

ON THE MECHANISMS OF COLOUR VISION

P. L. WALRAVEN



INSTITUTE FOR PERCEPTION RVO-TNO
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INTRODUCTION

Theories of colour vision have to account for a large number of experimental facts. Two main trends are apparent in the literature, both of which present the fundamental fact of colour vision: the colour mixture laws. Nevertheless, one of them explains without complications a number of phenomena, which the other cannot account for without including unreasonable assumptions, and vice versa.

These main theories are well known as the Young-Helmholtz theory and the Hering-theory. In both theories it is thought that the message of the colour is coded by the receptors into three components. In the Young-Helmholtz theory these are thought as the red, green and violet contributions of the colour, while in the Hering theory these are the amounts of white or black, red or green, and yellow or blue, which signals have therefore an antagonistic character. A large number of theories are advanced which include elements of both, and also the possibility is suggested that both are valid, but each at different levels in the transmission.

It is clear therefore, that there is still much doubt and controversy in this field, but there seems to be a trend in the literature, which indicates that a solution is certainly nearer than it was for instance ten years ago. Much help comes from the objective methods as measurements of absorption spectra of the visual pigments in the retina and electrophysiological work. These fields of study are a necessary complement of the psychophysical studies, to which this thesis is restricted, which never provide definitive answers to such questions.

It seemed to us appropriate to connect some of these objective data with those psychophysical functions, which must have a close relationship with them. In the first place we dealt with the chromatic Stiles-Crawford effect, which is the hue shift, when the point of entry of light into the pupil moves over the pupil. This effect has a close relationship with the physical absorption properties of pigments, which leads therefore to a determination of the absorption curves of the visual pigments in the cones (Ch. IA). We used for this determination also the luminosity curve after strong chromatic

adaptation, in which these pigments are also involved. In the second place we considered the possibility of whether the well known saturation effects in nerve transmission with increasing stimulation become apparent in psychophysical functions. We thought the Bezold-Brücke effect, the change in hue with increasing brightness, as such a function. Quantitative treatment necessarily involves the assumption of the ratios of stimulation of the different nerve inputs, or in other words the spectral absorption curves of the different visual pigments (Ch. IB). Relating this first chapter to the literature and anticipating Ch's II and III leads to a discussion on the mechanisms of colour vision in § 5 of Ch. IB. We have here presented what we consider as the current trend towards a solution of the physiological problems posed by colour vision.

Consideration of the physics of the light absorbing matter, the visual pigment, suggested whether the physical nature of the light itself has any bearing upon psychophysical functions. The quantum nature of light in particular has been considered in Ch.'s II and III. Inherent to the quantum nature are the statistical fluctuations in the number of quanta when light falls upon the retina. On the one hand the statistical fluctuations are correlated with the variability in colour naming (Ch. II). On the other the discrimination ability of the eye has been considered as a signal to noise problem, in other words the eye is a physical light sensitive instrument in which the noise is due to the fluctuations in number of incident quanta (Ch III).

As mentioned before, some of the results are appropriate for the discussion at the end of the first chapter, because the data of the experiments and the assumptions made in order to carry out quantitative calculations, are related with the ideas about the mechanisms of colour vision.

CHAPTER I

HUE SHIFT

A. THE HUE-SHIFT ASSOCIATED WITH THE STILES-CRAWFORD EFFECT

1. Introduction

Stiles and Crawford (1933) showed that the sensitivity of the retina varies with the place of entry of the light in the pupil, and thus with the direction of incidence of light upon the retina. This dependence of luminous efficiency on the direction of incidence is known in the literature as the Stiles-Crawford effect. The hue-shift associated with the Stiles-Crawford effect was discovered by Stiles and Crawford (1937) in a further study of the retinal direction effect (see also Stiles 1937).

Recently Vos (1960) gave a review on this effect. He showed that a quite rounded picture, albeit rather qualitatively, has been formed about the directional sensitivity, but other phenomena, associated with this proper effect, such as the wavelength dependence of it, the hue shift mentioned and the change in colour mixture functions are still not sufficiently explained.

The purpose of this part of the chapter is to connect the several aspects of the Stiles-Crawford effect (SC-effect) by consideration of the relationship between the shape of the spectral response curves of the colour mediating systems in the eye and the angle of incidence of the light in the receptor.

The theory affords strong support for the Young-Helmholtz theory as far as the receptor layer is concerned, and is based on a detailed analysis of the physics of light absorption in the receptor (Walraven and Bouman 1960).

First we will review data and interpretation of the directional sensitivity of the retina and associated phenomena. Then we will give our own theory and afterwards a critical consideration of other theories, which led, in our opinion, to a misinterpretation.

2. Literature review about the directional sensitivity of the retina and associated phenomena

a. The data

1. The Stiles-Crawford effect

If η is the efficiency of the light required to evoke a sensation of light for peripheral entry in the pupil at radius r , the efficiency through the centre of the pupil being 1, the relationship between η and r along the horizontal central traverse of the pupil is expressed by

$${}^{10}\log \eta = -pr^2 \quad (1)$$

p being about 0.05 (r in mm). The dependence of η upon r for the observer P.L.W. is shown in Fig. 1a. These measurements are

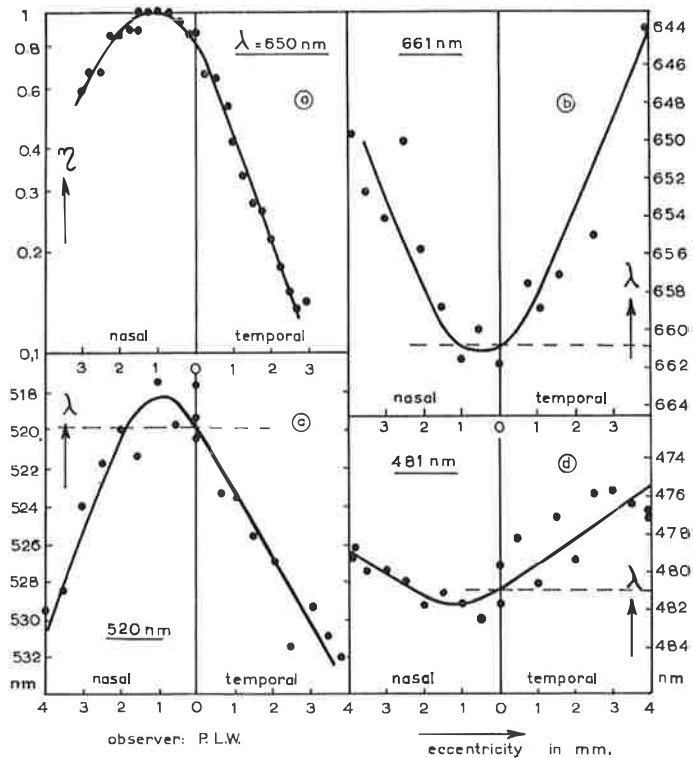


Fig. 1a. The variation of the luminous efficiency η as a function of the point of entry along a horizontal traverse of the pupil.

b, c, d. Lines of equal hue for the indicated wavelengths.

done with use of the apparatus shown in Fig. 3. The highest efficiency is here not in the middle of the pupil. In this case the formula must be modified as follows:

$$^{10}\log \eta = -p (r - r_0)^2 \quad (2)$$

where r_0 is the radius with maximum efficiency (Stiles 1933).

2. Dependence of the Stiles-Crawford effect on wavelength

A detail in the data, very important in relation to the theory of the hue shift, is the dependence of p on wavelength. According to Stiles (1939) p varies between 0.047 (at 570 nm) and 0.059 (at 400 nm). The reciprocal of the efficiency at an entry radius in the pupil of 3.5 mm is given in Fig. 2. This graph shows, that the SC-effect is smallest in the middle of the spectrum, while on the blue side it is still stronger than on the red side. We refer to the data at 3.5 mm in particular, because all our calculations are carried out for this radius.

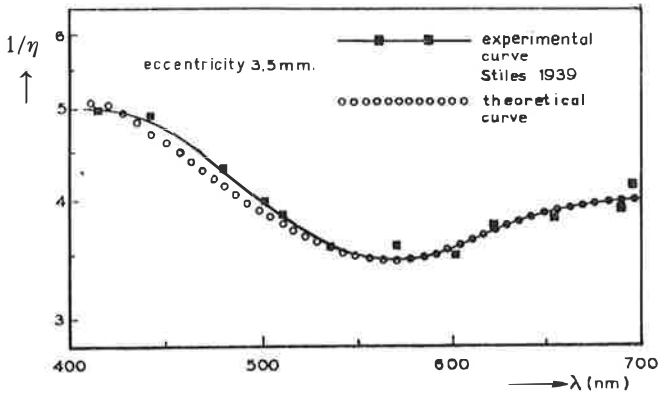


Fig. 2. $1/\eta$ as a function of wavelength according to Stiles' measurements and according to theory.

