THE BRITISH JOURNAL OF OPHTHALMOLOGY

NOVEMBER, 1948

COMMUNICATIONS

VISUAL PURPLE AND THE PHOTOPIC LUMINOSITY CURVE*

BY

H. J. A. DARTNALL

FROM THE VISION RESEARCH UNIT, MEDICAL RESEARCH COUNCIL,
INSTITUTE OF OPHTHALMOLOGY, LONDON

Introduction

THE precise relationship which has been established between the scotopic luminosity curve and visual purple (Dartnall & Goodeve, 1937; Wald, 1938) leads one to expect that the photopic luminosity curve is similarly related to some "photopic" pigment or pigments. This latter hypothesis has given rise to considerable speculation, particularly since the evidence for the existence of retinal pigments, other than the various forms of visual purple, is not unequivocal. In any case there is no evidence for such additional pigments in the human retina.

Visual purple mediates scotopic vision by virtue of the photochemical changes it undergoes on exposure to light. The rate of

* Received for Publication, July 12, 1948.

any photochemical change is governed by the value of the product γI_a where γ is the quantum efficiency of the process and I_a the intensity of the absorbed light expressed in quanta per second. Since the eye in the photopic condition is much less sensitive than in the scotopic state it follows that the value of γI_a must be correspondingly smaller for the photopic process.

This low value of γI_a for the photopic process could arise in the following ways:—

(i) γ very small. In this case it is conceivable that the active pigment could be overlooked as being "photostable".

(ii) I_a very small. This could be due to: (a) a very low value for the extinction coefficient or concentration of the active pigment. In these cases detection and isolation would be difficult; or (b) the development in a light adapted retina of a stable pigment in a sufficiently high optical density to prevent all but a very slight absorption of light by the active pigment.

The many possibilities are reduced by Granit's (1941) observation with carp and tench retinæ. In these retinæ, which contain the porphyropsin variety of visual purple (absorption maximum at 540 m μ), the photopic curve has its maximum at 600-610 m μ instead of 556 m μ as in the case of retinæ with the rhodopsin variety of visual purple. This observation affords strong evidence that the photo-sensitive material mediating the sensation of photopic luminosity is related to the particular form of visual purple possessed by the species.

The simplest assumption accounting for this observation is that visual purple itself is the mediator of photopic luminosity and that the shift in the luminosity curve from its scotopic to its photopic position is the result of other factors which come into play when the eye is light adapted. Thus the bleaching of visual purple results in the formation of yellow substances. The presence of these in a light adapted retina will have two effects. Firstly, there will result an overall reduction in sensitivity owing to the fact that only a fraction of the total light absorbed by the retina will be absorbed by the visual purple. Secondly, because the (yellow) photodecomposition products of visual purple have a heavier absorption in the blue, there will be a relative depression of sensitivity in the short wave end of the spectrum, resulting in a shift of the maximum of sensitivity towards the longer wave end of the spectrum. This possibility of accounting for the Purkinje shift was cursorily examined by Lythgoe (1938). These effects will be enhanced by the fact that the photopic luminosity curve is measured at the central retina which is permeated with the yellow macular pigment, whereas the scotopic luminosity curve is

measured in a more peripheral region of the retina, free from this pigment.

Thus the present hypothesis that visual purple mediates the luminosity sensations of both scotopic and photopic vision offers a *prima facie* explanation of the reduced sensitivity of photopic vision and also of the Purkinje shift associated with light adaptation. This paper is concerned with the quantitative consideration of this hypothesis.

The effect of the presence of photodecomposition products on the light absorbed by visual purple

When solutions of visual purple are exposed to light the red colour fades to a light or deep yellow, depending on the hydrogen ion concentration. Thus in alkaline solutions the colour of the bleached solution is pale yellow, while in acid solutions it is deep chrome yellow. Lythgoe (1937) has called the product of the bleaching with this dependence of colour on pH, "indicator yellow."

At low temperatures (5° C. or less) and in neutral or slightly alkaline solutions an intermediate substance which Lythgoe (1937) has named "transient orange" appears on bleaching visual purple. This substance is rapidly converted to indicator yellow on allowing the temperature to rise.

The retina is stated to become acid on exposure to light and transient orange has not been demonstrated in the bleaching of an acid solution of visual purple. Further, it seems reasonable to suppose that if transient orange were formed under retinal conditions, it would decompose extremely rapidly at blood temperature (37° C.) to indicator yellow. In other words it may be assumed that there is no appreciable concentration of transient orange in a light adapted retina at equilibrium.

