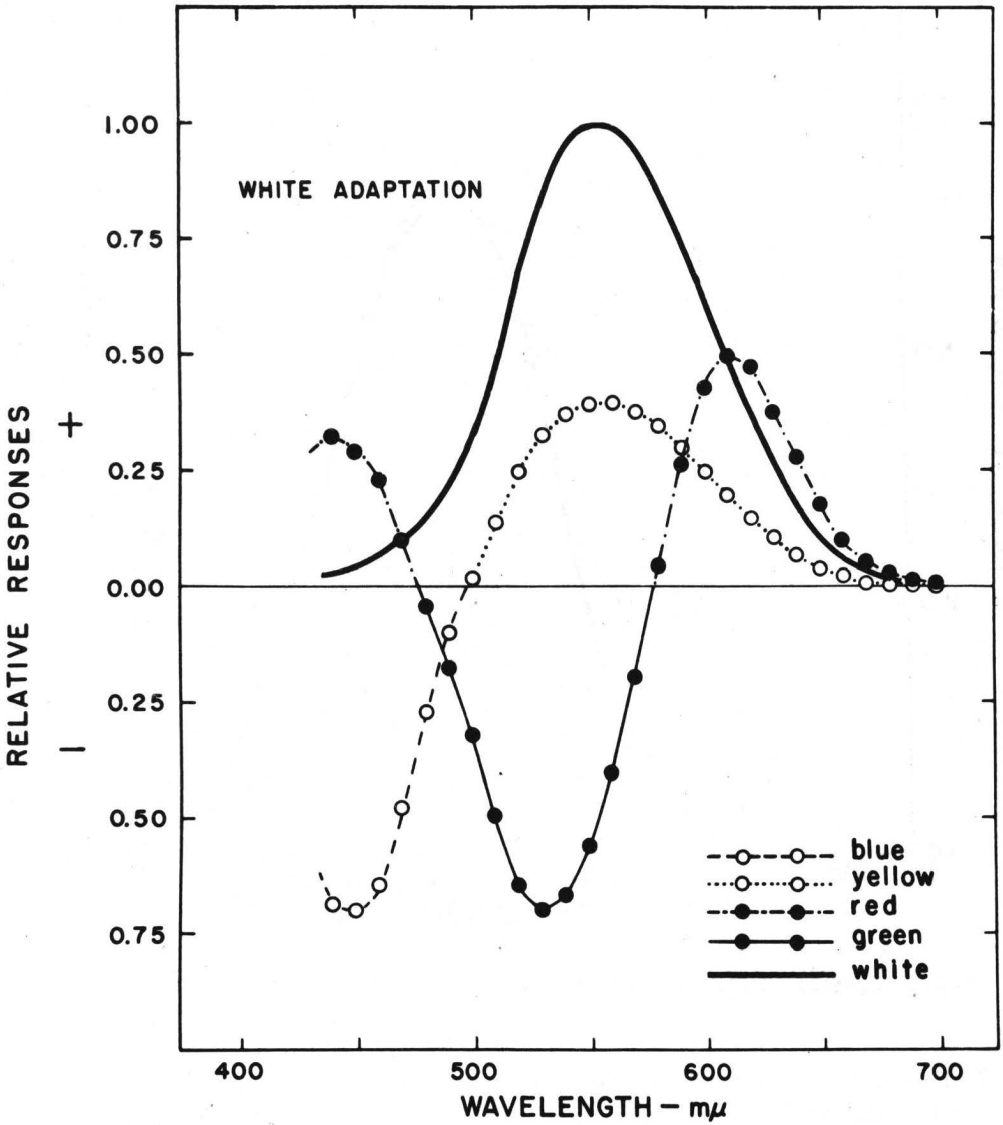


Fig. 1. Chromatic and achromatic response functions for equal energy spectrum for C.I.E. standard observer.

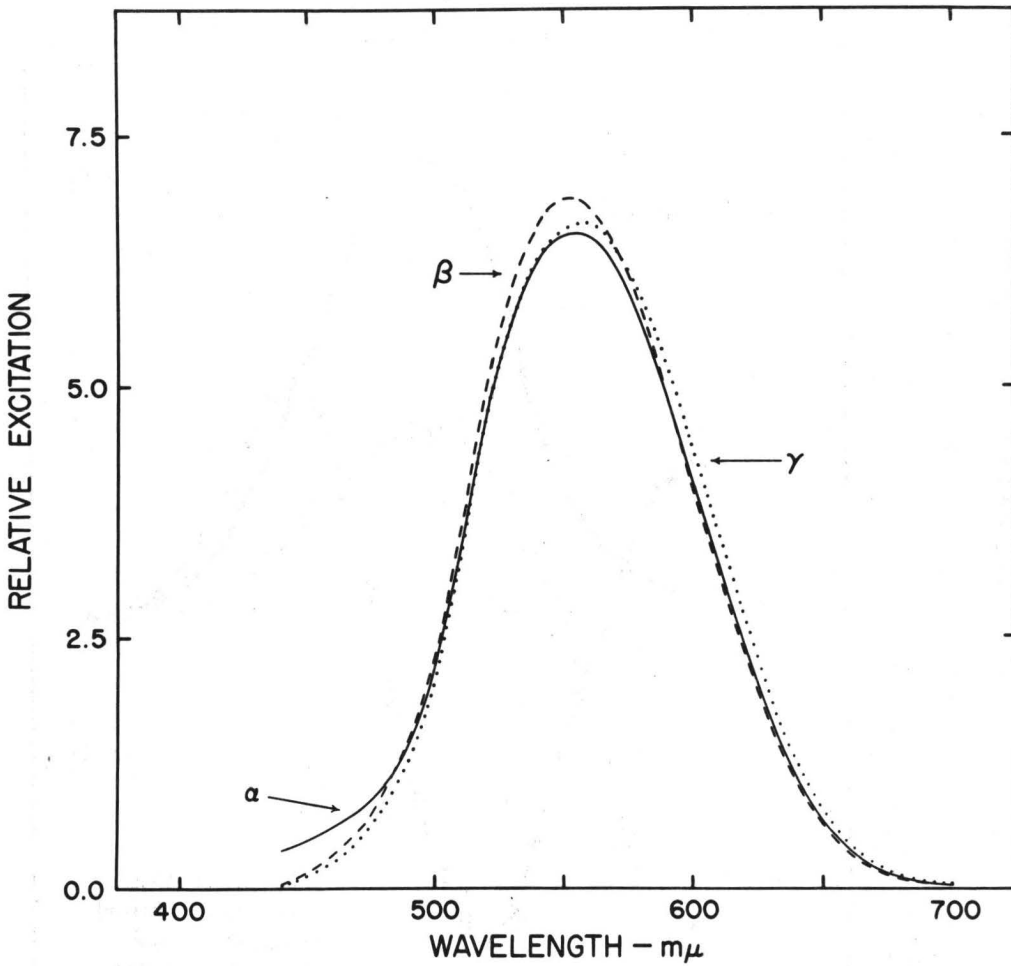


Fig.2. Spectral distribution curves derived for three receptor substances.

Had we postulated a set of linkages different from those just outlined, one which assumes, for example, that the α photopigment excites only the blue response system, β the yellow, green, and white response systems, and γ only the red system, then the family of photopigment distribution curves that we would have derived would be identical with the familiar C.I.E. tristimulus functions, $\bar{z}_\lambda$, $\bar{y}_\lambda$, and $\bar{x}_\lambda$. The shortcomings of the C.I.E. curves as photopigment functions become apparent however, when one attempts to correlate them with chromatic adaptation effects.

As matters now stand, the selective visual photopigments in the human eye have not been identified. Consequently, the visual theorist has no choice but to make *a priori* postulates concerning either the absorption

curves themselves or the relations between photosensitive excitations and visual response processes. Once the photopigment absorptions have been determined directly there will, of course, be no need for such *a priori* postulates, and the relations between the precisely identified light-mediating substances and the directly measurable chromatic and achromatic response functions can be deduced from the two knowns. Recent progress in the area of photopigment measurement gives us confidence that this desirable situation is not too remote *(refs. 9-11)*. Meanwhile, the particular spectral distributions and interrelations that we have postulated simply satisfy the psychophysical requirements of our working hypothesis.

As for the number of independent variables in the opponent-colours theory, a triple set of functions is necessary and sufficient for the treatment of normal colour vision, and both the three pairs of opponent chromatic and achromatic response functions and the derived α, β and γ distributions satisfy this requirement. However, in what we had hoped would be the interests of clarity, we have treated the three independent photopigment functions as grouped in four units, *B*, *G*, *Y*, and *R*, where the four units are composed of α, β, γ in the following way;

$$B = 2\alpha,\ G = 2\beta,\ Y = \beta + \gamma,\ R = \alpha + \gamma, \qquad (1)$$

This conceptual device was intended only to simplify the interrelations postulated between photochemical excitations and the paired visual response processes as shown by the alternative diagrams in *fig. 3*. Unfortunately, as an unforeseen by-product of this conceptual simplification, we seem inadvertently to have been responsible for giving the pointless "three-*v* four-variable" argument a little fuel to work on.

Although the respective views of Helmholtz and Hering are usually contrasted as three-*v* four-colour theories *(refs. 12-15)*, the fundamental difference between the two types of theory is not one of three-*v* four independent variables. Hering made it quite clear that the assumed physiological basis of his own theory was a three-dimensional one *(refs. 16, 17)*. Helmholtz's view of Hering's theory as a three-variable schema is found in the second edition of his Physiological Optics. "E. Hering's much discussed theory," wrote Helmholtz, "is a modification of Young's theory which seeks, through the choice of other Grundempfindungen, to be in better agreement with what it believes must be regarded as the immediate facts of introspection" *(ref. 18)*. Helmholtz then went on to illustrate by means of three linear equations, how the three paired variables of the Hering theory relate mathematically to his own three-variable schema.

The real theoretical issue, therefore, has never been a matter of the number of independent variables assumed, but the manner in which the different theories conceive the relations of the three variables to visual experience and to the action of the stimulus *(ref. 19)*.

The way in which the conception of paired, opponent chromatic response processes relates to the paired hue losses that are experienced at low levels of excitation will be discussed in the following section.

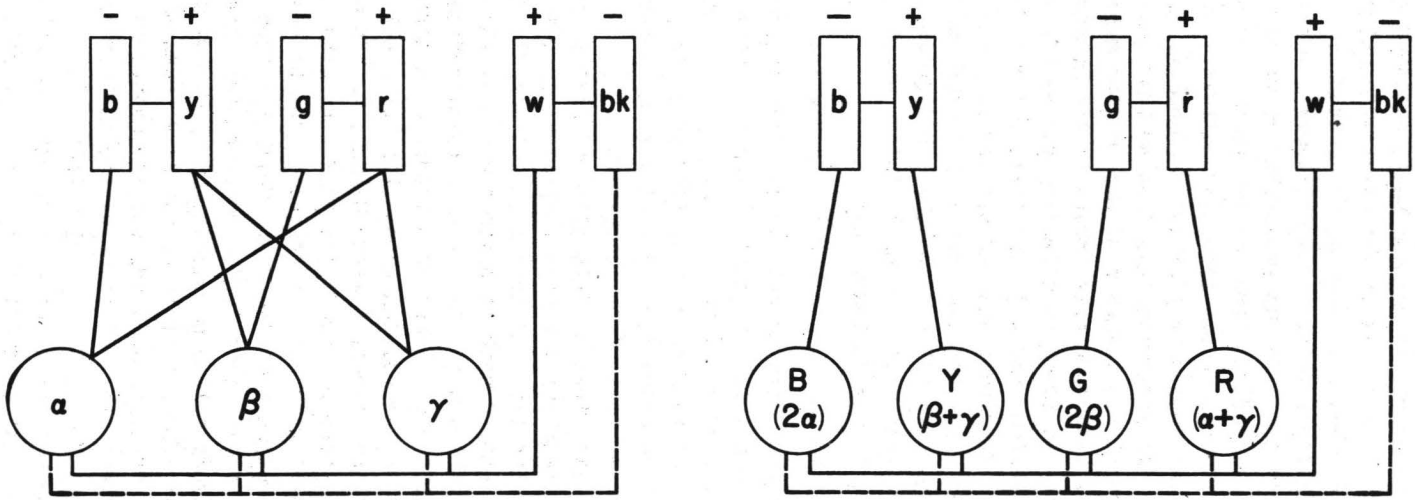


Fig.3. Schematic diagram showing the assumed relations between photoreception and visual response. α, β and γ are the three independent photochemical substances of which the *B*, *G*, *Y*, *R* photoreceptor units are constituted.