3. The hue shift

The reality of the hue shift as measured by Stiles and Crawford (1937) seems generally to be accepted. Only very recently the effect has been remeasured (Walraven and Bouman 1960, and Enoch and Stiles 1961), although Hansen (1946) measured the

practical consequences of it in working with the Pulfrichphotometer. Measurements made with the apparatus described in the text of Fig. 3 are in agreement with the earlier and the recent data. In Fig. 1b, c and d the hue shift at several wavelengths for the observer P.L.W. is shown. The meaning of these figures becomes clear by consideration of the experimental procedure. Referring to Fig. 1b the lower halffield (see Fig. 3) is filled with light of 661 nm. If the other

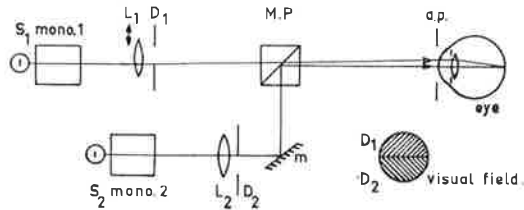


Fig. 3. Schematic arrangement of the apparatus. The exit slit of monochromator 1 is focused on the pupil of the eye. By shifting L_1 as indicated by the arrow, the point of entry of the light moves over the pupil. The place of L_1 is thus a measure of the eccentricity. The place of entry of the second beam, via mirror m and mixture cube M.P. remains in the centre. The eye sees in Maxwellian view two half fields, the upper D_1 of the first, and the lower D_2 of the second beam. Close to the eye is placed a slit shaped artificial pupil. On the ends of the artificial pupil two point sources are placed, which throw two shadows of the pupil edge on the retina. For centring the pupil the two half fields have to be seen just between the shadows of the pupil. The observer matched the two half fields by varying the wavelength of mono. 1, while the brightness could be changed by varying the currents through the filaments of S_1 and S_2

halffield is filled with light of adjustable wavelength, the observer will, if both beams go through the centre of the pupil, adjust the wavelength for equal appearance at 661 nm. The spread around this value is determined by the colour discrimination ability of the observer. If now the point of entry of the light with adjustable wavelength is changed, the wavelength will be shorter. This means that the appearance of the oblique light is the same as the perpendicular 661 nm, or in other words, with increasing eccentricity the hue becomes redder. The effect is reverse at 520 nm, and the graph shows that at 481 nm the hue change is again towards longer wavelengths. These hue changes were measured by the observers P.L.W. and H.J.L. for a series of wavelengths (both observers have normal colour vision). The results at an eccentricity of 3.5 mm are given in Fig. 4, together with the results of Stiles'

observers W.S.S. and B.H.C. The recent measurements of Enoch and Stiles (1961) are in accordance with the other. The 3.5 mm is the distance ($r - r_0$) of equation (2), the distance from the point of maximum efficiency. It can be seen in Fig. 1, that this point coincides with the maxima and minima in the curves of equal appearance of hue. The measurements thus indicate, that the hue shift may involve the same mechanism as the Stiles-Crawford effect proper.

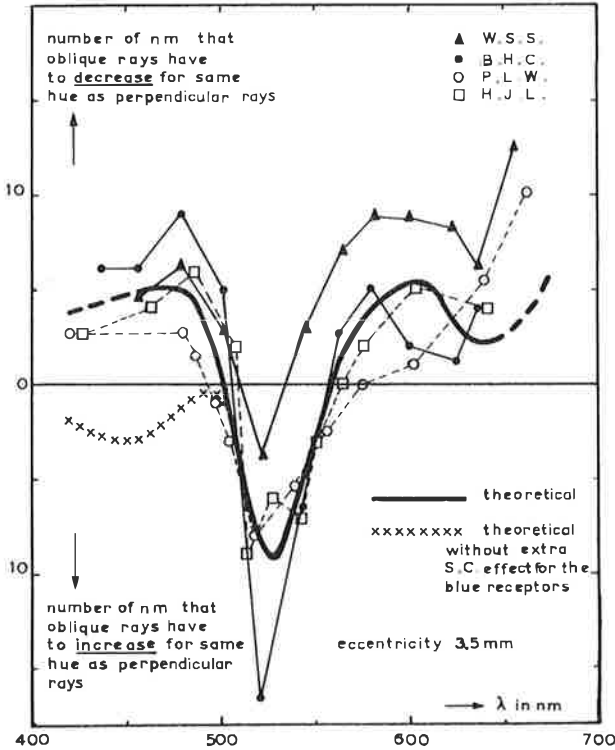


Fig. 4. Hue shift at 3.5 mm. eccentricity for four observers, together with the theoretical curve.

Some details have to be added to these experimental results. Stiles (1937) made the remark, that it is not always possible to get a correct match. We observed that in the red end of the spectrum the hue for oblique light becomes somewhat purple. In the yellow part there is a small desaturation, while in the violet part again a desaturation is visible. The recent findings about anomalous trichromats (Walraven and Leebeek 1962) will be left out of discussion now.

4. The change in colour mixture functions

Brindley (1953) observed that two lights of different spectral composition, which match when rays reach the retina from the centre of the pupil, may not match when the rays reach it from the periphery. Fig. 5 shows the way in which the amounts of R (680 nm) and G (550 nm) required to match various monochromatic lights altered (expressed in $\Delta \log R$ and $\Delta \log G$), when the light came to pass through a region about 3 mm above the centre, instead of through the centre. This change becomes also apparent in the observed hue change. In the case of the anomaloscope-setting,

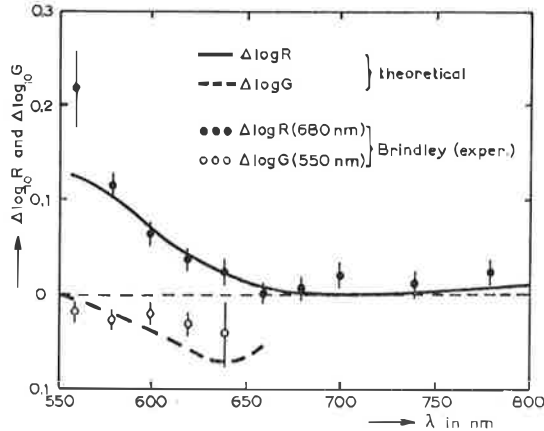


Fig. 5. Changes produced by moving the point of entry of the light from centre to edge of the pupil in \log_{10} (amount of red) and \log_{10} (amount of green) to match lights of different wavelengths.

the Rayleigh match (544 nm + 670 nm \rightarrow 589 nm) as used for the detection of colour anomalies, the hue shift of the monochromatic yellow is towards red, while the composite yellow shifts towards green.

b. The interpretation

Stiles and Crawford (1933) showed that the effect must be a property of the receptors themselves. Starting from this finding Wright and Nelson (1936) gave an explanation, which is based on the fact that the refractive index of the receptor is somewhat higher than that of the surrounding tissue (Brücke 1844). Measurements (Barer 1957) showed that the ratio of the indices of the

cone and the surrounding tissue is about 1.03. Rays entering the receptor only slightly obliquely (Fig. 8) are caught by total reflection, whereas more slanting rays partially pass to the tissue outside. So only the perpendicularly incident light is totally gathered into the outer segment, and thus being more effective than oblique light. If the maximum efficiency is not in the middle of the pupil, the cone is thought to be standing a little obliquely in the retina.

Toraldo di Francia (1949) emphasized the importance of wave-optics in allowing for the tiny dimensions of the cones with respect to the wavelength of the light. Considering the cone as a dielectric antenna, it is possible to calculate the radiation pattern, and thus the sensitivity as a function of the direction of the incident light. O'Brien (1951) showed with experiments on models that for the dimensions of the cone the treatment with geometrical optics is good enough. In the following this optical refinement will therefore be left aside.

The dependence of the effect on wavelength remained in the literature unexplained.

As far as the hue shift is concerned, Stiles (1937) explored whether different degrees of directional sensitivity (different p 's in equation (1)) for the different types of colour receptors could explain the facts. This failed. He came to the conclusion that the spectral response curves have to be deformed for an explanation of the hue shift. The measurements by Brindley (1953) on the change in the anomaloscope setting are a confirmation of this conclusion.