The presence of indicator yellow in the light adapted retina will affect the amount of light absorbed by the visual purple and hence also the luminosity curve. The degree of this effect will clearly depend on the amounts of visual purple and indicator yellow present and also on the pH of the light adapted retina since this latter determines the absorption spectrum of the indicator yellow.

The amount of indicator yellow in the light adapted retina. During the process of light adaptation indicator yellow will tend to accumulate in the retina. Lythgoe's work has made it clear that indicator yellow is stoichiometrically related to visual purple, that is, any given amount of indicator yellow corresponds to a definite amount of photochemically changed visual purple. It is also clear from the close relation between the scotopic luminosity curve and

the absorption spectrum of visual purple that the *dark adapted* retina must be substantially free from indicator yellow and, indeed, free from any substances with non-uniform absorption in the visible spectrum. In consequence, it follows that all indicator yellow present in a light adapted retina is derived from visual purple.

It cannot be assumed from this, however, that the maximum possible amount of indicator yellow in a light adapted retina is merely that resulting from the complete conversion of the "dark" concentration of visual purple as this would imply that the system

is a "closed" system, *i.e.*, that there are no precursors to visual purple. It will be sufficiently general for the present purpose to assume a scheme such as the following,

in which the formation of visual purple from precursors is shown as a reversible reaction to account for the fact that visual purple does not accumulate indefinitely in a retina removed from light.

It will be supposed that the production of visual purple from its precursors is a rapid process in comparison with regeneration from its decomposition products. With this assumption, it follows that large quantities of indicator yellow can accumulate in a retina which has been exposed to high intensities for considerable periods provided that the dissipation of indicator yellow by thermal decomposition is not great. This latter condition is satisfied provided the pH is *outside* the range 3.5 to 6.5 (Lythgoe and Quilliam, 1938).

The amount of visual purple in the light adapted retina. After exposure to intense lights for prolonged periods the retinae of frogs may still contain considerable amounts of visual purple (Lythgoe, 1940). This is probably due to the protective action afforded by the migration of the pigment epithelium which occurs on light adaptation. Though this migration is marked in fishes and birds it is not so distinct in reptiles, whilst in mammals it has not certainly been demonstrated. Oguchi (1924) failed to find it in man. Since pigment migration is absent in man it might appear reasonable to suppose that the amount of visual purple is very much less in the light adapted than in the dark adapted state. This, however, does not necessarily follow because indicator yellow also will act as a protective filter, particularly at the shorter wavelengths. If visual purple is rapidly formed from its precursors it

is possible that considerable amounts may be present even in a retina adapted to an intense illumination since, under these conditions the concentration of indicator yellow would be very high and, in consequence, only a small fraction of the total light absorbed would be available for the photochemical decomposition of visual purple. It is also apparent that the concentrations of visual purple and indicator yellow in a light adapted retina will depend not only on the intensity of the adapting light but also on its wavelength distribution of energy, as this latter will affect the degree of internal filter protection accorded by the indicator yellow.

There is no trustworthy measurement of the optical density of the visual purple in a dark adapted human retina. Dartnall and Goodeve (1937) assumed that the value would be similar to that for the dark adapted frog retina and, using extraction data then available for this species, calculated the density at 502 m μ (the peak density) to be 0.1. Broda, Goodeve and Lythgoe (1940) subsequently found, when all precautions against loss were taken, that the density in situ in the dark adapted frog retina is 0.54. It is, however, unlikely that the effective peak density in the human retina can be greater than (say) 0.2 as otherwise the correspondence between the percentage absorption curve of visual purple and the scotopic curve would be lost.

On exposure of a dark adapted retina to light the concentration of visual purple will fall. When the retina has again reached equilibrium (become adapted to the light) the visual purple may regain its former concentration. It is even conceivable that it could exceed it as the presence of a large amount of indicator yellow might disturb the equilibrium between visual purple and its precursors. It does not seem likely, however, that the concentration of visual purple in a light adapted retina would ever greatly exceed its "dark" concentration.

Theory. It will be assumed that the effect of indicator yellow in the retina on the light absorbed by visual purple is identical with that obtaining in a *homogeneous* solution or mixture of these two substances.