YELLOW-BLUE LOSSES, MACULAR PIGMENT AND CENTRAL FOVEAL COLOUR VISION

SPECIFIC colour distortions and confusions that occur in small foveal areas are frequently related to and described as reductions of normal trichromatic colour vision toward tritanopia *(ref.20)*. Compared with the normally trichromatic foveal area (one to two degrees) a small central foveal area (20', 10' or less) seems to exhibit 1) considerably reduced luminosity in the short-wave region of the spectrum, 2) loss of saturation of most spectral hues, and 3) specific reductions in yellow and blue hue responses. The usual proposal made to account for these changes is that, in the foveal centre the physiological elements are similar or identical to those assumed to be present in the eye of the congenital tritanope *(refs.21,22)*. Thus it is assumed that the photosensitive substance primarily responsible for the absorption of short-wave light is missing, in which case the centre of the normal fovea is completely dichromatic, or else that this material is considerably reduced in this area, and hence the central fovea tends toward complete dichromacy.

This view minimizes two rather important facts. One is that the yellow-blue losses associated with very small stimulus areas are not confined to stimuli at the centre of the fovea, but can be demonstrated for any retinal area. The numerous researches of Hartridge more than adequately document the generality of this effect in non-foveal as well as foveal regions of the retina *(refs.23,24)*. The second important fact is that the small field saturation and hue losses in any retinal region are not dependent solely upon the size of the stimulated area, but are also related to the stimulus luminance. If the stimulus energy is sufficiently increased, even a tiny foveal area is decidedly not "blue blind"--a fact that can be established by a look *(refs.25-27)* and that frequently comes as a surprise to those who have taken literally the "foveal blue-blindness" misnomer that originated with König *(ref.28)*. Reciprocal relations between area and intensity are, of course, common in vision *(ref.29)*, and they have also been reported at the neural level in electrophysiological studies *(ref.30)*. With specific reference to small field colour losses, Hartridge *(ref.31)* has called attention to the inter-dependence of luminance and area, and Farnsworth *(ref.32)* has made this a major point in a recent report on this subject.

These two facts, i.e., 1) the non-specificity of the small field effects with respect to retinal area, and 2) the dependence of the effects on stimulus luminance, led us to suggest in an earlier paper that the paired yellow-blue losses in small area responses might be considered an extreme of the Bezold-Brücke phenomenon, and that they might be accounted for by the same properties of the paired response processes that account for the Bezold-Brücke hue changes with change in stimulus luminance *(ref.3)*. Although Farnsworth *(ref.32)* makes a similar suggestion concerning the relation of the area and luminance phenomena, it is difficult to see how

his proposed reduction in the ratio $b/(r+g)$ would account for yellow, as well as blue losses with reduction in excitation.

In our development of the opponents theory, the assumed relations between chromatic and achromatic responses and photochemical excitations are as follows:

$$\begin{aligned} y - b &= k_1(\beta + \gamma - 2\alpha) \\ r - g &= k_2(\alpha + \gamma - 2\beta) \\ w - bk &= k_3(\alpha + \beta + \gamma) - k_4(\alpha + \beta + \gamma). \end{aligned} \tag{2}$$

In these equations, the coefficients k_1, k_2, k_3 and k_4 have been introduced expressly to take into account what seems to be a systematically different property of the three response systems. That is, in the theoretical model, neither the response thresholds nor the functions relating increase in response to increase in stimulus energy (or photochemical excitation) are identical in the three paired systems.

The general nature of the assumed differences in the energy *v.* response functions is illustrated in *fig. 4.* The achromatic response system, associated with luminosity and whiteness, is assumed to have a low intrinsic threshold and to exhibit responses that increase directly with, say, the logarithm or some power function of the stimulus energy. The paired red-green process has a somewhat higher intrinsic threshold for response, and increases at a somewhat lower rate, whereas the yellow-blue process has the highest intrinsic threshold but shows a higher rate of response increase with increase in stimulus energy than does the red-green pair. Thus, for a given field size, at some intermediate luminance level, say 10mL, the spectral hues will appear as indicated by the spectral response functions shown in *fig. 1.* At a considerably higher luminance level, the theory requires that the yellow-blue response function will be magnified relative to the red-green one, and the spectrum will thus show a predominance of yellow and blue hues. On the other hand, at very low luminances, the yellow-blue responses will be uniformly reduced relative to the red-green pair, and the spectral hues will be predominantly red and green. These changes can be handled quantitatively by assigning different specific values to k_1 and k_2 for different luminances in equations (2), and quantitative predictions of Bezold-Brücke hue changes, and of changes in wavelength and saturation discrimination that result from this treatment are found to be in good agreement with experimentally measured functions *(ref. 8).*

Since the level of excitation can be reduced by reduction in stimulus area as well as by reduction in luminance for a fixed area, the same quantitative treatment can be applied to small field phenomena. We should be able to predict, for example, the changes in chromaticity required when colour matches are made between stimulus areas of different size. Such predictions are plotted for four colours in *fig. 5.* In each case, the point of origin of the arrow represents the matching chromaticity for the standard observer for the usual condition of a bipartite two degree field, and the arrow head indicates the changed matching chromaticity when the

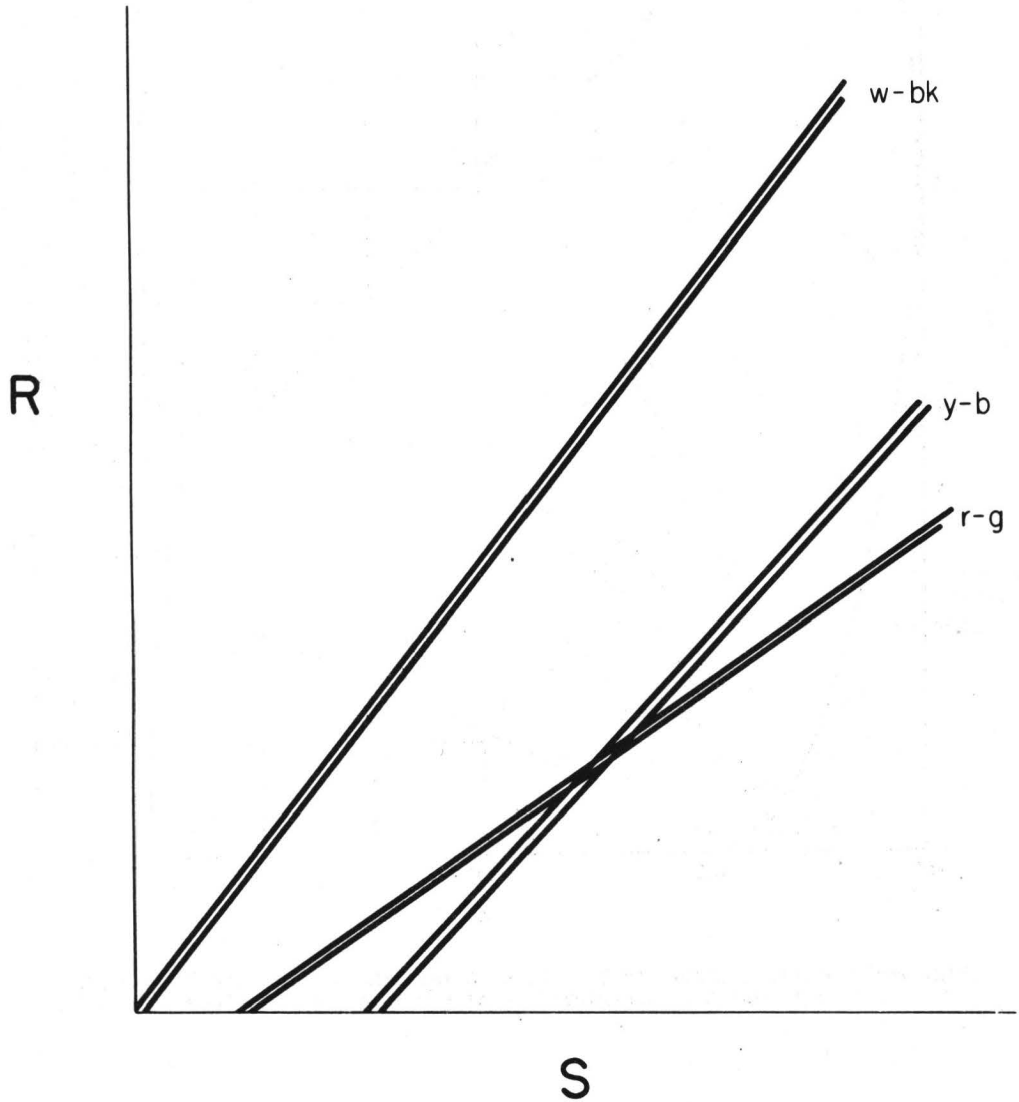


Fig. 4. Schematic representation of the relation between the paired chromatic and achromatic response systems and stimulus magnitude (photosensitive excitation). This graph does not represent the varying excitations of the three response systems by stimuli of different wavelength. See *fig. 1.*

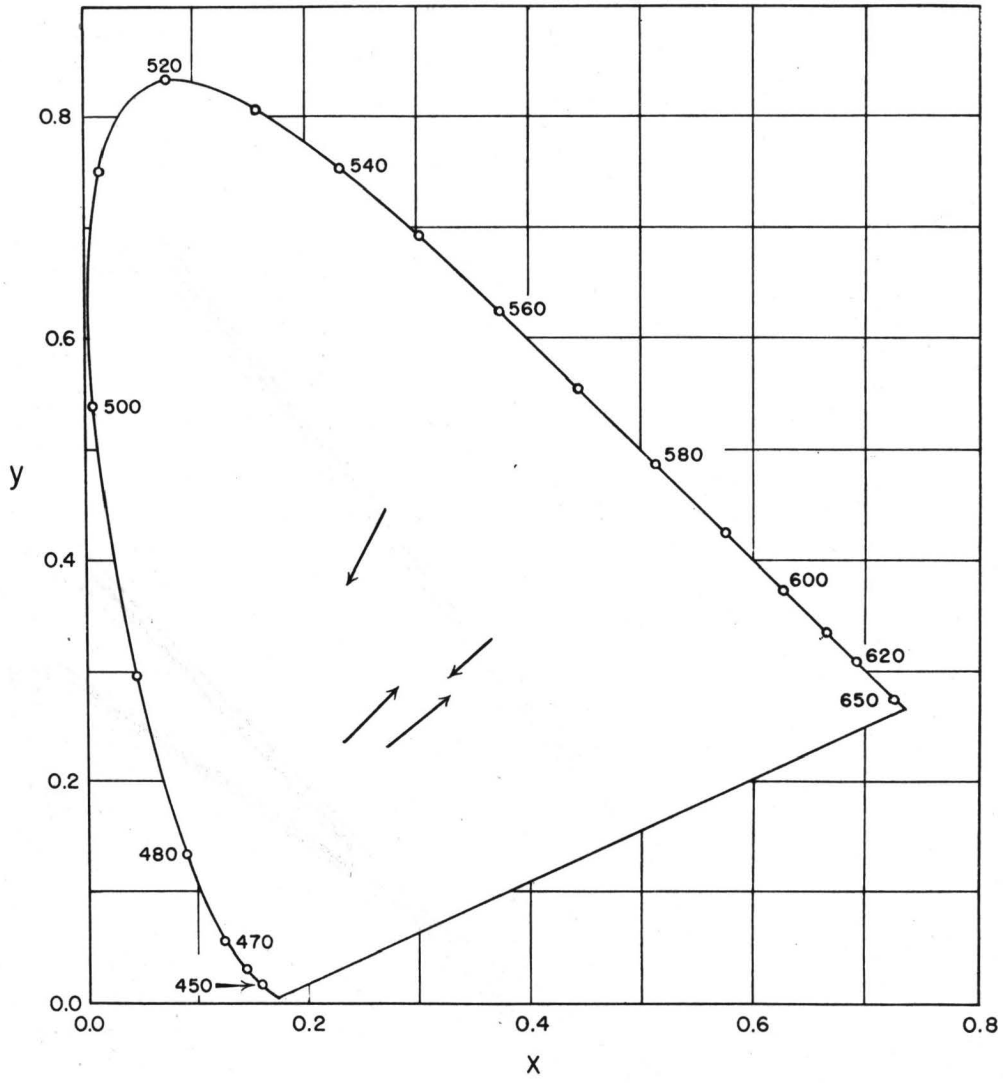


Fig.5. Theoretical chromaticity shifts in matching stimuli for four colours of fixed spectral distributions with size reductions from 2^{0} to 25'.

one half of the bipartite field containing the same test stimulus is reduced in size to, say, 25' or so. To compute the theoretical chromaticity values it was assumed that, for the excitation level associated with the small area stimulus, the relative responsiveness of the blue-yellow system has dropped to about one-third of its value for the standard condition. The perceived colour changes correlated with these predicted chromaticity shifts are reductions in yellow and blue hues and a general reduction in saturation.

Fig. 6 shows experimental data for such colour matches where the field sizes were 1^{0} x 2^{0} and 25'. These measurements are from part of a study by Burnham and Newhall *(ref. 33)*. The individual colours are shown in separate blocks. The thin arrows in each block show separately the average shifts measured for each of seven observers, and each heavy line is a theoretical prediction for the standard observer taken from *fig. 5*. The trends predicted on the basis of the theoretical assumptions for the standard observer are generally similar to the measured chromaticity changes.