Stiles and Crawford (1933) assumed that for the explanation of the SC-effect proper the cones should be enwrapped by a sheath of pigment, so that oblique light is easily absorbed in it, but perpendicular rays can enter the cones freely. For the explanation of the hue shift Stiles (1937) suggested the following idea: "Suppose each cone to be filled with a photochemical substance which attenuates the light in its passage through the cone. As a consequence the photochemical action will also decrease in amount in passing from the inner to the outer extremity of the cone. (Stiles thought the whole receptor filled with visual pigment). Since the pigment sheath gives rise to the intensity effect (the SC-effect) by shielding the outer extremity of the cone from obliquely incident light it follows that the intensity effect will be less the less the contribution of the outer extremity of the cone to the photochemical action. Thus at the wavelength at which the absorption of the photochemical sub-

stance is the greatest the intensity effect will be the smallest and there will be a variation in intensity effect with wavelength corresponding to the absorption curve of the photochemical substance. Admitting that the different types of cones must contain different spectral absorption curves it is clear that the ratio of the intensity effects for the different types of cones will vary with wavelength".

No doubt Stiles was very aware of the highly speculative aspect of his suggestion as such a sheath of pigment has never been found in higher vertebrates. This will be perhaps the reason that Stiles did not work out his own suggestion.

However it is at this point we will take up again the theoretical analysis by showing that the main features of his arguments remain valid in the Wright-Nelson explanation of the SC-effect.

Brindley (1953) followed the suggestion by Stiles. He stated: "Light which enters the receptors obliquely will pass through a smaller total density of pigment than light which travels along their axes". Whether he thought this in the framework of the pigment sheath hypothesis or along other lines is not clear. Although our results differ from Brindley's, our line of thought is the same. (Walraven 1959a). Before discussing Brindley's theory in detail, we will at first give our own theory.

3. Drawing in outline of theory

In order to bring a cone into action a critical amount of light has to be absorbed in its photo pigment. We think this critical amount does not itself depend on where it is located or how it is spread in the pigment container of the receptor. Next a part of the light — when oblique — passes through the walls of the pigment container to the surrounding tissue (Wright-Nelson explanation). This means that the critical amount of decomposed photochemical material is built up for oblique rays more near the place of entrance in the photo pigment container. In other words it works as if the effective length of the cone were shortened. Shortening of the pathway through a not very diluted solution corresponds with a narrowing of the spectral absorption curve (Stiles' idea), together with lower absorption and thus lower sensitivity. Dartnall (1957) gave a clear exposition of this behaviour of the absorption curve (Fig. 6).

Fig. 7 shows the train of thought. Fig. 7a represents two possible absorption curves of two different classes of receptors. To be

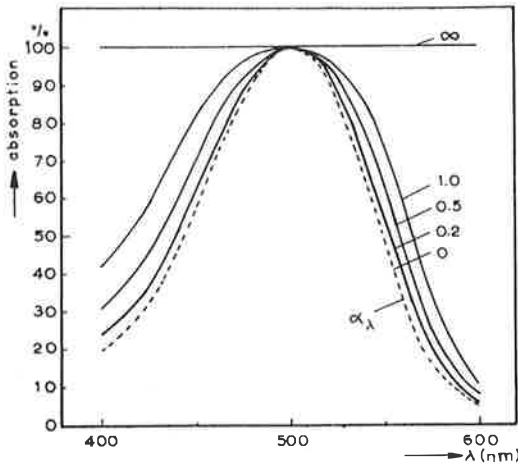


Fig. 6. Example of absorption spectra of visual purple solutions of various concentrations, plotted as percentages of their respective maxima. Parameter is the density in the maximum.

(Reproduced from Dartnall: "The visual pigments" pag. 16)

concrete we will speak of the red and the green system, although they do not represent a real proposal of fundamental curves.

The solid lines are the absorption curves for perpendicular light, the dotted for oblique light. The absorption of light is lower by the shorter pathway through the solution. For easy comparison, however, of the shapes of the absorption curves the peak values for oblique light have been made the same as for perpendicular light (Fig. 7b). Two things become now clear. In the first place the loss in sensitivity is largest at the flanks of the curves, and lowest at the peak. (Fig. 7c). This means that the variation of the SC-effect as a function of wavelength can be attributed to narrowing of the spectral absorption curves. In the second place the hue shift is due to the narrowing of the curves. The same hue is seen, if the ratios of the absorptions in the two types of receptors are equal. This means that wavelength p (Fig. 7b) has equal appearance for oblique as for perpendicular incidence: the decrease of absorption due to narrowing is the same in the red and the green receptors, hence the ratio does not change. At wavelength r the ratio of the absorptions in the red and green receptors is 5 : 2 for perpendicular incidence, while at wavelength q the ratio is the same 5 : 2 for oblique incidence. Hence q gives the same hue sensation for oblique, as r gives for perpendicular incidence. The hue changes thus

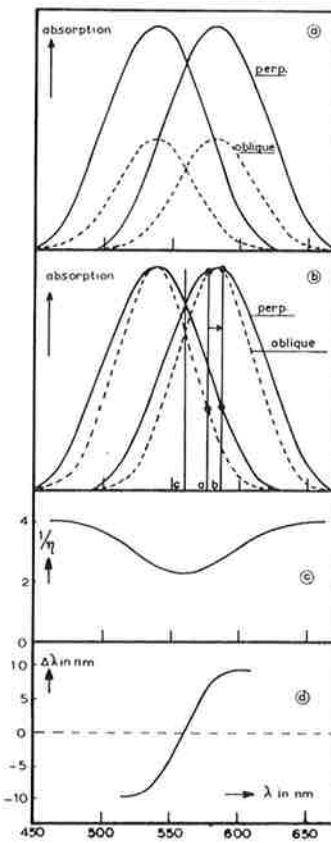


Fig. 7. Drawing in outline of theory.

7a. "Red" and "green" absorption curves for perpendicular and oblique light.

7b. Absorption curves for perp, and oblique light, given the same peak value, show the narrowing of the curves for oblique light. This is caused by the lower density as a result of the shorter pathway of the light through the pigment.

7c. The variation of $1/\eta$, a result of the narrowing of the curves.

7d. The hue shift, a result of the narrowing of the curves.

towards red with increasing obliquity at the red side of the spectrum (Fig. 7d). Because of the same reasoning the hue become greener in the green portion of the spectrum with increasing obliquity. It is assumed for this treatment that the peak densities are equal, and large enough to give narrowing. This means at least 20 % absorption in the peaks. The results with different densities will be discussed later (§ 5a).

The SC-effect proper is caused by the lower absorption, or in other words by leak out the receptor, whether out the inner, or out the outer segment. The hue shift is caused by the leak only out the outer segment, assuming that this is filled with the photo pigment.

We will compare now the quantitative development of the theory with the experimental data.

4. Quantitative development of the theory

a. Mathematical treatment

The change in the spectral absorption curves of the several pigments are now set in the framework of the Wright-Nelson explanation. As a first approximation it may be said that the pathway through the pigment is shortened for oblique light. This results in a lower density, and thus in a narrowing of the absorption curves. It is however not a simple density loss, because it is thought that only a fraction of the light which reaches the walls, passes through the tissue, and an other part is reflected again into the cone. It may thus be said that over the length of the pigment container there is an extra density (a leak), independent of wavelength and not contributing to the visual act. Although it has not been ascertained by histological findings, we assume in analogy with the rods that only the outer segments is filled with the visual pigment. Fig.'s 8 and 9 show the outer segment of the cone with length l .



Fig. 8. The gathering of light in a receptor by total reflection and the leak of light by non-total reflection in the inner segment (α) and the outer segment (ξ).

If α_λ is the extinction coefficient of the visual pigment, c the concentration of it and ξ the fraction of light leaking away per unit of length at a given angle of incidence of the light, then

$$-dI = I (\alpha_\lambda c + \xi) dl \quad (3)$$

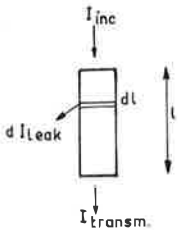


Fig. 9. The schematic outer segment, with a representation of the basis of Eq. (3).

Integrating from 0 to l we get, assuming α_λ and ξ independent of l

$$I_{trans}/I_{inc} = e^{-(\alpha_\lambda c + \xi)l} \quad (4)$$

Thus

$$I_{\text{not transmitted}} = \left\{ 1 - e^{-(\alpha\lambda c + \xi)l} \right\} I_{\text{inc}} \quad (5)$$

From every dI a fraction $\alpha\lambda cl / \alpha\lambda cl + \xi l$ contributes to the absorption by the pigment, and thus to the visual act. This means:

$$I_{\text{abs. by pigment}} = \frac{\alpha\lambda cl}{\alpha\lambda cl + \xi l} \left(1 - e^{-(\alpha\lambda c + \xi)l} \right) \quad (6)$$

The terms $\alpha\lambda cl$ and ξl are the respective densities of pigment and leak. It has to be emphasized that our definition of density is based on the natural logarithm. Often in the literature the density is defined on the basis of the common logarithm. For comparison our density values have to be multiplied by 0.43.