Assuming Beer's and Lambert's laws to hold, the fraction of the total amount of light absorbed by any single component of a homogeneous solution containing several absorbing substances is given by the optical density of the single component divided by the total optical density of the solution. Thus in a solution containing both visual purple and indicator yellow, the *fraction* of the total absorbed light of wavelength λ which is absorbed by visual purple is given by

$$\frac{D_{\lambda}}{D_{\lambda} + D'_{\lambda}}$$

where D_λ is the density of the visual purple and D'_λ that of the indicator yellow for light of wavelength λ .

The total fraction of incident light absorbed by the solution is

$$(1 - 10^{-(D_\lambda + D'_\lambda)})$$

By combining these two terms, the fraction of incident light of wavelength λ which is *absorbed by visual purple* in a solution containing both visual purple and indicator yellow is, therefore,

$$\frac{D_\lambda}{D_\lambda + D'_\lambda} \cdot (1 - 10^{-(D_\lambda + D'_\lambda)}) \dots\dots\dots (1)$$

The assumption that visual purple is produced rapidly from its precursors implies, as previously stated, that considerable amounts of indicator yellow can accumulate during the course of light adaptation. Consider a solution in which the amount of visual purple is kept constant but that of the indicator yellow continuously increased. The effect of the accumulation of indicator yellow will be twofold. In the first place there will be a continuous overall decrease in the amount of light absorbed by the visual purple at all wavelengths. This may be called the "depression" effect since any process which is dependent on the amount of light absorbed by visual purple (such as vision) would be correspondingly reduced in sensitivity. Secondly, because the absorption of indicator yellow is not uniform throughout the spectrum, the amount of this decrease will vary with wavelength. In other words, the *form* of the curve obtained by plotting the amount of light absorbed by the visual purple against wavelength will change. Actually, since indicator yellow absorbs most strongly at the short wave end of the spectrum, the result will be to displace this curve towards the longer wavelengths.

As the amount of indicator yellow increases, the value of the term $(1 - 10^{-(D_\lambda + D'_\lambda)})$, for the total fraction of light absorbed by the solution approaches its maximum value of unity. In addition the density of visual purple, D_λ becomes less significant in comparison with D'_λ , the density of the indicator yellow. Thus as the amount of indicator yellow increases, the expression for the amount of light absorbed by visual purple approaches D_λ/D'_λ .

As D'_λ tends to an infinitely large value, the amount of light absorbed by the visual purple, D_λ/D'_λ , tends to zero. The "depression" effect thus proceeds continuously with increasing indicator yellow concentration to the limit where no light is absorbed by the visual purple. The "displacement" effect can be isolated from the "depression" effect by plotting the curves

for the wavelength distribution of light absorbed by visual purple as percentages of their respective maxima. The limit of the "displacement" effect is thus given by plotting the values of D_λ/D'_λ , as percentages of the maximum value, against wavelength.

Calculations. Owing to the pH dependence of the absorption of indicator yellow, it is first necessary to arrive at a value for the pH of the light adapted retina. No measurements appear to have been made of the variation of the pH of the retina with adaptation. Lythgoe (1938) has assumed the value 6.5 for the "light adapted" retina. Unfortunately, the absorption spectrum of indicator yellow at this pH is not given by Lythgoe in his 1937 paper, the nearest determinations being at pH 7 and pH 6.1. Provisionally the value 6.1 will be assumed.

The densities of visual purple and indicator yellow solutions at pH 6.1 are shown in the first and second columns respectively of Table I. These figures (Lythgoe, 1937) are the densities of an

TABLE I

The densities at various wavelengths of a visual purple solution and the corresponding indicator yellow solution obtained by photochemical bleaching (columns 2 and 3 respectively) and the values of the ratio of visual purple density to indicator yellow density (column 4). pH 6.1. (From Lythgoe (1937)).

Wavelength $m\mu$	Densities at pH 6.1		Ratio
	Visual Purple	Indicator Yellow	
420	0.35	0.61	0.57
430	0.42	0.54	0.78
440	0.49	0.47	1.04
450	0.60	0.39	1.54
460	0.71	0.33	2.15
470	0.82	0.27	3.04
480	0.92	0.23	4.0
490	1.00	0.18	5.6
500	1.03	0.14	7.4
510	1.01	0.12	8.4
520	0.93	0.09	10.3
530	0.80	0.07	11.4
540	0.65	0.05	13
550	0.47	0.04	12
560	0.31	0.02	15
580	0.12	0.01	12
600	0.04	0.01	4

unbleached and bleached solution and include absorption due to impurities. Lythgoe attempted to estimate the amount of absorption by the impurities, but his methods were not sound and the uncorrected figures are more reliable. It is clear from a study of his paper that his solutions were almost photometrically pure, the density of absorbing impurities being very small, particularly at the longer wavelengths.