It seems clear that the same systematic properties of the visual mechanism that account theoretically for changes in perceived colour with reduction in stimulus luminance allow us to predict, at least approximately, changes in perceived colour with reductions in stimulus size. These changes are related entirely to assumed differences in the energy v response functions in the paired chromatic and achromatic processes and they do not involve in any way changes in the relative amounts of the different photosensitive materials responsible for light absorption.

We have, nevertheless, explored the latter possibility, namely, that the foveal centre might be deficient in the short-wave sensitive light substance and hence more closely related to a condition of congenital tritanopia than to normal colour vision at low excitation levels. One of the characteristics of typical tritanopia, and one that seems to require a deficiency in one of the photosensitive materials, is that, along with loss in yellow-blue sensitivity, there is also a distortion of the remaining red-green spectral response function such that the secondary red response in the short-wave region is sharply reduced or even completely absent *(ref. 3)*. The tritanope, who has no blue response, does not see a neutral point in the region of the spectrum where the normal observer sees a unique blue. The normally blue spectral region seems to be green for the tritanope, and the neutral point, if it can be found, is located at the extreme voilet end of the spectrum *(ref. 34)*. If the centre of the normal fovea lacks the same photosensitive material that the tritanope lacks, the normal observer should, for very small central stimuli, see a neutral point at a spectral locus that is displaced toward the short wavelengths from the normal pure blue. Or, if the short-wave substance is present, but in reduced amount, and there is a vestigial blue response, we should expect a shift in the pure blue locus from the wavelength at which it is normally seen in, say, a two degree field, to a significantly shorter wavelength in a central field of say, 10' or so. Judd's interpretation of small field phenomena in terms of

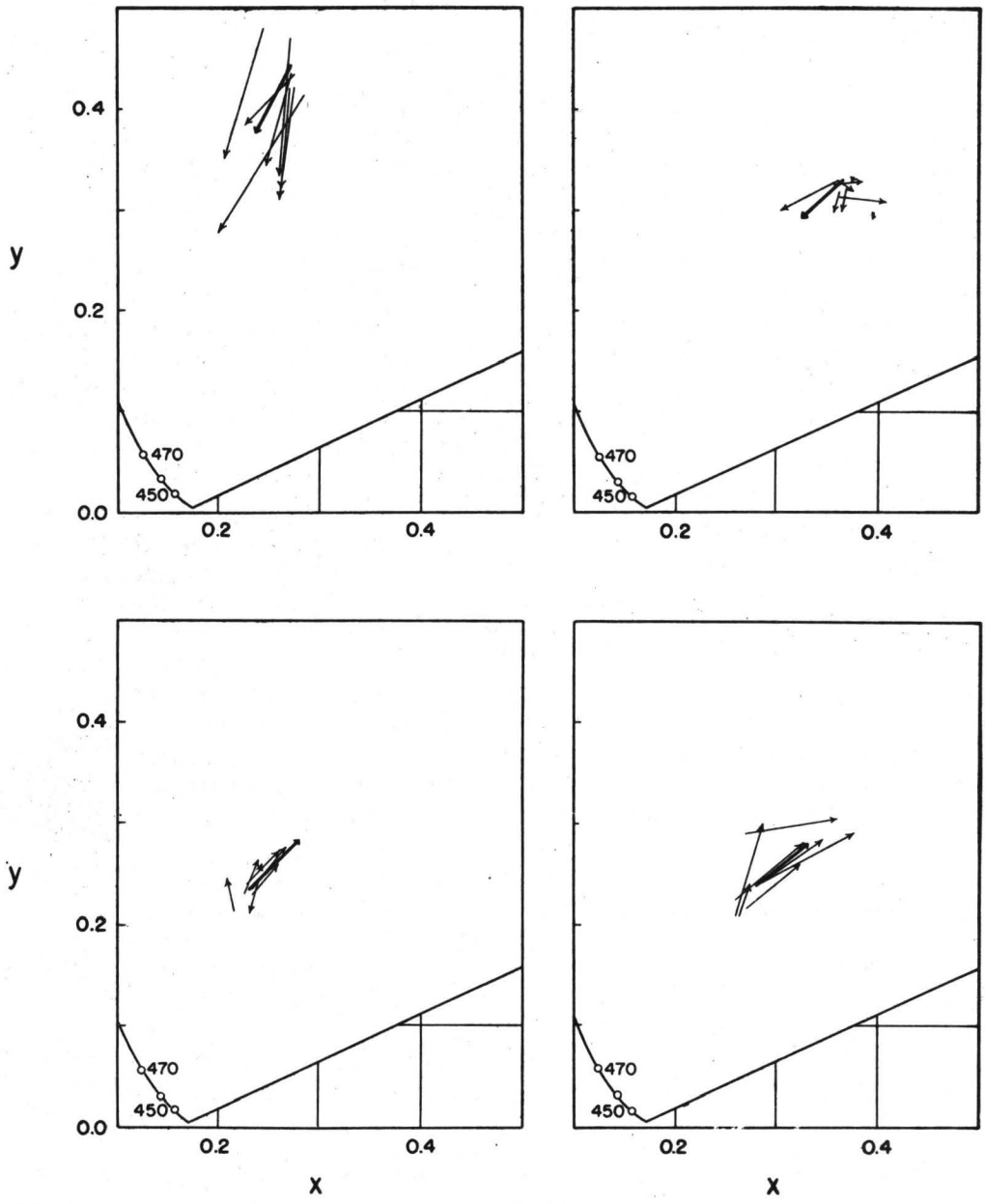


Fig.6. Chromaticity shifts in matching stimuli for four colours of fixed spectral distributions with size reduction from 1^0 x 2^0 to 25'. Thin lines are results for each of seven observers *(ref.33)*. Heavy lines are predicted chromaticity shifts from *fig.5*.

losses or reduction at the second stage of the Müller zone theory leads to the same expectation, i.e., a shift in the pure hue locus toward shorter wavelengths *(ref. 35)*.

We have subjected this hypothesis to an experimental test, and the results for three observers are shown in *Table I.* In the experiment, the observer selected that wavelength that appeared neither reddish nor greenish, but either pure blue or neutral. (For a detailed discussion of measurements of pure hue loci see *ref. 36.)* The stimulus was actually indentifiable as pure blue (in both cases) but it appeared both less bright and less saturated in the 10' field than it did for the 2^{0} field. The luminance level was approximately 15mL and all observations were monocular (left eye). Although the variability of the determinations increased for all three observers when the stimulus area was reduced from 2^{0} to 10' it is clear that there is no appreciable shift in the average wavelength selected to meet the "neither reddish nor greenish" criterion. The results clearly fail to confirm the hypothesis that there may be a short-wave

TABLE 1

PURE BLUE LOCUS

	Field Size			
	2^{0}		10'	
Observer	λ	σ	λ	σ
A	476.2	$\pm$ 3.3	476.1	$\pm$ 7.7
B	477.1	$\pm$ 2.8	475.4	$\pm$ 5.2
C	473.0	$\pm$ 3.9	473.5	$\pm$ 7.3

pigment reduction in the central fovea. Whatever histological differences there may be between the tiny foveal centre and the larger 2^{0} retinal region, they do not seem to involve the reduction of one type of photopic receptor or receptor substance.

What of the variations in macular pigment within the central two degrees of the retina? What role, if any, does the macula play in differentiating colour perception in the foveal centre from the immediately surrounding 2^{0} region? Unfortunately, reports of histological examinations of macular distributions in the retina are not decisive since there is a disagreement about the foveal centre *(refs. 37,38)*. This is mostly because, when the retina is removed for microscopic examination, the centre of the fovea usually tears away, leaving a tiny hole in just that region about which we would like to have more information.

It should be possible, however, to estimate the macular variations in the living intact eye by observations that involve stimuli from different

parts of the spectrum that are known to be differently absorbed by the macula *(refs.39,40)*. We can, for example, make the same kind of observations that we have made for the determinations of the unique blue in the spectrum, but this time with binary mixtures of two different wavelengths rather than a single spectral line of variable wavelength. In this way, we may be able to detect whether the selective macular absorption is the same or different in the two areas, and thus estimate whether the average density of the macular pigment in the 10' central area as compared with its average density in the central 2^{o} region is the same, or by what amount either greater or less.

The binary stimulus used for these determinations was a mixture of 450 mμ and 530 mμ, the latter being absorbed by the macula to a much lesser extent than the former. The observer's task was the same as in the preceding experiments. He was required to determine the mixture ratio for which the sensation was neither reddish nor greenish, but simply blue or neutral. The same three observers were used and the luminance level was higher than 15mL. The results are summarized in *Table 2*.

TABLE 2

PURE BLUE RATIO -- 450mμ/530mμ

	Field Size			
	2^{o}		$10'$	
Observer	*R*	σ	*R*	σ
A	2.13	± 18.1%	5.86	± 20.0%
B	2.50	± 7.8%	5.11	± 10.3%
C	3.70	± 10.0%	5.35	± 17.9%

There is some increase in variability for the small field determinations, but in this experiment there is also a striking change in the average mixture ratio for the different stimulus areas. For each observer, a greater amount of the 450 mμ stimulus was required for the 10' field determinations than was needed for the 2^{o} field. The differences are not identical for all three observers, but on the average they would be accounted for if the density of macular pigment in the central 10' fovea is about 1.4 times its density in the central 2^{o} of the retina. A similar deduction of increasing macular density toward the foveal centre has been reported recently by Grützner *(ref.41)*. Grützner's technique involved colour equations in bipartite fields of various sizes, and the changes in these equations for test fields decreasing in size from 4.2^{o} through 1.5^{o} to 0.6^{o} were interpreted as indicating a macular gradient of increasing density toward the foveal centre. A macular density increase in the foveal

centre is consistent with the fact that there is an apparent loss of short-wave luminosity in the tiny central fovea *(refs.32,42)*, which seems greater than that which occurs in congenital tritanopia *(ref.22)*. The relatively greater absorption of the short-wave stimuli would also account for the kinds of colour distortions that seem to occur in this region and not in other retinal areas when spectrally heterogeneous stimuli are viewed.

The general nature of the effects correlated with reduced yellow-blue responses and increase in macular pigment density in the central foveal area is summarized in *figs.7* and *8*. *Fig.7* shows lines in C.I.E. space along which stimuli would be expected to be confused at low luminances and small field sizes. The perceptions of stimuli falling along these lines normally differ mainly in the degree of yellowness and blueness, and with reduction in yellow-blue responses they tend to look more and more alike. The centre line, for example, that passes between about 475 mμ and 578 mμ represents chromaticities that normally vary from maximally saturated pure blue, through neutral, to pure spectral yellow when observations are made with the normal 2^{0} foveal area at moderate luminances. Viewed either at very low luminances or in fields restricted in size the yellow-blue differences tend to disappear, and in the extreme case with both area and luminance sufficiently reduced so that a true dichromacy results, all chromaticities that plot on this line will appear uniformly neutral. All chromaticities on the upper line will also be confused in the extreme case of reduced area and luminance but will have a greenish tinge in common. Similarly for the chromaticities on the lower line, which will be confused with one another but in this case they will all have a reddish hue. These lines have all been determined on the basis of the chromatic response functions given in *fig.1*.

These are the confusion lines that we should expect from plots of confusion stimuli seen by retinal areas with the average macular density in the central two degree area. Stimulus distributions that pass through an interposed filter such as an increased density of macular pigment before impinging on the photosensitive retinal elements are also expected to fall on these chromaticity confusion lines provided that this selective filter is taken into account in plotting the stimulus chromaticities. If the filter is not taken into consideration distorted apparent confusion lines will result. Thus, for example, we may suppose that one of the points indicated by the circles on the theoretical confusion lines in *fig.7* represents a mixture of 450 mμ, 530 mμ and 670 mμ that has been selectively attenuated by the assumed macular filter increment in the central 10' area of the fovea. Knowing the chromaticity values, we can solve for the amounts of the mixture primaries in this attenuated mixture. Knowing also the macular filter transmittances for the density difference involved, we can also solve for the amounts of the mixture primaries at the eyepiece of our instrument.