The ratio of $I_{\text{abs. (perp.)}}$ and $I_{\text{abs. (obl.)}}$ for equal $I_{\text{inc.}}$ we can define as the efficiency factor η^* , in analogy with the definition of η in § 2a. For the whole receptor we can define an η_c (cone) also in analogy with η . We mention that this is the combined effect of the η_c 's of the several receptor systems. To distinguish the η_c 's we will call them later η_r (red), η_g (green) and η_b (blue). If we define q by $\eta_c = q\eta^*$, we can regard q as a leak factor in the inner segment at a given angle of incidence of the light.

From the definition of η^* follows:

$$\eta^* I_{\text{inc}} \left(1 - e^{-\alpha\lambda cl} \right) = I_{\text{inc}} \frac{\alpha\lambda cl}{\alpha\lambda cl + \xi l} \left(1 - e^{-(\alpha\lambda c + \xi)l} \right) \quad (7)$$

This equation fixes the relationship between η^* , $\alpha\lambda cl$ and ξl . This means that for a given set of parameters the narrowing of the absorption curves is represented in this equation.

For the case of low absorption, as in the extremities of the absorption curves ($\alpha\lambda cl \ll 1$), and a relatively large leak in the outer segment ($\xi l \gg \alpha\lambda cl$)

$$\text{then} \quad \eta^* \alpha\lambda cl = \alpha\lambda cl / \xi l \quad \text{or} \quad \xi l = 1 / \eta^* \quad (8)$$

This equation fixes the values of ξl , if η^* in the extremities of the absorption curves is known. It has to be emphasized that we want to keep the treatment as simple as possible. The results of the calculations compared with the experimental data have to justify our approximations. We take therefore the factors ξ and q independent of wavelength for a particular receptor type. In order to obtain a marked narrowing of the absorption curves high peak densities are required. The peak densities are chosen so as that by them the

experimental facts can be described. Our choice as regards the peak densities is free, because no data are available in the literature.

Resuming there are the following parameters: the leak fraction ξl , the inner segment factor q , and the peak densities of the several absorption curves D_m . All these parameters are possibly different for each type of receptor. ξl and q are dependent on the eccentricity.

b. Choice of the absorption curves

The results which we will get by quantitative treatment of the suggestions made before, are very much dependent on the choice we make regarding the fundamental sensitivity curves of the different types of cones. In our opinion there is much in favour of the curves derived by Pitt (1944), which are expressed in luminous terms. In the first place as pointed out by Wright (1946): "We can assume, that Pitt's determination fits in most successfully with the various data which are available at the present time". Secondly the bleaching experiments by Rushton (1957) demonstrate good agreement as far as the green mechanism is concerned. Later on the results obtained with other proposed fundamental curves will be discussed.

The fundamental curves have to be corrected, in order to obtain the absorption curves of the pigments, for the absorption in the eye.

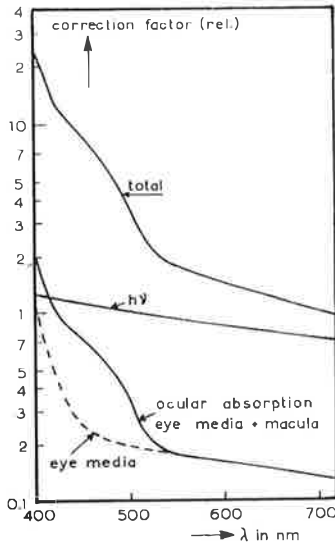


Fig. 10. The correction factor for transforming Pitt's fundamental curves into absorption curves on a quantum basis.

We used the data of Ludvigh and Mc Carthy (1938) and of Wald (1945), which are in accordance with the most recent measurements by Brindley (1952), for the absorption in the ocular media and in the macula lutea respectively. The correction factor as a function of wavelength is given in Fig. 10 on a relative scale. In order to bring a cone into action a critical number of quanta has to be absorbed in its photo pigment (Bouman 1950). So the absorption curves as a function of wavelength have to be based on an equal quanta spectrum, rather than on an equal energy spectrum. So Pitt's curves, which are based on an equal energy spectrum, have to be transformed for this purpose according to the equation $E = h\nu$. The magnitude of this correction is also presented in Fig. 10. Both corrections have now to be multiplied. The total correction factor has been chosen 1 at 700 nm. The resulting absorption curves are shown in Fig. 11 on a logarithmic scale.

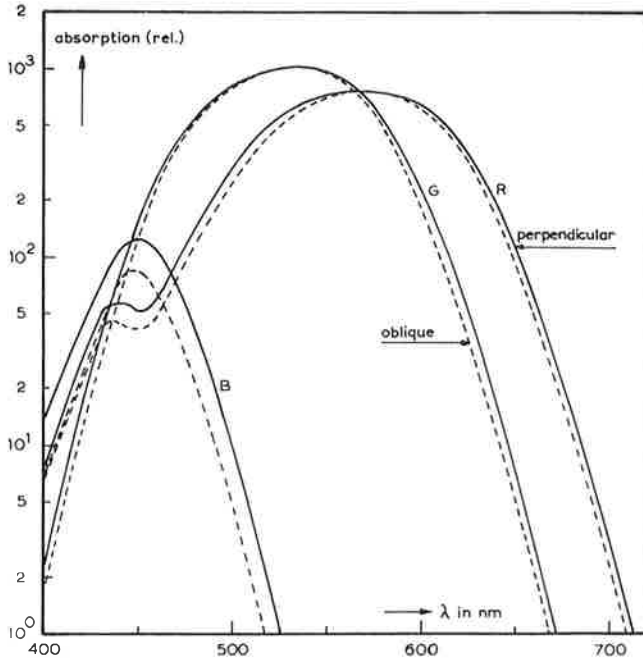


Fig. 11. The absorption curves for perpendicular and oblique light, obtained by correcting Pitt's fundamental curves according to Fig. 10. The change in shape by the narrowing of the curves and the extra Stiles-Crawford effect for the blue receptors is calculated for an eccentricity of 3.5 mm, assuming peak absorption of 80% for perpendicular light.

c. *Choice of the available parameters to explain the facts*

We will limit the calculations to an eccentricity of 3.5 mm and start with the red-green region of the spectrum. As pointed out an essential point in the theory is that the difference in $1/\eta$ between the middle and the end of the spectrum is caused by the narrowing of the absorption curves. Because we think that the hue shift is also caused by this narrowing, there must be a direct relationship between the dependence of $1/\eta$ on wavelength, and the hue shift. According to Stiles (1939) $1/\eta$ at the red end of the spectrum is equal to 4.00, and 3.50 in the middle of the spectrum. These data indicate the amount of narrowing of the total luminosity curve, which is considered as the sum of the three fundamental sensitivity curves.

Because the luminosity curve is the addition of Pitt's red and green curves in the red-green portion of the spectrum, the narrowing of these curves can be calculated from the narrowing of the luminosity curve (see Fig.'s 7b and 7c). It turns out by numerical analysis that the variations in $1/\eta$ mentioned, corresponds with a decrease in sensitivity at the flanks of Pitt's red and green curves of 20% with respect to the peak. It is then assumed that the densities at the maxima of the red and green curves are equal, because this assumption gives the best agreement with experiment. We refer here to the invariable hue (see details § 5a). Such a narrowing of the absorption curves causes a hue shift of 5 nm at 600 nm. This is quantitatively in accordance with the measurements. This proves that there is indeed a direct relationship between the dependence of $1/\eta$ on the wavelength and the hue shift.