The expression (1) for the amount of light absorbed by visual purple consists of two factors. The factor within the bracket evaluates the total light absorbed, that is, by the visual purple and indicator yellow combined; the remaining factor, $\frac{D_\lambda}{D_\lambda + D'_\lambda}$, gives

the fraction of this total which is absorbed by the visual purple.

The amount of visual purple in a retina at any given stage of light adaptation cannot, at present, be assessed. It may be very small or it may be of the same order as in the dark adapted retina or, conceivably, even somewhat greater. It depends, among other things, on what degree of protection from bleaching is afforded by the accumulated indicator yellow and this, in turn, depends on the wavelength distribution of the adapting light.

All possibilities will, however, be covered by considering two extreme cases. In the first case the effect of increasing amounts of indicator yellow on the light absorbed by visual purple having a density of 0.5 at 502 m μ will be considered. This concentration of visual purple has been intentionally chosen as being, in all probability, much higher than would ever occur in a light adapted retina. In the second case the effect of increasing amounts of indicator yellow on the light absorbed by visual purple of infinitesimally small peak density will be considered. These two cases constitute upper and lower extremes respectively.

First Case. In Fig. 1 are shown two series of curves. The A-series curves, calculated from the expression $(1 - 10^{-(D_\lambda + D'_\lambda)})$, show the total fraction of light of each wavelength absorbed by solutions containing (in every case) visual purple of peak density 0.5 and indicator yellow of concentration indicated by the numeral for each curve. The numerals actually represent the peak density of the parent visual purple solution, this being a convenient measure of indicator yellow concentration since visual purple and indicator yellow are stoichiometrically related. Conversion to actual indicator yellow densities may be carried out using table I. Thus from table I and simple proportion the indicator yellow arising from the photodecomposition of visual purple of peak density 10 for example has an actual density of 4.56 at 440 m μ 0.88 at 520 m μ , etc.

FIG. 1.

A series curves.—The total percentage of incident light absorbed by mixtures of visual purple (peak density 0.5 throughout) and indicator yellow of various concentrations. The numerals are measures of the indicator yellow concentrations and refer to the peak density of the visual purple from which they are derived.

B series curves.—The "depression" and "displacement" effects, at various indicator yellow concentrations, on the percentage of incident light absorbed by visual purple of peak density 0.5. The curve marked "O" refers to visual purple alone; other numerals are as for the A series curves. The intersection of the dotted curve connecting the maxima of the curves with the wavelength axis indicates the limiting displacement of the maximum at infinite indicator yellow concentration.

The B-series curves of Fig. 1 have been calculated from expression (1) and show the fraction of incident light absorbed by the visual purple. The "depression" and "displacement" effects are clearly shown. The limiting curve of the B-series is the wavelength axis of the graph or, in other words, when the concentration of indicator yellow is infinite the light absorbed by the visual purple is nil. The limit of the "displacement" effect is indicated by the dotted line which passes through the maxima of the curves. By re-plotting the B-series curves as percentages of their respective maxima the "displacement" effect can be isolated. If this is done it is found that the limiting curve of the family has a maximum at about 550 mμ,

Second Case. In this extreme case, where the concentration of visual purple is vanishingly small, D_λ may be neglected by comparison with D'_λ in expression (1) which accordingly may be rewritten

$$\frac{D_\lambda}{D'_\lambda} \cdot (1 - 10^{-D'_\lambda})$$

By evaluating the factor $(1 - 10^{-D'_\lambda})$ for various concentrations of indicator yellow, a series of curves similar to the A-series curves of Fig. 1 may be obtained. Such curves illustrate the normal broadening of an absorption band with concentration and show that, in the case of indicator yellow, the wavelength up to which virtually complete absorption occurs advances with increasing concentration towards the red end of the spectrum.

The value of the remaining factor, D_λ/D'_λ , is vanishingly small in the present case. Therefore, in order to illustrate the "displacement" effect isolated from the "depression" effect, the ordinates of the curves described in the previous paragraph are multiplied by the appropriate values of the ratio of visual purple density to indicator yellow density from Table I. The resulting curves are plotted as percentages of their respective maxima in Fig. 2.