Given the latter stimulus distribution, we can now also specify the CIE chromaticity in the standard way without including in the computations the

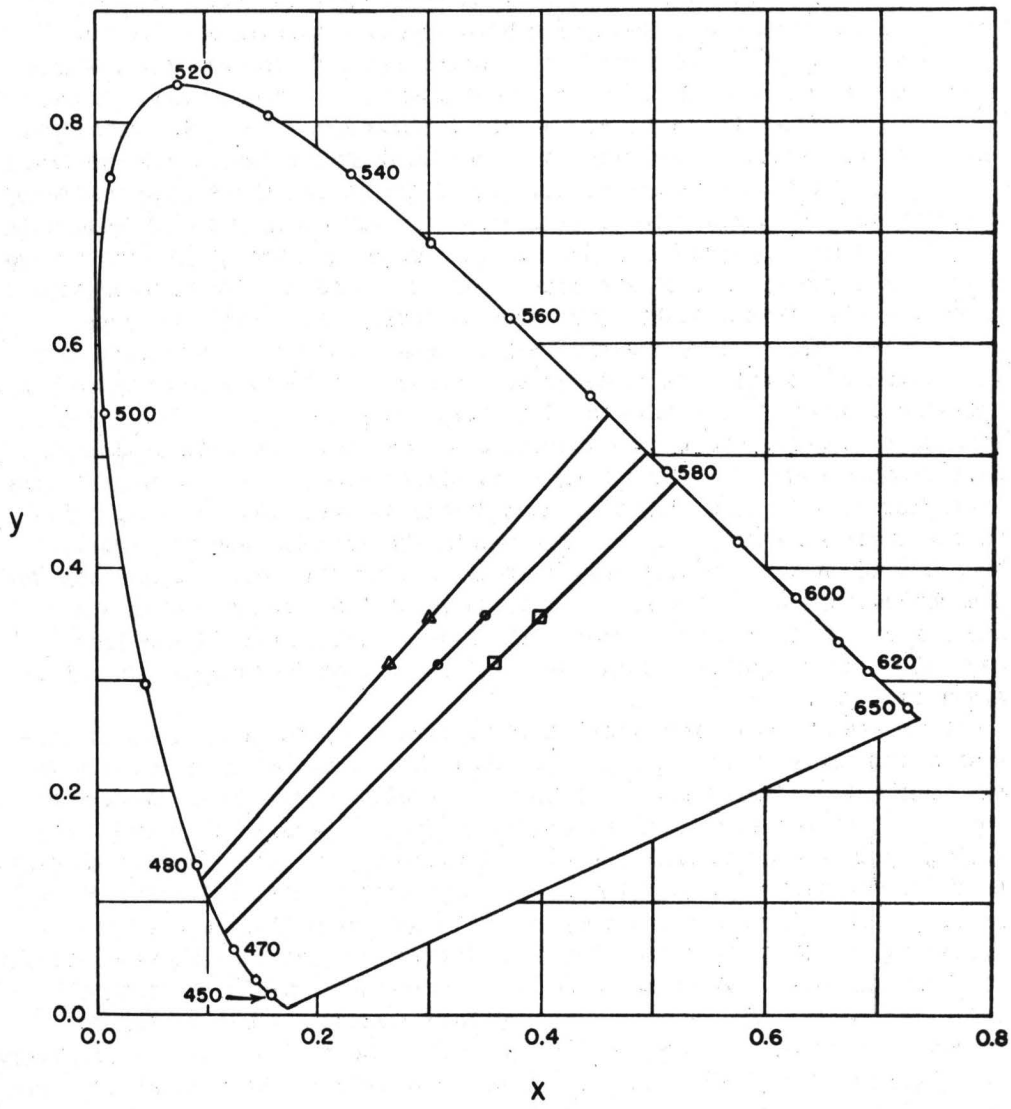


Fig.7. Theoretical chromaticity confusion lines for small fields and low luminances.

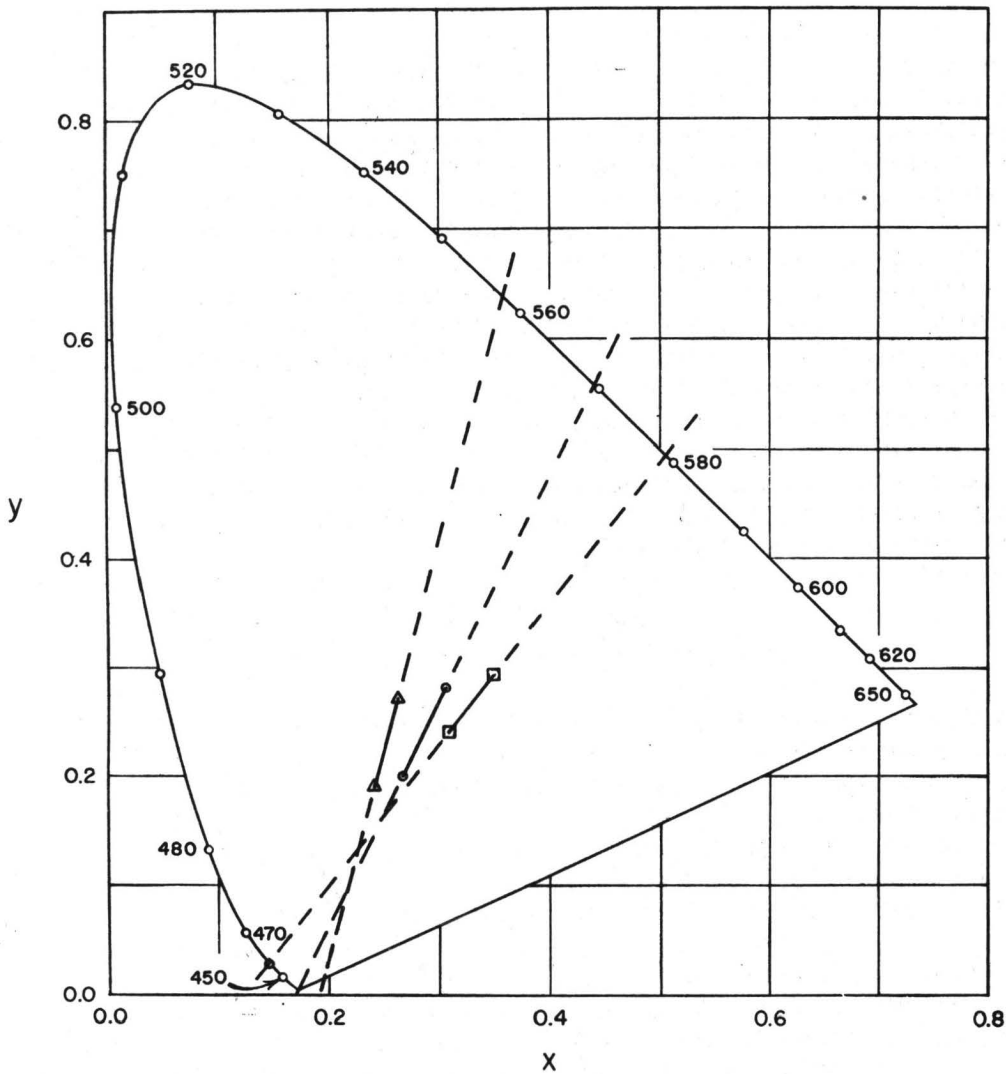


Fig.8. Theoretical apparent confusion lines for small fields and low luminances in fovea.

filter increment through which the retina is actually assumed to be "seeing" the stimulus. When such a computation is made for the pairs of stimuli indicated by the symbols plotted on each of the theoretical lines shown in *fig. 7*, the corresponding uncorrected apparent foveal confusion loci are those shown in *fig. 8*. As we see, the uncorrected confusion loci predicted for these stimulus mixtures for the foveal centre show a tendency to converge toward the short-wave extreme of the spectrum locus, and in this respect they are similar to experimental results for both small field observations by normal observers and observations made by congenital tritanopes *(refs. 32,34)*. The actual convergence of the lines within the spectrum locus is a tendency that is not found for congenital tritanopes, but one that has been reported by Farnsworth and his co-workers for central confusion loci determined for normal observers *(ref. 43)*.

The exact directions of these apparent confusion lines will, of course, depend on the particular stimuli used to determine the confusion loci, since the effects on the chromaticity of increased macular absorption will depend on the spectral distributions of the stimuli used in a given experiment. It is to be expected, also, that confusion zones determined for small fields outside the central fovea in some less densely pigmented retinal area will more closely resemble those plotted in *fig. 7*. Changes in chromatic adaptation will, of course, have some influence on all such determinations, and it is to a consideration of the more general problem of visual adaptation that we should now like to turn.

SENSITIVITY CHANGES AND INDUCTION EFFECTS

THERE are two possible ways of looking at the influences that underlie changes in sensation produced by changes in adaptation, whether chromatic or achromatic. One way is to emphasize sensitivity or excitability and to consider the relevant changes as ratio effects: i.e., a given change in adaptation means that the process in question has become twice or half as excitable, and so on. The other way is to emphasize the process or activity itself and to consider the relevant changes in terms of increments or decrements in activity: i.e., a change in stimulus conditions induces an increment or decrement of given amount in the activity in question. It is our notion that adaptation phenomena will not be fully understood unless the simultaneous existence of both these kinds of change is taken into account. To make the situation clear, let us consider first the phenomena of achromatic brightness, before going on to the more complex phenomena involving changes in chromatic excitability and response activity.

For some given state of adaptation, perceived brightness increases with luminance according to a relation that is approximately a cube-root function of luminance *(refs. 44,45)*. When the state of adaptation is changed by exposure of the eye to a stronger illumination, if the change is only a matter of a changed state of excitability to, say, one half the previous

level, then the response to each stimulus on the luminance continuum will simply be reduced to one-half its previous magnitude, and the new brightness function for the less sensitive state will have the same slope as the original function, but it will be displaced downward on the ordinate by 0.3 log unit. If, however, a brightness decrement of *constant amount* is induced in the new adaptation situation, the effect of this constant arithmetic subtraction from the apparent brightness function will be relatively small at the high levels of brightness response and relatively great at the low response levels. That is, the apparent brightness of the low luminance stimuli will be diminished by a relatively large percentage and the apparent brightness of the high luminance stimuli by an almost negligible factor. In this case, of course, the new sensory magnitude function would have a steeper slope than the original one at the lower level of bright adaptation.

When we turn to experimental data on just this point we find that the function relating magnitude of apparent brightness to luminance does indeed vary in slope from one level of bright adaptation to the next, and in the manner expected if a constant induction effect is influencing the form of the function. Stevens and Galanter report a cube-root relation, slope equal to 0.3, for the brightness magnitude function with zero adapting luminance, but a much greater slope for a comparable function with a medium level of photopic bright adaptation *(ref. 46)*. A recent report by Hopkinson *(ref. 45)* also indicates a steady increase in the slope of the brightness magnitude function with increase in level of bright adaptation: for a 2^0 test patch, seen within a 120^0 adapting field, the exponent of the brightness v luminance function increases with the luminance of the adapting field, from 0.3 in a dark surround to 1.0 at an adapting luminance of 450 foot-lamberts.

These results are, of course, important for the problem of brightness constancy. If the change in adaptation level were simply a matter of a given multiplicative change in brightness sensitivity, and the slope of the brightness magnitude function were constant for all states, then a given contrast ratio between a pair of luminances for one state of bright adaptation would be associated with the same perceived brightness contrast at all levels of adaptation. Since the classical studies carried out by Hess and Pretori *(ref. 47)*, it has been clear, however, that perfect brightness constancy is by no means the rule. A central test area of given reflectance may increase in apparent brightness with increase in general illumination, it may appear to remain constant and independent of increase in general illumination, or it may even decrease in apparent brightness as the illumination is increased. Which of these results will obtain depends on the ratio of test to surround luminances. Thus, a test area of very high reflectance on a low reflectance surround will appear to increase in apparent brightness with increase in luminance of both test and background areas; a very low reflectance test patch in a surround of high reflectance will appear darker with increase in luminance of both test and background

areas; and for some intermediate relation of test and background reflectances, the apparent brightness of the test area will remain constant. These results of Hess and Pretori as well as his own qualitative observations were basic to Hering's detailed treatment of induction effects, both temporal and spatial, in exploring the psychophysical relations between perceived brightness and stimulus luminance *(ref. 48)*.

The situation with respect to chromatic adaptation and its effects on perceived colour is surely no less complex. Although the well known von Kries coefficient law is a statement of the simple multiplicative factor hypothesis with respect to the three independent excitability variables of the chromatic system, von Kries himself recognized that his simple law could not be attributed a universal validity *(ref. 49)*. He specifically stated that the law would not be found to hold exactly for situations in which the test colour has a considerably lower luminance than the adapting luminance. It is at the lower luminances, of course, where we should expect induction effects of constant magnitude whether chromatic, achromatic, or both, to exert the greatest influence on the perceived effect.

The fact that the coefficient law does not hold for all stimulus levels means that one of the rules of colour arithmetic, namely that colour equations are independent of stimulus luminance, although perfectly valid for those situations where the state of adaptation and induction effects are the same for both sides of the colour equation, is no longer a valid assumption when we are dealing with colour comparisons for different states. Confirmation of this breakdown in colour arithmetic has accumulated throughout the years. Among others, Walters observed it in his experiments on chromatic adaptation in 1942 *(ref. 50)*, Wright reports it in the summary of his extensive adaptation studies in 1947 *(ref. 51)*. Failure is therefore not surprising when attempts are made to use the von Kries law to derive fundamental sensitivity curves from colour matches for different states of adaptation that involve observations for a variety of luminance levels *(refs. 52,53)*. If all the laws of colour arithmetic are not valid for these circumstances, then the coefficient analysis cannot legitimately be applied to data involving a single adapting luminance and a variety of test luminances. It is for this reason that we have in the past, explicitly limited our own admittedly simplified coefficient treatment of adaptation data to observations involving test colours at a single level of luminance that approximates the luminance of the adapting stimulus *(ref. 5)*.