This decrease of 20 % in sensitivity at the flanks of the absorption curves with respect to the peak, causing hue change of 5 nm at 600 nm, can however be obtained for a large range of peak absorption values, and well from 50 to 99%. Which of these absorption values has to be chosen? For several absorption percentages in the peaks the relationship has been established between $1/\eta^*$ in the extremity of the absorption curve and the amount of variation of $1/\eta^*$ as a function of wavelength. Fig. 12 shows that for the value $1/\eta^* = 4.00$ the absorption in the peak must be 50 %. The value $1/\eta^* = 4.00$ means, that as $1/\eta = 4.00$, that $q = 1$, or in other words, that the whole SC-effect proper is located in the outer segment. The cause of the SC-effect proper is however not

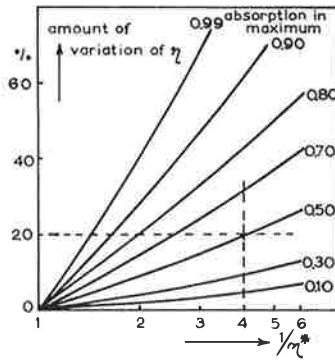


Fig. 12. Relation between the reciprocal of the efficiency factor η^* of the outer segment, and the amount of variation of η for several peak absorption percentages of the pigment.

located only in the outer segment, and this means that the absorption percentage in the peak has to be higher than 50%. Choosing the absorption very high, the minimum in the hue shift curve at 650 nm becomes more pronounced. The spread in the experimental points about this dip is too large to draw fargoing conclusions from it for a determination of the absorption percentage. No doubt however a percentage higher than 99 differs too much from the experimental points.

For the most probable value we suggest $D_{max.} = 1.60$ (abs. 80%), and accordingly $q = 0.5$ (see Fig. 12) and $\xi l = 2$.

As far as the measurements by Brindley (1953) on the change in colour mixture functions are concerned (§ 2a4), our theory has to be in agreement with them. In Fig. 5 the theoretical curves are given. These curves are obtained by narrowing of Pitt's curves in such a way that there is a quantitative agreement with experiment. Unfortunately no data of the variation in $1/\eta$ are available for the place of entry in the pupil used by Brindley. The agreement between theory and experiment is satisfactory. We corrected Pitt's curves according to the measurements by Brindley (1955b) for wavelengths longer than 700 nm in order to make the calculations in the very red end of the spectrum.

Finally we arrive below 500 nm in the blue end of the spectrum, where we have to consider the blue absorption curve. The data on the hue shift have to be considered with suspicion. Especially around 450 nm Pitt's red, green and blue curves intersect each

other in a rather complex way. We noticed that a marked increase in saturation goes together with the hue shift with increasing eccentricity. Another complication arises from the uncertainty of absorption in the ocular media, which is especially important on the short wave side of the spectrum. Be that as it may, we tried again with equations (7) and (8) to estimate ξl , q and D_m .

If we should assume that the peak absorption of the blue pigment is also 80%, and that also q and ξl are equal to those of the red and green systems, one does not get the hue shift as measured (see dotted theoretical curve in Fig. 4). This is however also not in accordance with the wavelength dependence of the SC-effect proper. We know from Fig. 2 that $1/\eta$ in the blue end of the spectrum is 5.00. Because the value of $1/\eta$ is determined by the values of $1/\eta_r$, $1/\eta_g$ and $1/\eta_b$ this means that $1/\eta_b$, the SC-effect proper of the blue receptors, must be greater than that of the other receptors. Stiles (1939) came also, using his two-colour threshold technique to the conclusion that the mean p-value (see equation (1)) of the blue cones is about 20 % higher than the mean value of the red and green cones. This means that either the leak factor in the outer segment, or the leak in the inner segment of the blue cones is greater than in the red and green cones. Calculations show, that a choice between these two possibilities cannot be made, because of the spread in the experimental results.

If we attribute the larger SC-effect of the blue receptors to a decrease in the inner segment factor, q_b must have the value 0.33. The theoretical curves in the Fig.'s 2, 4 and 5 are calculated with the following parameters: $D_{mr} = D_{mg} = D_{mb} = 1.60$ (abs. 80%); $q_r = q_g = 0.5$ and $q_b = 0.33$; and $\xi l_r = \xi l_g = \xi l_b = 2.00$. These curves are satisfactory in agreement with the experiment.

If we choose a low density of the pigment in the blue receptors, and thus no narrowing of the blue curve, q_b has to be chosen equal to 0.42. In this case the theoretical curve of the hue shift is also in fair agreement with experiment, so that no conclusions can be drawn from the experimental results about the density. Measurements about the colour mixture functions in the green-violet part of the spectrum have to be done to solve the questions about the density.

It is however very attractive to speculate on the possibility that the peak density of the blue pigment is as high as in the other systems. If one quantum suffices per receptor for a reaction in the

receptor (Bouman 1950), the effective area per cm^2 in the retina is for the green 9 times and for the red system 7 times as large as for the blue system. This is because of the ratios of about 9 and 7 between the peaks of the absorption curves of the green and red systems on the one hand and the blue on the other. If the effective area of all the individual receptors should be mutually equal it would mean that there are 16 times as many green and red receptors per cm^2 together as there are blue. Evidently it is easy to think in these terms because small field tritanopia fits in with this speculation. Moreover, the measurements by Brindley (1955a) and Blackwell and Blackwell (1960) show a low visual acuity if only the blue receptors are involved in the perception.

d. Discussion

We will consider again the fraction of 80 % absorbed by the photo pigment in the peak of the absorption curve. When the amount of photo pigment per cm^2 in the cones for a homogeneous spread out over the retina is comparable with the amount of rhodopsin in the dark adapted rods 10 to 20 % absorption is estimated by different authors. The agreement between Hecht's (1942) and Bouman's (1950) results of accurate measurements of absolute thresholds as a function of wavelength, and the absorption curves of rhodopsin for a diluted solution points to the fact that in the individual rods the maximum absorption does not exceed 30 %. Direct estimates of the active fraction of the light incident in the eye — also deduced from absolute threshold data (Bouman 1950) — result for rod vision at the maximum of the sensitivity curve in about 7 to 10 % and for the cones in about 1 %. From the light on the retina, fractions about twice as large are active because of the losses in the ocular media. In vivo in the individual cones the absorption according our theory is much larger. Also Rushton (1957) in his Teddington paper concluded that there is a much higher (about 7 times) absorption power of the receptors in vivo, as the comparable amount of visual pigment should have in solution.

As far as the smaller value of p_b of the blue receptors is concerned, we may think about the larger dimensions of the inner segment, according to the calculations by Toraldo di Francia (1949). If we have to attribute the larger SC-effect to the leak factor in the outer segment, we can think of a smaller difference in refraction index

between the cone and the surrounding tissue, caused by the existence of the "blue" pigment.

For the sake of completeness we again stress the fact that according to our theoretical analysis the minimum in $1/\eta$ in the middle of the spectrum is due to the narrowing of the absorption curves by the existence of the leak factor ξl . We suggested the peak absorption to be about 80 %. Under high brightness conditions the density is decreased by bleaching.

$1/\eta$ raises then in the yellow-green up to the value in the red end of the spectrum. At a brightness of 200 cd/ft^2 (pupil area 10 mm^2 , thus about 2×10^4 trolands) Stiles (1937) indeed found an increase of the directional effect in the middle of the spectrum.

In the description of the properties of the hue shift (§ 2a3) we mentioned a shift of the deep reds towards purple. This remains unexplained.

As a matter of great importance we have to emphasize the great concordance of different experimental data with our theory, which is based on Pitt's curves. In the first place this is reinforcement for the Young-Helmholtz hypothesis, as far as the receptor layer is concerned. Secondly it supports the validity of the fundamental curves as derived by Pitt (1944). Rather different curves, as will be seen in the next section, do not give such a good concordance.

5. Critical consideration of other hypotheses

a. *The use of other fundamental sensitivity curves and other densities*

Many authors have tried to find the shape of the fundamental curves. As far as a qualitative explanation along the lines of the previous sections has to be given, all curves with a Young-Helmholtz character can be used, except Hecht's (1932) curves. Quantitatively we have a crucial check for the red-green region by the wavelength of invariable hue. If we assume the peak densities to be equal, and the p-values for the several receptor systems involved also equal, these wavelengths of invariable hue can be calculated for the several fundamental curves proposed. These wavelengths are given in Table I. The curves derived by Brindley, Judd, Motokawa, Stiles en de Vries are in this respect not satisfying, the theoretical values lie rather far from the mean experimental value 560 nm.

Table I

Bouman (1950)	556 nm	Pitt (1944)	560 nm
Brindley (1953)	542	Stiles (1939)	552
Granit (1945)	564	De Vries (1948b)	550
Judd (1948a)	552	Walters (1942)	563
Motokawa et al (1955)	568	Wright (1946)	556

If the peak densities are not equal, the wavelength of invariable hue lies at an other place than indicated in the table. Unequal densities give however an asymmetrical curve around the wavelength of invariable hue. Choosing different p -values (see equation (1)) for the several systems involved can partly compensate this, but gives nevertheless less satisfactory results. Especially the dependence on wavelength of $1/\eta$ does in that case not correspond with the experimental data. The fundamental curves derived by Granit, Walters and Wright look much alike Pitt's, as far as the red and green curves are concerned. Our conclusion is that with still more reason we can confirm the opinion of Wright (1946) that Pitt's curves fit in most succesfully with the various data which are available.