The values of the ratio of visual purple density to indicator yellow density in Table I are rather uncertain at wavelengths beyond 520 mμ owing to the small absorption of the indicator yellow solution at the longer wavelengths. The resulting irregularities in the derived curves of Figs. 1 (B-series) and 2 accordingly become increasingly apparent as the maximum moves towards the longer wavelengths. Now the *limiting* curve of Fig. 2 is given by the ratio D_λ/D'_λ alone since here the remaining term $(1 - 10^{-D'_\lambda})$ is equal to unity. To show the limiting curve of this series more clearly, therefore, it has been plotted from the values for the ratios D_λ/D'_λ of Table I after they have been

FIG. 2.

The "displacement" effect of various concentrations of indicator yellow on the light absorbed by visual purple of very low concentration. The curve marked "O" is the absorption spectrum of visual purple. The curve marked " ∞ " is the limiting curve of the series, attained at infinite indicator yellow concentration.

smoothed by the "method of fitting parabolas of degree 2 or 3" (Whittaker and Robinson, 1924).

The results of the calculated examples may be summarized as follows. The absolute value of the "depression" effect (reduction in sensitivity) for a given state of light adaptation cannot be assessed without a knowledge of the concentrations of visual purple and indicator yellow in the light adapted retina. The "displacement" effect (Purkinje shift), on the other hand, proceeds to a limit which is independent of the visual purple concentration. Further, although this limit is attained only when the concentration of indicator yellow is infinite, it is, as shown by Figs. 1 and 2, closely approached at finite concentrations of indicator yellow.

The effect of absorption by the macula lutea and the pre-retinal ocular media

The determination of photopic luminosities is carried out in the central retina where absorption due to the macular pigment takes

place. In the measurement of scotopic luminosities, however, the retinal region employed is beyond the macula.

Sachs (1891) determined the mean coefficients of transmission of monochromatic light by the yellow pigment from the macula of human eyes (nine specimens) and obtained the results shown in Table II.

TABLE II

The variation of transmission with wavelength at the macular region of the retina.

Wavelength m μ	Transmission of macula lutea (per cent.)	Transmission of ocular media (per cent.)	Combined Transmission (per cent.)
420	67.0	16.0	10.7
430	67.0	24.8	16.6
440	67.0	31.8	21.3
450	67.0	38.8	26.0
460	67.1	42.6	28.6
470	67.5	43.8	29.6
480	68.0	45.8	31.1
490	70.0	48.1	33.7
500	74.0	49.5	36.6
510	80.0	51.0	40.8
520	90.5	52.5	47.5
530	94.1	54.0	50.8
540	95.1	55.9	53.2
550	96.2	57.0	54.8
560	97.1	57.2	55.5
580	99.1	59.4	58.9
600	100.0	61.0	61.0

A further source of preferential light absorption is that by the aqueous, lens, and vitreous. This absorption is, of course, always present irrespective of the retinal region investigated. Ludvigh and McCarthy's data (1938) for the transmission of the ocular media are also shown in Table II.

In the last column of the table the combined effect of these two factors is shown.

Derivation of the photopic luminosity curve

In order to complete the comparison with the photopic luminosity curve, the ordinates of the curves of Figs. 1 (B series) and 2 require to be multiplied by the transmission factor appropriate to each wavelength (shown in Table II). The families of curves so

FIG. 3.

Experimental and calculated photopic luminosity curves.

--- luminosity curve (experimental) on the basis of an equal energy spectrum.

— ditto on the basis of an equal quantum intensity spectrum.

○ calculated values assuming pH = 7.0.

● ditto assuming pH = 6.1.

◐ ditto assuming pH = 5.2.

obtained represent luminosity curves for different levels of light adaptation (different concentrations of indicator yellow), the limiting curve corresponding to the condition of complete adaptation to a very high intensity (infinite concentration of indicator yellow). As this latter condition is approximated when the photopic luminosity curve is measured it is appropriate to select the limiting curve for the purpose of comparison. When the ordinates of the limiting curve (the ratios D_λ/D'_λ of Table I) are multiplied by the appropriate transmission factors of Table II and the values obtained adjusted proportionately so that the maximum is 100, the values shown by filled circles in Fig. 3 are obtained.