Failure to recognize this necessary limitation of the coefficient analysis of adaptation data may lead to theoretical treatments that are inconsistent with the more well established facts of colour vision. For example, MacAdam's conclusion that a trichromatic coefficient law is not valid, but that the data can be accounted for by a coefficient analysis in more than three independent variables, carries with it the implication, as MacAdam recognizes, that metameric colour equations must break down even when the equations are made between homogeneously adapted visual areas *(ref. 53)*. That such breakdowns do not occur for the stimulus levels in

question has, however, been repeatedly demonstrated *(refs. 50,54-57)*. Induced effects, which cause departures from the coefficient law, would, of course, be identical for both sides of a colour comparison in the homogeneously adapted condition, and there would be no breakdown in the equality of metameric stimuli already established for some other homogeneous state.

The effect of chromatic induction on perceived colour can easily be demonstrated. When the eye has been exposed to a non-selective reflecting surface uniformly illuminated by a non-neutral light source, this adapting surface will tend in time to lose in apparent saturation and to approach an achromatic appearance. A central test patch of approximately the same reflectance as the background will then appear achromatic. A test patch of higher reflectance than the background will, however, take on the appearance of the illuminant colour, whereas a test patch of much lower reflectance will appear in a hue that is complementary to the illuminant colour. This is a general result based on extensive series of observations reported by Helson and Judd *(refs. 58,59)*. If we think of this situation as involving, in addition to multiplicative excitability changes, a constant chromatic induction of a hue complementary to that of the adapting illuminant, this constant chromatic increment will be relatively ineffective at the high level of activity associated with the high luminance test stimulus, and will not be sufficient to cancel the hue of the illuminant. At an intermediate level of luminance and chromatic activity, the complementary induction is just enough to cancel the illuminant hue, and at the low luminance and activity level associated with the low reflectance test patch, the induced effect will actually be stronger than the direct stimulus effect, and the test patch will appear in a hue complementary to the illuminant hue.

Our own recent experiments have been concerned with changes in colour appearance that occur with changes in chromatic adaptation, and our hope is to obtain enough systematic data under a sufficiently wide range of stimulus conditions to be able to specify some general relations concerning the relative contributions of multiplicative changes in excitability and of additive changes in chromatic induction. This experimental programme is still in progress, and we are yet far from having reached our stated goal. We shall therefore limit our present discussion of these experiments to an illustrative set of results that simply indicate the order of magnitude of some of the changes that will have to be taken into account in a generalized formulation.

In the experiments with which we are concerned, a binocular adaptation and matching technique is used. The left eye is adapted to a near neutral adapting and surround field, and the right eye to a spectral stimulus of high physical purity. The test stimulus is seen by the right eye in the centre of its adapting and surround field, and the comparison field, made up of a variable mixture of 460 mμ, 530 mμ and 650 mμ is seen by the left eye. The arrangement is such that in binocular vision the observer sees a

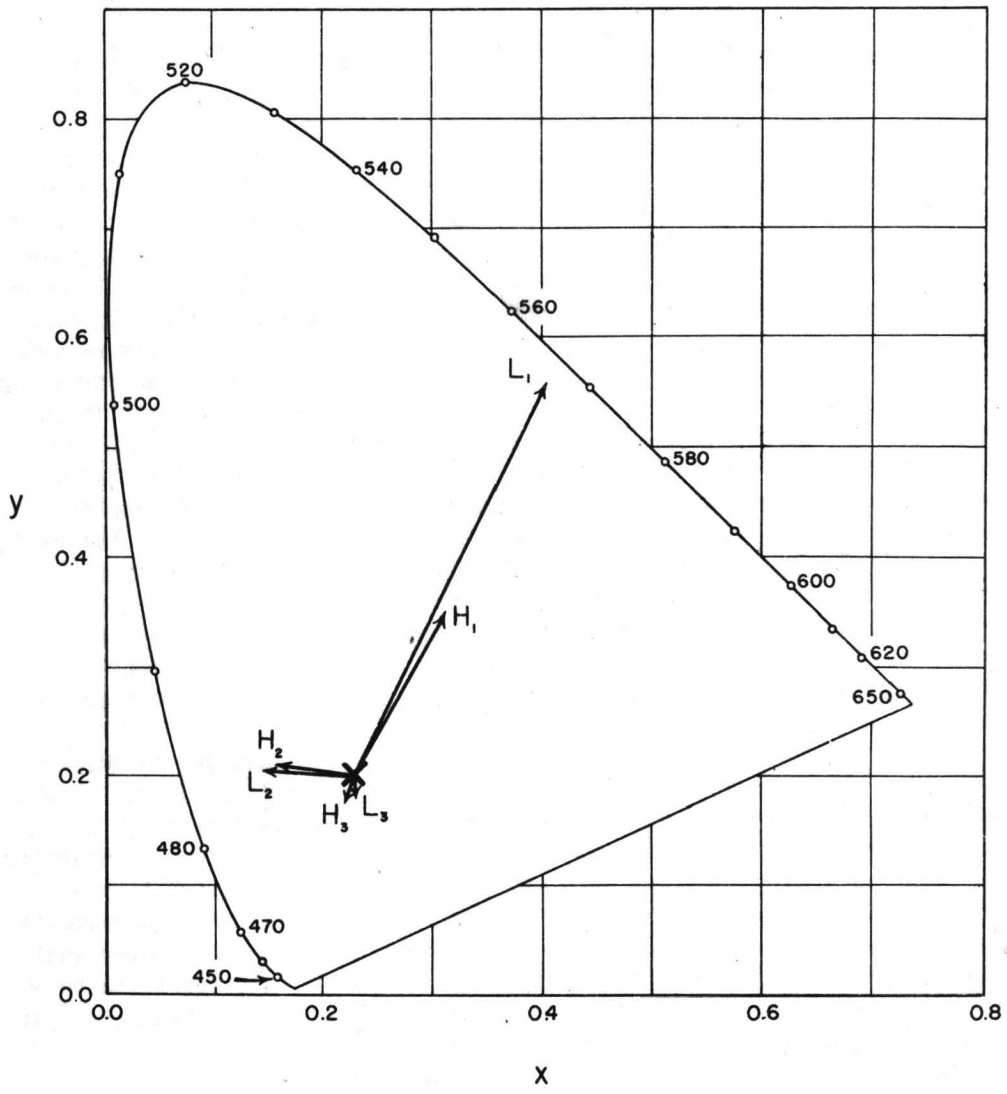


Fig.9. Chromaticity shifts for a single test colour at two luminance levels for three pairs of binocular adaptations.

large surround with a central area of about 2^{o} that is either dark when the test and comparison fields are not exposed, or a vertically divided bipartite field made up of the test stimulus seen by the right eye and the comparison field seen by the left. The observer's task is to produce a colour match between the two halves of this divided field. For the experiment illustrated in *fig. 9*, the spectral distribution of the test field was constant, and colour matches were made at two different levels of test luminance. When no surround was present in either eye, the C.I.E. chromaticity of the matching stimulus is indicated by the large X in the diagram for both test luminances. When the left eye was adapted to a heterogeneous, near neutral distribution, and the right eye to a 450 mμ stimulus of the same luminance, the match for the high luminance test stimulus was the chromaticity indicated by the arrow head at H_1 on the chart, and for the same adapting and surround conditions, the match to the low luminance stimulus was at the point labelled L_1. When the experiment was repeated with all conditions the same except for a change in the wavelength of the right eye adapting stimulus to 610 mμ, the comparable matches for the two test field levels were at the points indicated by the arrow heads at H_2 and L_2, respectively. The arrow heads designated H_3 and L_3 are the matching chromaticities for the same experiment with the right eye adapted to 550 mμ. It is clear from this illustrative set of results that the chromaticity shift required to match the changed colour perception produced by a change in chromatic adaptation can be expected to vary depending on the luminance of any given test stimulus. Moreover, the extent of this dependence will be a function of the particular states of chromatic adaptation being compared. In these experiments, the luminance of all adapting fields was approximately 10 mL, and the test luminances were about 10 mL and 1 mL respectively.

The von Kries coefficient analysis alone, without consideration of the incremental chromatic induction effects, would, of course, lead to the expectation of a single chromaticity shift for each pair of adaptations, with identical results for both luminances of the test field of constant spectral distribution. That such effects as those reported here are not limited to what might be considered extreme situations involving chromatic adaptation to spectral stimuli, may be seen from an examination of binocular adaptation results recently reported by Burnham, Evans, and Newhall *(ref. 60)*. From a least-squares matrix analysis of chromaticity matches for pairs of adaptations, generalized equations relating the matching C.I.E. tristimulus values for each pair of adaptations were derived that provide an excellent description of the experimental data. These empirically derived prediction formulas differ from those usually proposed in that they include, not only coefficients relating the tristimulus values for the two states of adaptation, but also a constant additive increment in each of the relations. Thus, the formula given, for example, for prediction of equal-appearing colour with Illuminant *A* adaptation when the Illuminant *C* colour is known, is:

$$X_a = 0.9132X_c + 0.4220Y_c - 0.1988Z_c + 0.0024$$
$$Y_a = 0.0299X_c + 1.0215Y_c - 0.1020Z_c + 0.0025 \quad (3)$$
$$Z_a = 0.0175X_c - 0.1378Y_c + 0.4708Z_c - 0.0019$$

The authors did not attribute any theoretical significance to the additive values required in their equations to minimize the residual errors between the general formulas and the experimental data. It seems reasonable, however, to assume that these values actually provide a quantitative expression of the incremental effects of chromatic induction.

The experiments from which the prediction formulas were derived involved matches to test colours at three different luminance levels, with C.I.E. Y values ranging from about 0.02 to 0.09. The increments in the adaptation formulas therefore represent a relatively small percentage of the tristimulus values for the test stimuli of highest luminance and a larger percentage of the values for the test stimuli of lower luminance. The incremental contribution (+0.0025) to the Y value, for example, represents less than 3% of the total Y for the highest luminance stimuli, but more than 12% of the total for the lowest level of test stimuli used. As indicated above, a constant chromatic induction is characterized by this property of providing an increasingly more significant contribution to the total chromatic effect with increasing reduction in stimulus luminance. From the authors' statement that the intercept value in their formulas turned out to be too small to make a significant contribution to the accuracy of the formula in two thirds of the cases, it may be assumed that the induction effect was significant relative to the spread of the results only for the test stimuli of lowest luminance which represented one-third of the cases in these experiments.

Whether the effects of chromatic induction will be found to be dependent only on the ratio of adapting to test luminances for any given qualities of adapting and test stimuli, or whether they will also show a dependence on the absolute level of stimulation cannot be decided at present. It is, however, one of the questions on which we expect our current experimental programme to provide some evidence.

In the next and concluding section of this paper that will consider the physiological plausibility of the opponent-colours theory, some of the evidence from experiments in electrophysiology will be seen to be of direct relevance for the interpretation of the complex phenomena of visual adaptation and contrast.

OPPONENT PROCESSES AND NEUROPHYSIOLOGY

OUR primary objective in developing the quantitative theoretical model with which we have been working has been to subsume and express in organized fashion the psychophysical relations between physical stimuli and their

associated visual responses. Such a theoretical construct obviously assumes certain basic physiological processes and events to underlie the psychophysical relations. Is the opponents theory plausible from the point of view of physiology? How do the assumed mechanisms relate to what is known today of neural behaviour? The basic assumptions of the opponent-colours theory are perhaps best understood by examining the physiological concepts basic to the thinking of the originator of the theory.

Hering believed that living tissue, including nervous tissue, is characterized by two fundamentally opposed modes of biochemical activity, and these two modes he called, by analogy with the basic processes of plant metabolism, assimilation and dissimilation *(ref. 61)*. In the absence of external stimuli impinging on the sensory apparatus, both kinds of activity are assumed to be occurring simultaneously and to be in balance, and in this condition the tissue was described by Hering as being in a state of autonomous equilibrium. Application of an external stimulus is assumed to cause an increase in one of these two opposed kinds of activity. This increase disturbs the autonomous equilibrium and brings with it a reduced disposition toward further increase of the kind of activity already excited, and conversely, an increased disposition toward the opposed mode of activity. This decrease in excitability of the excited process and simultaneous increase in excitability of the opposed, non-excited process has specific consequences. With continuing, constant stimulation, there is a tendency for equilibrium to be re-established between the two opposed modes of activity, although now the ("allonomous") equilibrium state occurs at a different level of total activity than that which characterizes the autonomous equilibrium condition. Moreover, with cessation of the external stimulus a reaction takes place in the initially non-excited process, which, in turn, gradually diminishes as the autonomous equilibrium condition is again approached.

Hering assumed, furthermore, that the individual elements of the physiological field are not isolated in their activities, but that they mutually interact with each other in such a way that stimulation of one of the basic modes of activity in a given element induces an increase in the opponent process in the surrounding elements *(ref. 48)*.

Specific differentiations within the two basic modes of activity were assumed to account for specific qualitative variations in sensory effect. For the three independent variables of the visual system Hering proposed three qualitatively different pairs of opponent activities within a given substance, or for simplicity of conception since he thought it the less likely possibility, three kinds of visual substance, each capable of two opposed modes of activity *(ref. 17)*.