With the absorption curves proposed by Hurvich and Jameson (1955) in the framework of their opponents colours theory (Hering theory) it turned out to be impossible to predict the experimental data. Therefore their theory, as far as the receptor layer is concerned, has to be rejected.

b. *Brindley's hypothesis*

As already mentioned, we followed the same line of thought as Brindley (1953). The procedure was however quite different, because 1. he used other fundamental curves, and well the curves derived by himself (Brindley 1953) and 2. he only tried to fit the experimental data to the change in colour mixture functions. Brindley came to the conclusion that the peak absorption of the red pigment must be about 90 % and that of the green one less than 20 %. In § 5a of this chapter we rejected already different densities in the several systems. When we calculate the hue shift using Brindley's own fundamental curves with his choice of densities, the theoretical curve is very different from the experimental one (Fig. 13).

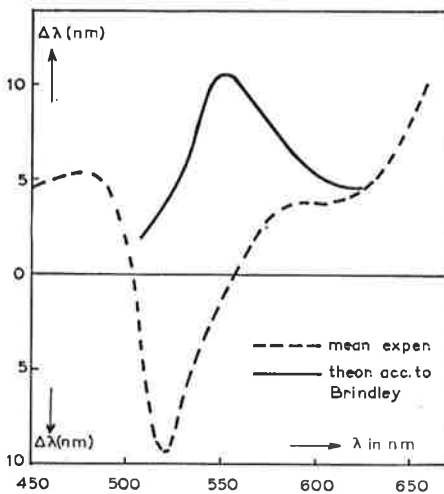


Fig. 13. The dotted curve is the mean experimental Stiles-Crawford hue shift. The solid curve gives the predicted one if Brindley's theory should be used.

Brindley is the first who followed and worked out Stiles' suggestion (§ 4b), and it is worthwhile to consider his line of thought with care. Other data were available, which led Brindley to the same conclusions regarding his fundamental curves. It is thus worthwhile and necessary to fit also these data in our explanation.

We will give at first point by point his arguments, and afterwards we will give our comment.

a. Brindley (1953) determined his red and green fundamental curves by bleaching with a combination of violet and red, and a combination of violet and blue-green light. The blue pigment is bleached away by the violet, while the red and green pigments are bleached away by the red and blue-green light respectively.

b. After adaptation as mentioned under a, one is during some ten seconds monochromat. Brindley concluded from this that therefore only one of the fundamental systems was present. This seemed thus to be a support for the validness of his determination of the fundamental curves.

c. Brindley observed that after very bright adaptation the Rayleigh-match changed. This was already observed by De Vries (1948a). This change is of the same kind as observed for oblique incident light (Ch. IA § 2). This is because of the same origin, the

decrease of density of the pigments. By bright adaptation the density decreases by decomposition of the visual pigment, while for oblique light the pathway through the pigment is shortened. Further it was observed that for each wavelength of the adapting field the same change in anomaloscope setting could be reached by an appropriate amount of bleaching light. Brindley determined these amounts of light as a function of wavelength, and measured thus the sensitivity curve for the same disturbing effect. This curve corresponds well with Brindley's red fundamental curve. This led to the conclusion that only the red system was the cause of the disturbance of the Rayleigh equation, and this agreed with the choice of a high density in the red and a low density in the green receptors.

Ad a. Brindley made, in our opinion, the error of thinking that it is possible to bleach one of the systems away. If at a certain wavelength the sensitivity of one of the systems is higher than that of the other, the sensitivity of the former will drop faster than that of the latter during adaptation with this wavelength. In our opinion, however, although the adaptation illuminance may be very high, the sensitivity of the former will never drop below that of the latter at this wavelength. In other words, the sensitivities of the systems involved will be equal at the wavelength used for adaptation, after the very high level of adaptation illuminance. Brindley used 658 nm as his adapting wavelength. According to Pitt's curves the ratio of the sensitivities of the unadapted red and green systems is 15 : 1 at 658 nm. If indeed the sensitivities of the systems will be equal at 658 nm after adaptation with very bright 658 nm-light, the red system is 15 times lower in sensitivity with respect to the green after adaptation, compared with before adaptation. Because the luminosity curve is the sum of the fundamental sensitivity curves, the luminosity curve following adaptation will be the green one + $1/15$ of the red one. In order to calculate the luminosity curve after strong chromatic adaptation we have also to take into account the narrowing of the absorption curves due to the decrease in density of the visual pigment caused by the decomposition of it. The correction of the curves by application of the narrowing of them is only a small one, but it should be incorrect to neglect its influence. Fortunately, data are available about the narrowing at the adaptation levels used by Brindley (1955). He measured the change in anomaloscope setting after adaptation to several high

illuminances. These changes are a direct measure of the narrowing which has to be applied. The calculated luminosity curve for adaptation at 658 nm is drawn in Fig. 14, indicated by R : G = 1 : 15. The agreement with experiment is satisfactory.

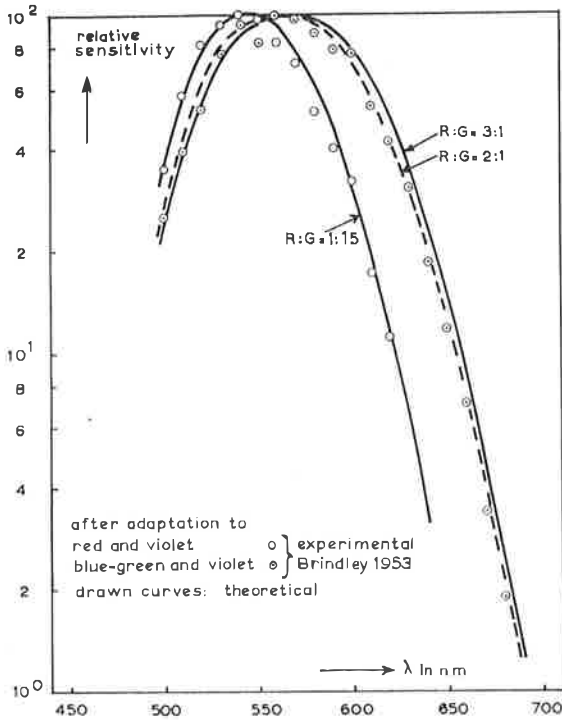


Fig. 14. The eye sensitivity curves after strong adaptation, compared with the theoretical predictions as described in the text, using Pitt's fundamental curves.

Brindley used for adaptation to blue-green light 497 nm. According to Pitt's curves the ratio of sensitivities of the red and green systems is 1 : 3. After adaptation the resulting luminosity curve will be the sum of the red and 1/3 of the green curve, this after correction for the narrowing. The theoretical curve is the solid one in Fig. 14, indicated by R : G = 3 : 1. This curve represents the case that at 497 nm the sensitivities of the red and green systems are equal following adaptation. A case, at which this stage of equal sensitivity is not yet reached is represented by the curve which is the sum of the red and 1/2 times of the green curve, indicated by R : G = 2 : 1 in Fig. 14. As a matter of fact the overall fit with

experiment should be better with a curve between $R : G = 3 : 1$ and $R : G = 2 : 1$. This may indicate that indeed nearly the stage of equal sensitivity of the red and green systems is reached at 497 nm following adaptation.

The correspondence between experimental and theoretical curves is a strong support for the validness of Pitt's curves, and in general for the Young-Helmholtz theory as far as the receptor layer is concerned. If we use the absorption curves of Hurvich and Jameson (1955) it is impossible to predict the experimental results. We mentioned already that it is impossible to explain the Stiles-Crawford effect with these curves. We find here a second reason to reject their proposed absorption curves.

Ad. b. The conclusion that during the state of monochromasy only one system is acting cannot be else than correct. But it is not necessary that this is one of the fundamental systems, it can and probably is a combination of all three. It is pointed out under Ad a. that at wavelengths longer than 500 nm anyhow two systems are involved in the state of monochromasy.

Ad c. If one calculates the change in the Rayleigh match with use of Pitt's curves, it turns out that it does not matter much in the outcome of the calculations, if only the red, or the red and the green curves together are narrowed. In the latter case the change is of course larger. This explains how it is possible that for all adapting wavelengths the change in the Rayleigh match is the same. Adaptation with red light narrows only the red curve, while with yellow and green light both red and green curves are narrowed. The sensitivity curve for equal disturbance of the Rayleigh match is therefore the red fundamental curve on the red side of the spectrum, and an intermingling of the red and green curves in the yellow-green region. This is just the experimental curve found by Brindley, which resembles his fundamental red curve.