In the foregoing calculations the pH of the light adapted retina was assumed to be 6.1. This is probably rather on the acid side. If the pH is taken as 7.0 and the value of D_λ/D'_λ for this pH are multiplied by the appropriate transmission factors of Table II, the luminosity values for this pH are obtained. These results are shown as unfilled circles in Fig. 3. Similarly derived values for pH 5.2 are shown as half-filled circles.

For comparison, the photopic luminosity curves based on an equal energy spectrum (dotted line) and on an equal quantum intensity spectrum (full line) are shown in the same figure. The ordinates of Fig. 3 are plotted on a logarithmic basis, so that equal percentage deviations of the calculated luminosities correspond to equal distances from the photopic curves.

It will be observed from Fig. 3 that the best agreement between the derived and experimental photopic luminosities is obtained at pH 6.1. Since the derived luminosities both for the less acid (pH 7) and the more acid (pH 5.2) cases deviate from the experimental curve in the same sense, it may be inferred that in the neighbourhood of pH 6.1 the derived luminosities are not closely dependent on pH. Thus Lythgoe's estimate of 6.5 as the pH of the light adapted retina is supported by the present results. It is possible that the variation between the luminosity curves of different individuals is due to pH variations.

It will also be noted that the derived luminosities agree better with the experimental curve when the latter is on an equal quantum intensity basis than when it is on an equal energy basis. This indicates that the primary part of the physico-physiological process in photopic vision (as in scotopic vision) is photochemical.

Discussion

The foregoing derivation of the photopic luminosity curve rests on two main assumptions. These are:

- 1, that the production of visual purple from precursors is a rapid process in comparison with regeneration from its photo-products;

2, that the influence of indicator yellow on the light absorbed by visual purple is that which would obtain in a *homogeneous* mixture of the two substances.

The first assumption allows the possibility of the accumulation of relatively large amounts of indicator yellow in a light adapted eye, provided that thermal dissipation is not too rapid. (At pH 6.5 this condition is satisfied.)

Insufficient is known about the production of visual purple from precursors to discuss this assumption profitably. It is, however, possible to make a rough estimate of the minimum amount of indicator yellow required to shift the *maximum* of the derived luminosity curve to its photopic position (550 m μ). The validity of the ratio D_λ/D'_λ as a measure of the fraction of incident light absorbed by visual purple, depends on the assumption that *all* the incident light is absorbed. Strictly speaking, this is true only when the density of the indicator yellow is infinite. Absorption is, however, complete for practical purposes (>95 per cent.) at densities of 1.3 and more. As the concentration of indicator yellow increases in the retina, the point in the spectrum up to which there is virtually complete absorption moves towards the longer wavelengths. The maximum of the limiting curve of Fig. 2 is at 550 m μ (approx.). Consequently when the concentration of indicator yellow becomes such that its density at this wavelength is equal to or greater than 1.3, then the derived luminosity curve will also have its maximum at this wavelength and will, moreover, correspond exactly with the limiting curve on the blue side of the maximum. Further increase in the concentration of indicator yellow will result in a raising of the ordinates on the red side of the maximum to their ultimate positions corresponding to the limiting curve of Fig. 2.

Now the photodecomposition of visual purple of peak density 1.0 yields indicator yellow of density 0.04 at 550 m μ at pH 6.1 and 0.05 at pH 7. Taking the mean density, 0.045, as applicable to a pH of 6.5 it is seen that to achieve a density of 1.3 would require the decomposition of visual purple of peak density $1.3/0.045 = \text{ca. } 29$. [This calculation refers to the extreme case where the concentration of visual purple in the light adapted retina is regarded as very small. If the other extreme (peak density 0.5) is assumed then the corresponding visual purple density at 550 m μ , namely, 0.23 must be subtracted from 1.3 since it contributes to the total density. In this case the amount of indicator yellow required is that derived from visual purple of peak density $1.07/0.045 = \text{ca. } 24$.]

These can only be regarded as rough estimates since the absorption of indicator yellow at 550 m μ is not very accurately known. They

indicate, nevertheless, that a considerable amount of photodecomposition of visual purple is necessary to produce sufficient indicator yellow to account for the whole of the Purkinje shift. It is for this reason that the first assumption has been made, namely that the production of visual purple from precursors is a rapid process. This is in distinction to the generally held view which regards the precursors as merely making good the inevitable katabolic losses of visual purple and its photoproducts.