Hering's notions of nervous activity found no immediate acceptance by other physiologists of his own day *(ref. 61)*, and most serious discussions of his colour theory have (even quite recently) tended to dismiss the proposed physiological base as implausible *(refs. 62, 63)*. Later attempts to describe physiological correlates for colour theories of the opponent type

have usually offered new speculations concerning specific chemical, physical, and neural mechanisms and linkages *(refs. 64-72)*. Rather than examine the merits of any of these widely varying proposals, let us see how Hering's own views fare with respect to the neurophysiology of 1957.

The conception of a neurochemical system in a condition of active equilibrium when "at rest", and capable of two kinds of opposed deviation from this equilibrium condition when disturbed by an external stimulus was rejected, when Hering first proposed it, in favour of the more familiar concept of a nerve fibre in either of two states, passive when at rest, or in a single mode of activity when stimulated. Throughout many subsequent years of experimentation with electrophysiological techniques, however, evidence for spontaneous neural action has accumulated and is now known to exist in the muscular, temperature, auditory and visual organs *(ref. 73)*. "Gradually," comments Granit, "the idea of spontaneous activity as an integral part of the performance of the sensory instruments has grown upon us." We now know that the effect of light stimulation may be either to increase or inhibit the spontaneous neural discharge, depending on the stimulus strength and the nature of the responding element, and the effects of stimulation of the mammalian retina are recognized as being displayed against a background of spontaneous activity *(refs. 73,74)*. Granit recognizes the advantage that accrues from this arrangement, and relates it to that of a galvanometer with its needle at the midpoint of the scale instead of at the end.

The existence of two fundamentally opposed neural processes is exhibited, not only in the form of either increased or decreased electrical activity away from the background level with application of an external stimulus, but still more strikingly in the two modes of response in individual nerve fibres. A fibre may respond to stimulation with an initial burst of electrical impulses which then diminish in frequency while the light remains on; when the light is turned off this discharge stops. This electrical pattern describes what is known as the on-effect. An opposite response pattern (off-effect) shows no impulses at all during illumination, but a vigorous discharge occurs when the light is turned off; this off-discharge usually subsides gradually. A third electrical pattern combines these two in direct succession (on/off effect). A short burst of impulses at high frequency occurs when the light is turned on, but after the initial burst there are no impulses at all as the light continues to shine steadily; another brief burst of impulses follows this silent period when the light is turned off *(ref. 75)*.

These different electrical patterns might readily be related to Hering's two basic processes by assuming that one process is characterized by electrical discharge whereas the opponent process is not. Thus when light stimulation excites the first process an on-discharge will be recorded. When the stimulus is removed, the second basic process predominates so as to restore the equilibrium condition, but with no associated electrical discharge. In the case of an off-effect, the stimulus might be assumed to

initiate process II in excess, with the subsequent off-burst indicating the back-reaction in process I as equilibrium is re-established. Strong alternations of the two opponent activities would account for the on/off discharge pattern. The assumption that an active process is occurring during light stimulation in the case where no electrical impulses are released and that the off-burst indicates a back-reaction of the opponent process is consistent with Lorente de Nó's assertion that "the nerve fibres never act as passive structures" *(ref.76)*, and is fully supported by the demonstrable dependence of the off-effect on stimulus strength and duration. Hartline has emphasized that the strength of an off-response increases both with the intensity and length of time the preceding light has been allowed to shine; it is completely absent following very short flashes *(ref.75)*.

In addition to the obviously opposite reaction to onset and cessation of illumination, there is other evidence that the processes associated with the on- and off-discharge patterns are antagonistic in nature. When conditions are such that both on- and off-discharges are elicited, reduction of stimulus duration does not lead to a simple summation of the two bursts at the ganglion cell when the two types of response ultimately collide, but rather they prove to be mutually exclusive. The two electrical patterns also seem to be closely associated with slow potentials of opposite sign in the retina. It is Granit's view that "all these results are a belated vindication of the essential truth of Hering's contention that there are two fundamental processes of opposite character in the retina, even though he could never have foreseen in what way his idea would come true" *(ref.73)*. Clearly we have learned much since Hecht wrote twenty-five years ago, "Hering's ideas of assimilation and dissimilation mean nothing in the modern physiology of sense organs and of nerves" *(ref.6)*.

There now seems little doubt that Hering's notion of an active state of equilibrium between two opposed processes, either of which may be excited in excess of the other by an external stimulus, of the associated decrease in excitability of the excited process, and of the reversal toward the equilibrium state in time and at the cessation of stimulation, is a picture consistent in its essentials with what is known today of neural behaviour. The importance of this picture for the temporal phenomena of sensory adaptation and after-image effects is too obvious to be laboured here.

The concept of mutual interaction among the various elements of the physiological field is of equal importance to Hering's concept of visual function and is also critical to an understanding of both areal effects and simultaneous contrast phenomena. Here again, we find ample support for the notion that individual nerve elements never act independently, and that visual function must be thought of in terms of the integrated action of all the units of the visual system *(ref.30)*. It has been found that even in the very simple Limulus eye "The discharge of impulses in any one optic nerve fibre, in response to steady illumination of the eye, depends not only upon the stimulus to the specific receptor unit from which that nerve fibre arises but also upon the spatial distribution of the stimulation over

the entire population of mutually interacting elements" *(ref. 77)*. In the Limulus eye the interaction is always exhibited as an inhibitory effect. In the vertebrate visual mechanism, however, interaction comprises both excitatory and inhibitory influences *(refs. 30, 73, 74)*. Granit summarizes the situation in the vertebrate visual system by enumerating four principles. They are: (1) the existence of two antagonistic systems: the on- and off-systems; (2) an organization consisting of overlapping receptive fields of very different sizes; (3) a minute organization which serves to emphasize the properties of the centre of each of these receptive fields, and (4) a functional dependence of the size of the receptive field on the state of adaptation. Thus Hering's concept of mutual interaction and induction among the various elements of the visual field, although still far from completely explored in either the psychophysical or the physiological realm, does emerge as a general principle well documented by the results of recent studies in electrophysiology.

Evidence for specific qualitative variations associated with variations in nerve response patterns is as yet only fragmentary and suggestive, at best. This situation is not surprising in view of the fact that much of the recent electrophysiological work has been limited to animals whose capacity to discriminate among colours is yet to be demonstrated. In view of the reversed polarities of the opposed neural processes, it is of some relevance therefore, to recall the early experiments of Purkinje, Ritter, Helmholtz, Schelske, and others showing that sensations of light can be elicited by passing an electric current through the human eye *(ref. 78)*. The sensation is generally of one colour when the polarity is in one direction, and a contrasting colour when the polarity is reversed. Because of the reversed polarities of on-and off-effects, these well known reports of electrically induced colour phenomena in humans stimulated Gernandt to investigate specific effects of polarizing currents on neural elements having different wavelength sensitivities *(ref. 79)*. The detailed experimental results yield a rather complex picture but there is some indication that, in general, sensitivity changes induced by electrical polarization are maximal for on- and off-effects respectively, in contrasting spectral regions. Although the evidence is far too meagre to attempt to associate specific neural patterns with the assumed opponent colour processes, there is reason to believe that the opponent neural activities may well be associated with contrasting chromatic, as well as achromatic, sensory responses *(ref. 80)*.

Much detailed information is still wanted and wanting, but the opponent-colours theory does seem today to be a physiologically plausible, as well as psychophysically useful working hypothesis.

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REFERENCES

1. HECHT, S. *Handbook of General Experimental Psychology* (edited by C. Murchison), Clark University Press, Worcester, 1934, p.804.
2. JAMESON, D. and HURVICH, L. M. *J. opt. Soc. Amer.*, 1955, **45**, 546.
3. HURVICH, L. M. and JAMESON, D. *J. opt. Soc. Amer.*, 1955, **45**, 602.
4. JAMESON, D. and HURVICH, L. M. *J. opt. Soc. Amer.*, 1956, **46**, 1075.
5. JAMESON, D. and HURVICH, L. M. *J. opt. Soc. Amer.*, 1956, **46**, 405.
6. HECHT, S. *Report of a Joint Discussion on Vision*, Physical and Optical Societies, Cambridge University Press, 1932.
7. WEALE, R. A. *J. Physiol.*, 1953, **121**, 322.
8. DARTNALL, H. J. A. *Brit. Med. Bull.*, 1953, **9**, 24.
9. COLLINS, F. D. *Biol. Rev.*, 1954, **29**, 453.
10. WALD, G., BROWN, P. K. and SMITH, P. H. *J. gen. Physiol.*, 1955, **38**, 623.
11. RUSHTON, W. A. H., CAMPBELL, F. W., HAGINS, W. A., BRINDLEY, G. S. *Opt. Acta.*, 1955, **1**, 183.
12. PARSONS, J. H. *An Introduction to the Study of Colour Vision*, Cambridge University Press, Cambridge, 1924, p.209.
13. TSCHERMAK, A. *Handb. Norm. Path. Physiol.*, 1929, **12**, 550.
14. HARTRIDGE, H. *Recent Advances in the Physiology of Vision*, J. and A. Churchill, Ltd., London, 1950, p.264.
15. PICKFORD, R. W. *Individual Differences in Colour Vision*, Routledge and Kegan Paul, Ltd., London, 1951, p.39.
16. HERING, E. *Sitzber. d. Kaiser. Akad. der Wissen. Wien. Math. Natur. Cl.*, 1875, Pt. III, **70**, 169, 186ff.
17. HERING, E. Introductory Remarks: HILLEBRAND, F. *Sitzber. d. Kaiser. Akad. der Wissen. Wien. Math. Natur. Cl.*, 1889, Pt. III, **98**, 70.
18. HELMHOLTZ, H. v. *Handbuch der Physiologischen Optik*, L. Voss, Hamburg and Leipzig, 1896, 2nd edit., p.376ff.
19. TROLAND, L. T. *The Principles of Psychophysiology*, D. Van Nostrand Company, Inc., New York, 1929, vol. II, p.197.
20. WILLMER, E. N. *Nature, Lond.*, 1944, **153**, 774.
21. WILLMER, E. N. and WRIGHT, W. D. *Nature, Lond.*, 1945, **156**, 119.
22. WILLMER, E. N. *Docum. ophthal.*, 1955, **9**, 235.
23. HARTRIDGE, H. *Nature, Lond.*, 1945, **155**, 657.
24. HARTRIDGE, H. *Philos. Trans. roy. Soc.* B., 1947, **232**, 519.

25. HERING, E. *Pflüg. Arch. f. ges. Physiol.*, 1894, **59**, 403.
26. KRIES, J. v. *Z. Sinnesphysiol.*, 1896, **9**, 81, p.109.
27. WILLMER, E. N. *Docum. ophthal.*, 1949, **3**, 194.
28. KÖNIG, A. *Sitzber. Akad. Wiss.*, 1894, (Berlin) 577.
29. PIÉRON, H. *Aux Sources de la Connaissance: La Sensation, Guide de Vie*, Librairie Gallimard, Paris, 1955, 3rd. edit., pp.284 and 288.
30. HARTLINE, H. K. *Harvey Lectures*, 1941/42, **37**, 39.
31. HARTRIDGE, H. *Recent Advances in the Physiology of Vision*, J. and A. Churchill, Ltd., London, 1950, p.210.
32. FARNSWORTH, D. *Die Farbe*, 1955, **4**, 185.
33. BURNHAM, R. W. and NEWHALL, S. M. *J. opt. Soc. Amer.*, 1953, **43**, 899.
34. WRIGHT, W. D. *J. opt. Soc. Amer.*, 1952, **42**, 509.
35. JUDD, D. B. *J. Res. Natl. Bur. Standards (U.S.)*, 1949, **42**, 1.
36. HURVICH, L. M. and JAMESON, D. *Science*, 1951, **114**, 199.
37. POLYAK, S. L. *The Retina*, University of Chicago Press, Chicago, 1941, p.222ff.
38. HOLM, E. *Arch. Ophthal.*, 1922, **108**, 1.
39. SACHS, M. *Pflug. Arch. f. ges. Physiol.*, 1891, **50**, 574.
40. WALD, G. *Docum. ophthal.*, 1949, **3**, 94.
41. GRÜTZNER, H. P. "Der Lichtverlust in der Macula Lutea und die Einstellung von Farbengleichungen auf kleinem und grossen Gesichtsfeld", Dissertation, Tübigen, 1955.
42. THOMSON, L. C. and WRIGHT, W. D. *J. Physiol.*, 1947, **105**, 316.
43. HILLMANN, B., CONNOLLY, K. and FARNSWORTH, D. MRL No. 257, Medical Research Laboratory, New London, 1954.
44. STEVENS, S. S. *Amer. J. Psychol.*, 1956, **69**, 1.
45. HOPKINSON, R. G. *Nature, Lond.*, 1956, **178**, 1065.
46. STEVENS, S. S. and GALANTER, E. H. Personal Communication, 1956.
47. HESS, C. and PRETORI, H. *Arch. Ophthal.*, 1894, **40**, 1.
48. HERING, E. *Grundzuge der Lehre vom Lichtsinn*, Julius Springer, Berlin, 1920, Chapter VII.
49. KRIES, J. v. *Nagel's Handbuch der Physiologie der Menschen*, F. Vieweg and Son, Brunswick, 1905, **3**, 211-212.
50. WALTERS, H. V. *Proc. roy. Soc.* B, 1942, **131**, 27.
51. WRIGHT, W. D. *Researches on Normal and Defective Colour Vision*, C. V. Mosby Company, St. Louis, 1947, Chapter 21.
52. BREWER, W. L. *J. opt. Soc. Amer.*, 1954, **44**, 207.
53. MACADAM, D. L. *J. opt. Soc. Amer.*, 1956, **46**, 500.
54. KRIES, J. v. *Arch. f. Anat. u. Physiol.*, 1878, **2**, 503.
55. HERING, E. *Lotos, Jahrb. f. Naturwiss. N. F.*, 1887, **7**, 177, See esp. Sections 28 and 40.
56. BÜHLER, K. "Beiträge zur Lehre von der Umstimmung des Sehorgans", Dissertation, Freiburg, 1903.
57. GREGORY, R. L. *Nature, Lond.*, 1955, **176**, 172.