Concluding we can say that all measurements by Brindley, mentioned in this chapter, fit with the theory we developed in the foregoing sections, and support Pitt's curves.

B. THE BEZOLD-BRÜCKE PHENOMENON

1. Introduction

The hues of most visual stimuli change with luminance. This fact, known as the Bezold-Brücke phenomenon, was first described by Von Bezold (1873) and Brücke (1878): at high luminance red and yellow-green spots are yellower, whilst those of blue-green and violet are bluer. Yellow, green and blue exhibit no hue change when luminance is increased. Purdy (1931), who made careful measurements about this topic, reviewed the existing literature up to his time. Several theories are put forward, but these turned out to be untenable. The most promising theory, which seems to be accepted for a long time, was developed by Peirce (1877), but was rejected by Purdy (1931). Peirce's theory was an explanation in terms of the Young-Helmholtz theory of colour vision. Purdy rejected this theory because he felt that it does not explain the wavelength of invariable hue in the blue, and is not in accordance with the law of additivity of brightness. Hering (1880) pointed out that his theory of colour vision with its antagonistic response pairs of red-green and yellow-blue is suited to give qualitative explanations of the BB-phenomenon. Judd (1948b) and Hurvich and Jameson (1955), using Hering's ideas, produced a quantitative picture, which Purdy's data closely duplicate. Boynton (1960) agrees with this picture in his theory of colour vision, but admits a discrepancy between theory and experiment in the green part of the spectrum. Judd (1948b) rejects an explanation in the framework of the Young-Helmholtz theory, because if it is correct, a reddish blue spot should change towards red, the reverse of the experimental result of Purdy (1931).

Is now really only the Hering-theory capable to explain the BB-phenomenon? Our point of view is that the answer is no, because with several reasonable additional assumptions Peirce's theory gives an even better approximation to the experimental results.

We will therefore revive Peirce's ideas, which are associated with the Young-Helmholtz theory, giving an extended quantitative picture of it, and refute the objections made by Purdy and Judd.

2. Experimental data

The circles in Fig. 15 give Purdy's (1931) experimental determination of the wavelength difference caused by increasing retinal illuminance from 100 to 1000 trolands. The invariable yellow, green and blue are at 570, 508 and 476 nm. Purdy (1937) did also some measurements of the amount of hue shift that occurs

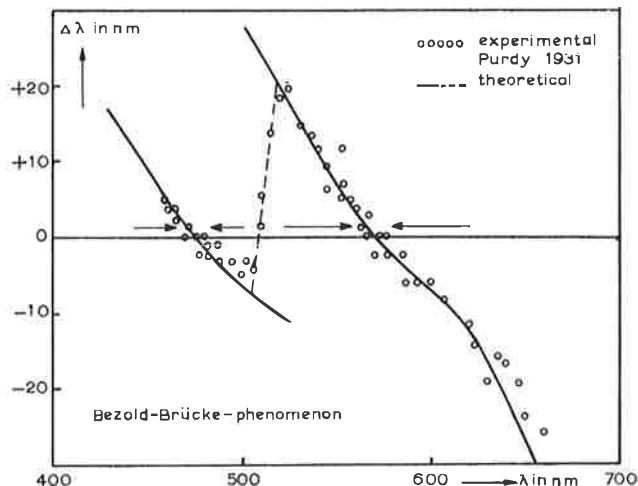


Fig. 15. The circles are Purdy's experimental determinations of the wavelength difference corresponding to the hue change caused by increasing retinal illuminance from 100 to 1000 trolands. The curves are theoretical. With arrows is indicated how the hue changes with increasing illuminance.

between various luminance levels (Fig. 16). The wavelength locations of the invariant hues are indicated by the three arrows in the upper part of the lowest figure.

As far as the purple region of the colour mixture diagram is concerned, Purdy (1931) reports that red purples shift towards violet, that violet purples shift also towards violet, and that there is one purple between the two, which give no hue shift at all. Because of this lack of quantitative data we did some measurements in the purple region (Walraven 1961).

We used mixtures of 415 and 650 nm. Because of the low transmission of the 415 nm interference filter it was only possible to

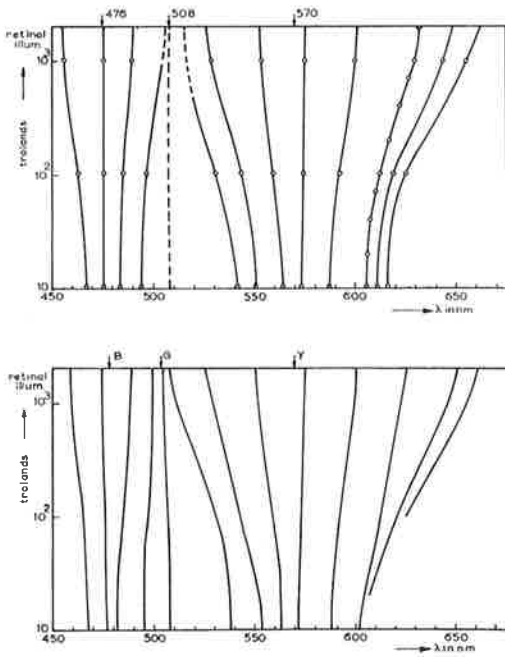


Fig. 16. Wavelengths having the same hue at different levels of retinal illuminance are indicated by the curves. The lower graph gives Purdy's experimental curves. The invariable hues are indicated by arrows. The upper graph gives the theoretical curves.

measure the hue shift between 10 and 100 trolands. A field size of 1° , fixated foveally, was chosen to avoid any influence by the rods. For plotting our results we employed the x_1, y_1 -diagram as developed by Judd (see Thomson and Wright 1953). This diagram makes use of recent luminosity data for the short wave portion of the spectrum. The lines in Fig. 17 connect the chromaticity points of 415 and 650 nm in the x_1, y_1 -diagram. The shifts measured experimentally are plotted vertically in the same scale, those towards red are plotted above the line, those towards violet below the line. Both observers H.J.L. and J.B. report essentially the same: the reddish purples shift towards violet, the violet purples shift towards red, and at a certain ratio of red and violet there is an invariable hue. These measurements are only partly in accordance with the measurements of Purdy.

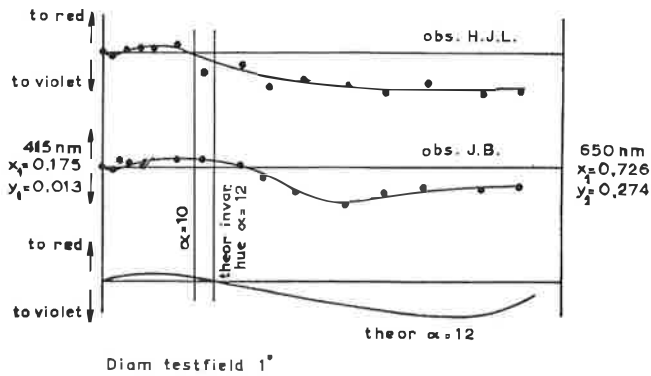


Fig. 17. Hue shift in the purple region of the colour mixture diagram. The horizontal lines connect the colour points of 415 nm and 650 nm in the x_1, y_1 diagram. The two upper graphs represent the shift measured by two subjects, upside towards red, downwards towards violet, plotted in the same scale, for increase in retinal illuminance from 10 to 100 trolands. The third graph represents the theoretical hue shift for $\alpha = 12$. For $\alpha = 10$ and $\alpha = 12$ the invariable hues are indicated.

3. Review of theories

a. Peirce's theory

Peirce (1877) pointed out that if there are three independent processes in the visual cone system, it is most likely that the responses are not linearly related to the intensity, but that the response of each of the systems increases relatively less at a high intensity level, thus according to a law of diminishing returns, such as the relation in Fig. 18. This means, if the response of the red system is larger than that of the green (e.g. orange), that with increasing intensity the response of the former does not increase relatively as much as that of the latter system. An essential idea in the theory is, that the colour impression is determined by the ratio of the responses of the three colour systems. According to the law of diminishing returns every ratio of responses not equal to 1, tends with increasing intensity to change towards 1. Orange changes thus towards yellow, if the latter is produced by equal stimulation of the red the green systems. At the wavelengths where the responses are equal, that is at the crossing points of the fundamental sensitivity curves, the hues are invariable: independent of illuminance.

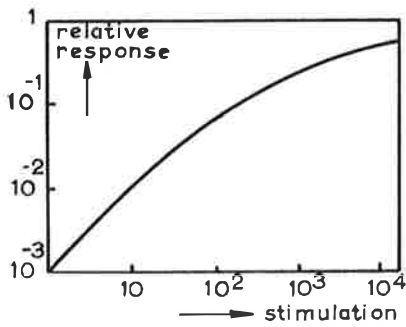


Fig. 18. Relation between stimulation and response, from which the theoretical curves of the Fig.'s 15, 16 and 17 are derived.