Information concerning the mode of occurrence of visual purple in the retina is insufficient to allow a discussion of the likelihood of the second assumption, namely that the division of absorbed light between visual purple and indicator yellow is such as would obtain in a *homogeneous* mixture of the two substances. In support of this assumption, however, is the fact that the displacement of the luminosity curve as light adaptation proceeds, that is, as the amount of indicator yellow accumulates, is not an indefinite process. *The limit beyond which no further change takes place corresponds to the photopic luminosity curve.* If, as an alternative hypothesis, it were assumed that the indicator yellow acts as an external light filter, its effect, as it accumulated in the retina, on the light absorbed by visual purple and hence on the calculated luminosity curve would be to shift the maximum further and further into the red.

If the above two assumptions are allowed then a number of visual phenomena are capable of explanation. Thus, the failure to find a photosensitive pigment corresponding to the photopic luminosity curve is due to the dual role of visual purple in acting as the mediator of both scotopic and (in the presence of indicator yellow) photopic luminosity. The Purkinje shift is *quantitatively* accounted for, the photopic luminosity curve being calculated as the *limiting* case of the effect of indicator yellow on the light absorbed by visual purple. The corresponding shift in the case of retinae containing porphyropsin is similarly explained. Further, the derived photopic luminosity curve agrees better with the measured curve when the latter is plotted, in accordance with photochemical principles, on an equal quantum intensity basis. The lower sensitivity of the light adapted retina is at least partly accounted for by the screening action of the accumulated indicator yellow.

A basis for the explanation of certain aspects of dark adaptation is also provided. As is well known the course of dark adaptation, as measured by the visual threshold at various intervals of time, depends on the previous history of light adaptation. For example, after exposures to light for short periods the rate of return of sensitivity is much more rapid than after exposures for long

periods even though the thresholds immediately after adaptation may be similar.

The presence of variable amounts of indicator yellow in the light adapted retina is consistent with these facts. Thus while a short exposure may be sufficient to reduce the visual purple concentration (and hence the sensitivity) to a low figure, the total amount of photodecomposition during the adapting period and hence the amount of indicator yellow formed may be relatively small. In consequence, on return to the dark, the concentration of visual purple will be rapidly restored from precursors and indicator yellow, any residual amount of indicator yellow being small and hence without great effect on the sensitivity. After exposures for long periods, however, the total amount of photodecomposition, and hence amount of indicator yellow formed, will be large. Consequently, although on return to the dark the concentration of visual purple will be equally, if not more, rapidly restored, indicator yellow will still at this point be present in large amount. Not until this "excess" has been discharged will the sensitivity of the retina return to its full value corresponding to complete dark adaptation.

The phenomenon of "rod monochromatism" (Wright, 1946) can also be accounted for. Subjects with this visual defect are unable to discriminate hues and, while having a normal scotopic luminosity curve, suffer from nystagmus, photophobia and poor visual acuity under conditions of illumination which, in a normal observer, would evoke photopic vision. An additional characteristic is an abnormally slow rate of recovery (dark adaptation) following exposure to a bright light. As the name implies, the usual explanation given for this type of defect is that vision is mediated by rods alone, cone vision being absent. This is little more than a description however. On the present hypothesis the absence of a photopic luminosity curve and the slow rate of dark adaptation are attributable to a reduction in the capacity for the production of visual purple from precursors. Thus the absence of a steady supply of visual purple would prevent the accumulation of sufficient indicator yellow in bright light to displace the luminosity curve to its photopic position. The photophobia presumably arises from the absence of the normal protective action afforded by the indicator yellow.

In the light adapted condition the eye is colour sensitive. It is outside the scope of this paper to discuss the mechanism of colour perception; it is mentioned merely for the purpose of clarifying the implications of the present concepts. The sensation of luminosity is generally regarded as an intensive property of the sensation of hue. While there are practical reasons for this there

are many phenomena, a number of which are given by Troland (1922), which indicate that the sensations of luminosity and hue are mediated by separate processes. The existence of a defect known as "cone monochromatism" (Pitt, 1944), in which the subject has normal dark adaptation, normal scotopic and photopic luminosity curves and yet no colour sense, is sufficient indication that luminosity and hue sensations are not necessarily related as intensive and extensive attributes.