58. HELSON, H. *J. exp. Psychol.*, 1938, **23**, 439.
59. JUDD, D. B. *J. Res. Natl. Bur. Standards, (U.S.)*, 1940, **24**, 293.
60. BURNHAM, R. W., EVANS, R. M. and NEWHALL, S. M. *J. opt. Soc. Amer.*, 1957, **47**, 35.
61. HERING, E. "Zur Theorie der Vorgänge in der lebendigen Substanz", Prague, 1888, Eng. Translation by F. Welby in *Brain*, 1897, **20**, 232.
62. LE GRAND, Y. *Optique Physiologique. II. Lumière et Couleurs*, Éditions de la Revue d'Optique, Paris, 1948, p.429.
63. GELDARD, F. A. *The Human Senses*, John Wiley and Sons, Inc., New York, 1953, p.79.
64. SCHJELDERUP, H. K. *Z. Sinnesphysiol*, 1910, **51**, 19.
65. TROLAND, L. T. *Amer. J. Psychol.*, 1914, **25**, 500.
66. FORBES, W. T. M. *Amer. J. Psychol.*, 1928, **40**, 1.
67. TROLAND, L. T. *The Principles of Psychophysiology*, D. Van Nostrand Company, Inc., New York, 1929, vol. II, Chapter 5, Section 59.
68. MÜLLER, G. E. *Z. Psychol. Ergänzungsb.*, 1930, **17**, 1, and **18**, 435.
69. HOUSTOUN, R. A. *Vision and Colour Vision*, Longmans, Green and Company, New York, 1932.
70. FRY, G. A. *J. opt. Soc. Amer.*, 1945, **35**, 114.
71. CIBIS, P. *Ber. dtsch. Ophthal. Ges.*, Heidelberg, 1948, 62.
72. TALBOT, S. A. *J. opt. Soc. Amer.*, 1951, **41**, 895.
73. GRANIT, R. *Receptors and Sensory Perception*, Yale University Press, NewHaven, 1955, Chapters 2 and 3.
74. KUFFLER, S. W. *J. Neurophysiol.*, 1953, **16**, 37.
75. HARTLINE, H. K. *Amer. J. Physiol.*, 1938, **121**, 400.
76. LORENTE DE NÓ, R. *Harvey Lectures*, 1946/47, **42**, 43.
77. HARTLINE, H. K., WAGNER, H. G. and RATLIFF, F. *J. gen. Physiol.*, 1956, **39**, 651.
78. HELMHOLTZ, H. v. *Handbook of Physiological Optics*, Optical Society of America, 1924, third English edition, vol. II, p.13ff.
79. GERNANDT, B. *J. Neurophysiol.*, 1947, **10**, 303.
80. GRANIT, R. *Rev. gen. Sciences*, 1948, **55**, 52.

PAPER 33

INDEPENDENCE OF WAVELENGTH OF THE THRESHOLD NUMBER OF QUANTA FOR PERIPHERAL ROD AND FOVEAL CONE VISION

By N. I. PINEGIN

N. I. Pinegin was born in 1902 and is at present a senior scientific worker at the State Optical Institute. He is a specialist in the field of physiological optics, and is interested mainly in questions of colour and light sensitivity, adaptation, quantum nature of vision and discrimination acuity. He is the author of about 40 published scientific works.

33. INDEPENDENCE OF WAVELENGTH OF THE THRESHOLD NUMBER OF QUANTA FOR PERIPHERAL ROD AND FOVEAL CONE VISION

By N. I. PINEGIN

SOME investigators *(refs. 1,2,3)* suppose that the threshold number of quanta n_0 depends on wavelength λ. Other authors *(refs. 4,5,6,7)*, on the contrary, put forward arguments in favour of the independence of n_0 and λ. At the same time, some authors *(ref. 5)* think that the threshold number of quanta n_0, being independent of wavelength, may be estimated to be not more than 2.

As this problem is extremely controversial and complicated, we undertook a new investigation of it.

Our experimental arrangement did not differ much, in principle, from those of Vavilov *(ref. 2)* and Hecht *(ref. 4)*. The observer viewed with his right eye circular monochromatic flashes of light of 0.01 sec. in duration. In the case of foveal vision a red point of dimensions 0.8' of arc served for fixation of the gaze in the short-wavelength region of the spectrum, a white point in the long-wavelength region. The fixation point was located close to the flash. The brightness of the fixation point hardly exceeded that of the threshold stimulus. In one series of experiments the point was replaced by a faintly gleaming ring 5^0 in diameter, and flashes were observed in the centre of a dark field, surrounded by the ring. In the case of foveal vision the results of the measurements of n_0 did not depend on the method of fixing the eye on the flash nor on the colour of the fixation point.

Peripheral observations of flashes were made for a portion of the retina at 10^0 of arc from the fovea centralis towards the temple. The same fixation points were used as in the foveal observations. The results of the measurements of n_0 in the case of peripheral vision also did not depend on the colour of the fixation point.

The brightness of the flashes B_λ, which is proportional to the number of quanta n_λ which are absorbed by rods and cones, could be decreased by means of photometric wedges so that the observer saw flashes with the probability P, varying from 1 to 0. As a result of the measurements, the experimental frequency-of-seeing curve was determined:

$$P = f(\log_{10} B_\lambda).$$

This curve was compared with the Poisson sum, which approaches it in shape:

$$P_{n_\lambda} = f_1(\log_{10} n_\lambda).$$

The parameter n_0 of the latter curve enables the threshold number of quanta to be determined unambiguously.

The present investigation was carried out with the help of four observers (one man and three women) from 19 to 27 years of age. The observers had normal colour vision and acuity. Every experimental frequency-of-seeing curve was plotted, using not less than ten experimental points. Each experimental point was characterized by a corresponding probability P found from the observation of a hundred monochromatic flashes. The determination of the frequency-of-seeing curve was repeated under identical conditions (of wavelength λ and flash size γ) not less than three times. Since the observers were trained, the curves had always the same shape and, consequently, the same parameter n_0.

The determination of the threshold number of quanta n_0 was done after the preliminary dark adaptation of about one hour, for seven wavelengths and for six sizes of flashes. The wavelengths were: 405, 450, 500, 550, 600, 650, 700 mμ. The sizes of flashes were the following: 0.5', 0.67', 1', 3.67', 13.3' and 22' of arc.

It has been found that the threshold number of quanta n_0 does not depend on the wavelength λ either for the peripheral rod or foveal cone vision. At the same time n_0 depends on the size of flashes:

γ	n_0 for rods	n_0 for cones
0.5'	2	2
0.67'	5	8
1.0'	8	15
3.67'	11	25
13.3'	12	30
22.0'	12	31

It should be noted that at $\gamma = 0.5'$ of arc, the threshold numbers of quanta for rods and for cones are identical and equal to 2. At $\gamma > 0.5'$ of arc the threshold number of quanta for cones becomes greater than for rods. The maximum number of quanta for cones is $n_0 = 31$, and for rods $n_0 = 12$, at the size of flash $\gamma = 22'$ of arc. Thus, $n_0 = 2$ represents only a particular case when the flash size corresponds to one light-sensitive retinal element (rod or cone).

The independence of wavelength of the threshold number of quanta for rods and cones satisfies all demands of photochemistry. Firstly, it takes place in the region of the absorption bands of rhodopsin and iodopsin extending (as follows from our curves of spectral sensitivity of rods and cones *(refs. 8,9)*) from $\lambda = 302$ to $\lambda = 950$ mμ of the spectrum. Secondly, although the absorption coefficient and, consequently, the absorption

probability are entirely different for quanta with different frequencies, nevertheless, in accordance with the Einstein law, an equal number of absorbed quanta causes, independently of their size, a decomposition of an equal quantity of molecules of rhodopsin and iodopsin (i.e. equal for different wavelengths) to produce the threshold visual effect for rods and cones.

The independence of wavelength of the threshold number of quanta indicates the independence of the quantum efficiency of the primary photochemical process in rod and cone vision. The independence of wavelength of the quantum efficiency is peculiar also to other processes, for instance, to the photoluminescence of solutions of complex organic dye molecules.

Vavilov *(refs. 10,11,12)* pointed out that this occurs in a wide spectral interval within the absorption band.

A more detailed exposition of the results of our investigation is given elsewhere *(refs. 13,14)*.

REFERENCES

1. VAVILOV, S. I. Transactions of the 1st Conference on Physiol. Optics, *Izd. Akad. Nauk., SSSR*, Moscow, 1936, 332.
2. VAVILOV, S. I. Microstructure of Light. *Izd. Akad. Nauk., SSSR*, Moscow, 1950, 42.
3. RIEZLER, W., ESPER, F. and MEURERS, H. *Z. Phys.*, 1954, **137**, 238.
4. HECHT, S., SHLAER, S. and PIRENNE, M. H. *J. opt. Soc. Amer.*, 1942, **32**, 42.
5. BOUMAN, M. A. and VAN DER VELDEN, H. A. *J. opt. Soc. Amer.*, 1948, **38**, 570.
6. BAUMGARDT, E. *Naturwiss.*, 1952, **39**, 388.
7. PIRENNE, M. H. *Progr. Biophys.*, 1951, **2**.
8. PINEGIN, N. I. *Dokl. Akad. Nauk., SSSR*, 1945, XLVIII, No. 4, 266.
9. PINEGIN, N. I. *Probl. physiol. Opt.*, Moscow, 1953, **8**, 8.
10. VAVILOV, S. I. *Phil. Mag.*, 1922, **43**, 307.
11. VAVILOV, S. I. *Z. Phys.*, 1924, **22**, 266.
12. VAVILOV, S. I. *Z. Phys.*, 1927, **42**, 311.
13. PINEGIN, N. I. *Probl. physiol. Opt.*, Moscow, 1957, **12**.
14. PINEGIN, N. I. *Dokl. Akad. Nauk., SSSR*, 1955, **103**, No. 5, 823.

PRESENTATION AND DISCUSSION OF PAPERS 24, 27, 37, 22 and 33, AND RESUMED DISCUSSION ON PAPER 28

DR. R. W. G. HUNT, before delivering his paper (24) gave an effective lantern demonstration of the persistence of a metameric match under differing adaptations.

PROFESSOR G. A. FRY, presenting his paper (27) said that some measurements had now been made with the new colorimeter. He had decided to abandon the triangulation method for locating the cyan fundamental colour and to rely on the Bezold-Brücke effect for determining the *y/b* equilibrium axis. He illustrated that for the four spectral sensitivity curves, which he had been challenged to produce, there was no unique solution; only the luminosity and the two response ratios could be determined and there were only three independent curves.

In his recent monocular adaptation experiments, following MacAdam's method, he had been able to measure along the line 680-520 mμ without leaving the spectrum locus, provided that he used about 8 seconds adaptation and then waited a further 3 seconds for the comparatively rapid *y/b* adaptation to be completed. Changes in the yellow-blue direction had been more difficult, and from greenish-yellow to violet was the best that had been done. In this case the match was judged immediately after removal of the adapting stimulus. Nevertheless it would seem that the monocular experiments suffered from induction effects and he would be returning to the binocular method.

In conclusion Professor Fry illustrated how his theoretical approach could be used to characterise defective colour vision, tritanopia for example meaning that the *y/b* mechanism was functioning as an *r/g* mechanism.