One of the many difficulties of the Duplicity Theory is in accounting for the rôle of the rods at high illuminations. This difficulty arises directly from the habit of regarding luminosity as the intensive property of hue. If the present hypothesis that visual purple mediates both scotopic and photopic luminosities is true, then it is possible that the rods are responsible for the mediation of luminosity both at scotopic and photopic levels, leaving the cones for the mediation of the hue sensations.

Summary

The hypothesis that visual purple is the mediator of photopic luminosity sensations as well as of scotopic is investigated. Two main assumptions are made in developing the hypothesis. The first of these is that the production of visual purple from its precursors is a rapid process in comparison with regeneration from its photoproducts; the second, that the influence of absorption by the photoproducts on the light absorbed by visual purple is equal to that obtaining in a homogenous mixture of the substances.

It is shown that the effect of the accumulation of photoproducts (indicator yellow) in a retina exposed to light, is to move the position of maximum light absorption by visual purple towards the longer wavelengths. This process is not indefinitely prolonged. As the amount of indicator yellow accumulates the light absorbed curve of visual purple rapidly approximates to a *limiting* position having a maximum at about 550 m μ . When this limiting curve is corrected for absorption by the ocular media and by the macular pigment, the resulting curve closely approximates to the photopic luminosity curve.

Apart from accounting for the Purkinje shift in a quantitative manner the hypothesis provides a basis for the explanation of a number of other visual phenomena, notably the reduced sensitivity of photopic vision and the dependence of the rate of dark adaptation upon the previous light history of the retina.

Acknowledgment. I wish to record my thanks to Miss M. A. Hooper for assistance with the computational work involved in the preparation of this paper.

REFERENCES

- BRODA, E. E., GOODEVE, C. F. and LYTHGÔE, R. J. (1940).—*Jl. Physiol.*, Vol. XCVIII, p. 397.
- DARTNALL, H. J. A. and GOODEVE, C. F. (1937).—*Nature, Lond.*, Vol. CXXXIX, p. 409.
- GRANIT, R. (1941).—*Acta physiol. Scand.*, Vol. II, p. 334.
- LUDVIGH, E. and MCCARTHY, E. F. (1938).—*Arch. Ophthal. Chicago*, Vol. XX, p. 37.
- LYTHGÔE, R. J. (1937).—*Jl. Physiol.*, Vol. LXXXIX, p. 331.
- (1938).—*Proc. phys. Soc.*, Vol. L, p. 321.
- (1940).—*Brit. Jl. Ophthal.*, Vol. XXIV, p. 21.
- LYTHGÔE, R. J. and QUILLIAM, J. P. (1938).—*Jl. Physiol.*, Vol. XCIII, p. 24.
- OGUCHI, Ch. (1924).—*v. Graefes Arch. Ophthal.*, Vol. CXV, p. 234.
- PITT, F. H. G. (1944).—*Nature, Lond.*, Vol. CLIV, p. 466.
- SACHS, M. (1891).—Quoted by Parsons, J. H. in "An Introduction to the Study of Colour Vision," p. 40. Cambridge University Press, 1915.
- TROLAND, L. T. (1922).—*Jl. Opt. Soc. Amer.*, Vol. VI, p. 3.
- WALD, G. (1938).—*Jl. gen. Physiol.*, Vol. XXI, p. 795.
- WHITTAKER, E. T. and ROBINSON, G. (1924).—"The Calculus of Observations." London: Blackie.
- WRIGHT, W. D. (1946).—"Researches on Normal and Defective Colour Vision." London: Henry Kimpton.

SCLERAL RESECTION IN THE TREATMENT OF RETINAL DETACHMENT

(A Preliminary Report)

BY

SEYMOUR PHILPS

LONDON

THE great majority of retinal detachments are cured by Gonin's operation of scleral diathermy over the site of the retinal tear, but there remains a percentage which is not cured by this means. This percentage varies from 20 to 30, and the causes of failure are various. Apart from those patients in whom inter-current disease or other factors make operation impossible, the causes of failure of the diathermy may be :—

(1) Failure to see and therefore to seal off the retinal tear.

(2) Retraction of the vitreous and shrinkage of the retina, making it too small to "fit" the eye, so that even after a successful diathermy operation the retina breaks away again.

Failure to see the Retinal Hole. If the media are transparent the whole of the retina can be examined ophthalmoscopically and a hole, if present, can be located. Lack of transparency of the media whether due to lens opacity, capsular remains or vitreous opacity may mean that the view of the retina is so poor that all efforts to locate a retinal tear are fruitless.