PROFESSOR E. N. YUSTOVA presented her paper (37) and, through her interpreter MRS. MILNER, added some comments on the work done on colour-adaptation. She said that, in connexion with Dr. MacAdam's work on this subject, of which she had heard only recently, she would like to speak briefly of her own measurements of the transformation of colour space under the influence of eye adaptation. Her measurements were carried out in order to define the axes *R G B* of the basic physiological system, the work being done in 1946 under the direction and following the ideas of Dr. Nuberg. It was published in the "Transactions of the Central Chamber of Measure and Weight" - a publication not sufficiently well-known. Modifications of colour equalities resulting from a preliminary adaptation to two mixed fields of different colours were measured. The measurements were done with the help of a special device she had constructed. That device made possible an immediate substitution of colorimetric fields with the fields of adaptation and *vice versa* without disturbance of fixation of the dividing

line. The aim of the experiment was the matching of visually indistinguishable pairs of colours under the conditions of a given adaptational shift. The instrument satisfied the necessary conditions for a simultaneous observation of three pairs of colorimetric fields, with the same preliminary adaptational shift. Such an arrangement was necessary in order to be able to examine experimentally whether the colour space transformation under the influence of adaptation was linear, and in order to justify the characterisation of each adaptational shift by a matrix of transformation. If that transformation had invariable axes, the same for each adaptational shift, then those axes would be the axes *R G B* of the Young-Helmholtz receptors. In that co-ordinate system alone was the transformation of colour co-ordinates reduced to a change of scales, and could the state of adaptation be characterised by three coefficients which represented the states of sensitivity of the receptors *R G B*.

The investigations of adaptation proved to be very difficult. It was true that the linearity of transformation was confirmed experimentally but the invariable axes of transformation were never defined. That failure was in her opinion explained firstly by the impossibility of accurate registration of the colour match at the moment of field substitution, the course of adaptation in the first moments being extremely rapid, and secondly by the special nature of the receptor *B*. The latter conclusion was based upon the results obtained experimentally. When the results of colour transformations were expressed in König's system *R G B* (no other data were then available) it appeared that the correlations between the co-ordinates $\bar{r}'/\bar{r}$ and $\bar{g}'/\bar{g}$ of the transformed colours actually remained constant for a given adaptational difference, but the fraction $\bar{b}'/\bar{b}$ could assume the most variable values. These experiments were terminated and work was begun on the determination of the axes *R G B*. She (Professor Yustova) was very glad that Dr. MacAdam's experiments on adaptation confirmed the axes which she had derived from tests of colour blindness but she wanted to point out that the accuracy of measurements of adaptation could not compete with the accuracy of the experiments with dichromats.

THE CHAIRMAN (DR. W. S. STILES) read in title the papers by Dr. L. M. Hurvich and Miss Dorothea Jameson (22) and Professor N. I. Pinegin (33).

PROFESSOR W. D. WRIGHT said that he agreed with Dr. Hunt's conclusions, and thought that Professor Fry's fourth fundamental colour was unnecessary. In his opinion the adaptation changes which he himself had reported at 460 mμ had been misunderstood.

He asked Dr. Hunt whether he had considered possible interdependence of the red, green, and blue adaptations. If these were not necessarily separate the non-linear relations might perhaps be avoided.

DR. HUNT replied that no distinction was involved since only in the case of luminance had a definite function been assumed. The other two functions had been kept as general as the evidence permitted.

PROFESSOR Y. LE GRAND asked what was the justification for the crook at the extreme violet end of the spectrum locus, which was shown both in the C.I.E. and in Fry's diagram to be pointing directly towards the red end of the locus.

THE CHAIRMAN said that recent N.P.L. data generally confirmed this crook; there were some indications that perhaps it pointed towards a reddish orange rather than towards the extreme red.

PROFESSOR FRY said that the crook shown on his diagram had been found experimentally for his own eye.

MR. F. J. J. CLARKE said that, if dichromasy occurred in the violet portions of the spectrum locus, he wished to ask why these wavelengths were not plotted as coincident points on the colour diagram.

PROFESSOR FRY replied that if a greenish-blue primary was used to change the match point to the region of 480 mμ then normal trichromatic measurement of *R G* and *B* was possible. The dichromasy applied only when two neighbouring wavelengths were being compared in a field of extreme saturation.

THE CHAIRMAN confirmed this point and said that a similar procedure had been found effective in the N.P.L. colour-matching investigation. Where a 445 mμ blue primary was used it was helpful to add green to both sides of the field but with a blue primary at 471 mμ no extra green was needed. For monocular colour-matching however the dichromasy was not so extreme.

DR. D. B. JUDD asked why, if as Professor Fry suggested the concentration of a visual pigment were reduced by a factor of fourteen, no change was found in its spectral absorption curve.

THE CHAIRMAN said that no change need be expected provided that the initial concentration was low enough.

DR. JUDD then asked whether in adaptation the sensitivity of the receptor could not be inhibited electrically at the synapse and not necessarily at the pigment level.

DR. W. A. H. RUSHTON said that the point about pigment concentration had been raised by Lythgoe in 1940. In ordinary light not more than about one or two % pigment change was produced and the illumination needed to reduce the pigment to 1/e of its dark-adapted value was about five times that required for rhodopsin bleaching. At these very high intensities, of the order of 50,000 trolands, metameric matches had begun to break down.

With regard to neurological adaptation, this did not necessarily take place at the synaptic layer. Most of the electroretinogram was generated, according to Dr. Brindley, at receptor level and the electroretinogram varied enormously with adaptation. The classical results of Hartline's work on Limulus fit in so well with this standpoint that we were led to believe the adaptation must have occurred earlier on, in the transducer performance of the receptor itself. This did not however exclude additional synaptic effects.

COMMANDER D. FARNSWORTH inquired whether Professor Fry's tetrachromasy was really necessary.

PROFESSOR FRY said that although he postulated four receptors he also specified one linkage between them and this was essentially trichromasy. The four corners in his colour-mixture diagram were needed to explain adaptation effects.

DR. D. L. MACADAM said that he agreed that non-linearity occurred most probably in the neural process and that a von Kries type adaptation was produced after the receptor stage.

DR. HUNT said that he did not specify where it occurred: in the past he had favoured the receptor stage but perhaps Dr. Rushton's experiments were conclusive. It might be that more attention to the time factor, as shown by the researches of Professor Wright, could be used to decide the balance between neural adaptation which tended to be quick and chemical adaptation which tended to be slow.

PROFESSOR G. WALD referred to Dr. Rushton's results, and to the fact that very high light adaptation, for example a thousandfold increase in threshold, required no more than 1% bleaching of rhodopsin. On a statistical mechanical basis a photochemical change of the first 1% of pigment was sufficient to explain the results. A problem which was much more difficult to explain was why light adaptation increased the number of effective quanta required to give a response.

Turning to Dr. Barlow's paper, PROFESSOR WALD said that the rise in required number of quanta, to which he had just referred, could perhaps be explained on the basis of signal/noise ratio. A second point was that, although there was a very close parallel between light and dark adaptation on the one hand, and pigment bleaching on the other, the long term effects of retinal interaction were also involved and it was difficult but important to assess their role.

DR. M. H. PIRENNE quoted a paper by M. Levy (*Rev. d'Optique*, 1947, **26**, 489) in which the incremental brightness threshold had shown a preliminary dip when the background intensity had been raised slightly from its initial value of zero. This result, which was similar for bipartite fields of 1^{0} and 10' angular diameter, was difficult to explain on a signal/noise basis, but making use of Polyak's work, and considering both noise and retinal interaction, one could predict an initial reduction of the threshold.

Dr. Pirenne then reported an experiment* in which the background field contained a black Landolt C and the threshold was determined for a small central test flash. With a dark background one quantum per rod per second was found to be sufficient, but with the background illuminated the threshold rose by a factor of three, four or five. This result had convinced him, in spite of Hecht's views in which he had been brought up, that lateral interaction was at work.

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* Pirenne, M. H. *J. Physiol.*, 1957, **137**, 48-49P.

Dr. Pirenne subsequently sent the following written comment on Dr. Barlow's paper:-

"It is easy to estimate the maximum amount of noise compatible with the absolute threshold value of the dark-adapted human eye for a stimulus 1 square degree in area and 0.1 sec in duration. The noise is found to be 40 to 50 molecular excitations for a light signal of 20 quanta acting upon the receptors (Denton and Pirenne, *J. Physiol.*, 1954, **123**, 417-422). It is assumed that a large retinal unit summates both light signal and noise within the area and time corresponding to the stimulus. Now when the stimulus area is reduced to 1/50 sq. degree, the threshold energy does not decrease by more than 50%. Assuming (a) that this smaller patch of light acts upon a functional unit having the same temporal summation properties as the large one, but only 1/50 sq. degree in area, and made up of a correspondingly smaller number of the same receptors which form the large unit, and (b) that this unit summates light and noise from its own area only, then it follows that the noise level here will have dropped to about 1 excited molecule, whereas the signal consists of about 10 quanta. This type of argument shows the theoretical possibility that, even if noise does limit sensitivity in some cases, it may become unimportant in others.

The preceding considerations were originally thought to refer to the noise in the rods only, for it was believed that the retinal units under consideration did *function* as pure rod systems. Anatomically, however, there are, according to Polyak (*Docum. ophthal.*, 1949, **3**), no pure rod systems in the human eye. All diffuse bipolars are related to both rods and cones, while the only other type, the midget bipolars, are related to cones only. All those ganglion cells which are related to rods must therefore be also related to cones. Thus it seems to follow from Dr. Barlow's theory that the cones should feed a great deal of noise into those units even if they do not themselves contribute to the detection of the light signal. This would upset various signal/noise considerations particularly with regard to differences between rods and cones."

DR. F. H. C. MARRIOTT said that what was actually observed from a neurophysiological preparation was a succession of spikes, so that over a given time interval there must be an equation relating the noise x to the number of spikes y.

It could be argued that if n was the number of quanta required for each discharge, then the mean spike frequency μ_y would be given by

$$\mu_y = \frac{1}{n}\mu_x \text{ where } \mu_x \text{ was the mean noise.}$$

On the other hand $\text{Var } y = \frac{1}{n^2} \text{ Var } x = \frac{1}{n}\mu_y$.

It was possible that the nerves did not behave in that way, but proceeding on that basis one found that the threshold was inversely proportional to the square root of the noise. That meant that the noisier the fibre the lower the threshold, the explanation being that more visual purple was present.

Dr. Marriott then said that Professor Pinegin's paper was very valuable in that it showed clearly that the form of the frequency-of-seeing curve was independent of wavelength. However, some of his detailed conclusions were open to question.

It had been shown *(1,2) that, provided presentations were randomized, n_o gave a lower limit for the threshold number of quanta - the mean number of quanta acting on the retina for 55% seeing. But shallower curves might be obtained, either because of biological variations, or because the absorptions were not simply additive, or perhaps because of "dark-noise".

Now for both rods and cones Ricco's law applied very closely for diameters up to at least 3.67'. If, therefore, there were 11 acting quanta for a 3.67' field for rods, there must be about the same number for a 0.5' field, and the flatter curve ($n_o = 2$) obtained must be due, not to quantum fluctuations, but to one of these disturbing factors. The same argument applied for the case of cone vision, but with rather less force, since the larger field might possibly extend to more sensitive parts of the fovea.

In fact the use of very small fields led to complications which might produce large biological variations. Small errors of fixation might displace the image of the field into insensitive parts of the retina - e.g. bloodvessels, or peripheral cones; multiple absorptions might occur in single receptors; the effects of diffraction and optical defects in the eye became more marked.

DR. H. B. BARLOW, replying to the discussion of his paper, thought that nothing fatal to his ideas had been put forward.

Professor Wald's request that neural noise be considered had surprised and gratified him. On the question of the rise in minimum quantum demand, he was not convinced that it occurred or that it could be inferred from the papers quoted. Indeed Clark, Jones and Rose had maintained that the quantum efficiency and also the photochemical concentration remained constant.

Dr. Pirenne had reported a result by Levy which apparently conflicted with his arguments, but in Levy's experiment variations in "degree of reliability" might be coming in. Stiles and Crawford had reported a similar case in 1934† where the addition of a background had caused a decrease in increment threshold which was attributed to improved focusing.

* (1) Pirenne, M. H. and Marriott, F. H. C., *J. opt. Soc. Amer.*, 1955, **45**, 909-912.
(2) Marriott, F. H. C., *J. opt. Soc. Amer.*, 1956, **46**, 661.
† Stiles, W. S. and Crawford, B. H., *Proc. roy. Soc.* B, 1934, **116**, 55.

Dr. Barlow suggested that the reason why Piper's law failed for small areas in the Riccò range was that there were no receptor units below this size which contained exclusively rods: if all the small units contained cones as well as rods then cone noise would be masking the response as suggested by Pirenne.

Dr. Baumgardt's conception of double hits did not necessarily conflict with his (Dr. Barlow's) ideas, in that noise could still be involved in addition: the double hit requirement would certainly be a valuable safeguard in discriminating against single thermal events.

Dr. Marriott had brought up the relationship between noise x and spike frequency y. A recent paper by Kueffler, Barlow and Fitzhugh had considered this point, and a further paper by Fitzhugh would show that a similar distribution occurred for both "on" and "off" units.

In conclusion, Dr. Barlow suggested to theorists that, if non-linearities were being introduced, then the visual processes postulated should be those for which evidence of non-linearity already existed, and in this connexion the threshold versus intensity curves would repay further study.

The proceedings ended with a vote of thanks, to the Chairman and to the National Physical Laboratory, which was proposed by PROFESSOR W. D. WRIGHT and seconded on behalf of overseas visitors by PROFESSOR G. WALD.

APPENDIX I

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