This theory assumes that for each system the quantitative relationship between stimulation and response is identical.

As already mentioned, Purdy rejected this theory for two reasons: (1) If the theory were correct, the mixture of two greens of equal luminance must be darker than the mixture of a red and a green both of the same equal luminance. This is contrary to the law of additivity of brightness. (2) An intersection point of the fundamental sensitivity curves does not lie at 476 nm, even though this was found to be an invariable hue. Purdy's argumentation on this point is not clear in his paper, but indeed, according to Pitt's curves, the intersection point lies at 445 nm. This is a large discrepancy.

For the sake of completeness we have to remember the theory by the Fjodorows (1935). They describe the BB-phenomenon by assuming that the colour impression is determined by $\log R/\log G$ and $\log G/\log B$, if R, G, and B represent the amounts of stimulation of the red, green and blue systems. This is in fact a non-linearity as suggested by Peirce. Their theory fails also in the violet.

4. Refinement of Peirce's theory, an explanation in the framework of the Young-Helmholtz theory

a. *The invariable hues*

According to Peirce's theory the invariable hues must be found at the intersection points of the fundamental sensitivity curves. Because of the favour of Pitt's curves, as pointed out in Ch. IA, we checked the intersection points of these curves. It turns out that

the invariable hue at 570 nm agrees very well with Pitt's curves, but that the invariable hue at 476 nm cannot be explained along the lines suggested by Peirce. We mentioned already that this was one of the objections of Purdy (1931) against Peirce's theory.

To overcome this difficulty we propose an extension of the Young-Helmholtz theory. In Y-H-theory the luminosity is thought of as the addition of the sensitivities of the three systems. The three fundamental sensitivity curves of Pitt do indeed give, if added to each other, the luminosity curve. As an extension of the Y-H-theory we propose to make a distinction between the brightness contribution of each of the three systems and their contribution to chromaticness. More precisely we think, according to Kremer (1953), that the contribution of the blue system to chromaticness is a times larger than its brightness contribution. In terms of hue experienced by an observer it would be better to speak about the violet system, but we are following the tradition of calling it a blue system. The factor a means that as far as colour phenomena are concerned, we use Pitt's curves, but with the height of the blue curve multiplied by a . This multiplication factor is determined by placing the crossing points of the blue and the "other" curve at 476 nm. When we speak about the "other" curve, we have in mind two possibilities (1) the green curve, and (2) the sum of the red and green curves (Fig. 19). The first possibility seems the most obvious one, the second, however, has to be considered too because of the colour discrimination data (see Ch. III). In case (1)

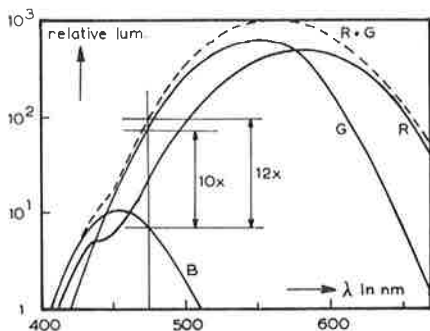


Fig. 19. Pitt's fundamental curves. The invariable hue at 570 nm is at the crossing point of the red and green curves. To get 476 nm at a crossing point, the blue curve has to be multiplied by 10 (crossing with green curve) or 12 (crossing with red + green curve).

the factor α is equal to 10, in case (2) equal to 12. The distinction between these two possibilities will be further under discussion in § 5 of this chapter.

The introduction of a multiplication factor for the blue system has already been done by Kremer (1953) and Walls (1955) for other reasons, but without giving a quantitative estimate of it. We will call α the chromaticness valence factor.

In the purple region of the colour mixture diagram the colour perception is governed by the interaction of the red and blue systems, because there the green system has a negligible sensitivity. If the introduction of the chromaticness valence factor has any value, the same α -value has to be chosen to explain the experimental facts along the purple line. The theoretical invariable red-violet ratios for $\alpha = 10$ and $\alpha = 12$ are indicated in Fig. 17. Indeed, for both α -values the agreement with experiment is satisfactory. The experimental data obviate the argument of Judd, mentioned in the introduction for rejecting the Young-Helmholtz theory.

It is difficult to predict exactly which will be the invariable hue in the green part of the spectrum. In our opinion the cause of the existence of an invariable hue here is that there is a tendency of the green hues to shift towards yellow, as well as towards blue. This means that there must exist an equilibrium wavelength, at which both tendencies are equal, and no hue change is visible. This offers an explanation that 508 nm is an invariable hue, because this wavelength is located in the sharp bend of the spectrum locus of the colour mixture diagram. The agreement of the theory with the experiment is therefore much better than that of the theoretical value 498 nm according to Hurvich and Jameson (1955). 10 nm may not be much in a wavelength scale, but it is a considerable colour difference. Boynton (1960) admits that no explanation of this discrepancy in the framework of the Hering-theory appears obvious at this time.

b. *Distinction between brightness and chromaticness information channels*

We mentioned in the introduction that Purdy rejected Peirce's theory because it is not in accordance with the law of additivity of brightness, Abney's law. The reasoning is, that if the theory were correct, the mixture of two greens of equal luminance must

appear darker than the mixture of a red and a green both of the same equal luminance. Although the validity of Abney's law is again under discussion in the literature, Sperling (1957) has shown that deviations in flicker photometry at 500 trolands never exceed 15 to 20%. According to the non-linear relationship between stimulation and response, as proposed by us in the next subsection (Fig. 18), the brightness of two greens together of each 250 trolands should be about 30 to 40 % lower than of a green and a red, each 250 trolands, together. Such a deviation is thus really in contradiction to Abney's law.

We meet this difficulty by assuming that the information about brightness is transmitted along a different channel than the information about the chromaticness. This means that the non-linear relationship between input and response, which causes the BB-shift, must exist in the chromaticness information channels. A similar transformation could be present equally in the brightness channel, and not affect the additivity of brightness. It is essential that the brightness signal be regarded not as the addition of the responses of the three colour systems, but as the additions of the inputs, and if not so (deviations of Abney's law), at least independent from the transformation in the chromaticness channels.

c. *Relation between stimulation and response*

The contributions to luminosity of the three colour receptor systems are $\int E_\lambda R_\lambda d\lambda$, $\int E_\lambda G_\lambda d\lambda$ and $\int E_\lambda B_\lambda d\lambda$, in which E_λ is the spectral distribution of the incident light in the eye, and R_λ , G_λ and B_λ the red, green and blue sensitivity curves respectively.

Under a. the chromaticness valence factor α was introduced to account for the invariable hue at 476 nm. At this point we can define the stimulation of the chromaticness channels for the red and green system as the inputs $\int E_\lambda R_\lambda d\lambda$ and $\int E_\lambda G_\lambda d\lambda$ and for the blue as the input times the chromaticness valence factor, namely $\alpha \int E_\lambda B_\lambda d\lambda$. If we consider in the green-violet region colour perception due to the interaction of the blue and the addition of the red and green systems, we think the stimulation as $\int E_\lambda (R_\lambda + G_\lambda) d\lambda$.

The relation between stimulation S and response R (Fig. 18) has been chosen so as to account for the experimental results as given in the Fig.'s 15 and 16. As mentioned earlier, it is assumed

that the relation between stimulation and response is identical for each of the three systems. It is an arbitrary choice, but as a start for a theory it seems appropriate to treat all chromaticness channels in the same way in order to keep the number of variables as low as possible. The correspondence of experiment with theory will be the justification of the assumptions made.

For the curve in Fig. 16 starting at 605 nm at 10 trolands a large number of values are calculated using Fig. 18, and are indicated in the graph. This calculation shows how well the typical shape of the curves in Fig. 16 are represented by the assumed relationship between stimulation and response. For the other curves only three points were calculated.

The theoretical curves in the neighbourhood of 508 nm are partly dotted, exact calculations were not made. This is caused by the fact that in this region of the spectrum a change in saturation accompanies the change in hue. In order to make calculations it is necessary to make an assumption about the place of the white point in the colour mixture diagram. To avoid an extra assumption we did not make exact calculations.

The shape of the left hand solid curves, describing the results in the green-violet part of the spectrum, is independent of the choice between the two possibilities for colour perception we considered in that region, namely the interaction of the blue with the green system, and the interaction of the blue with the red + green system, provided an appropriate value of α was picked in each case. This means α equal to 10 in the former case, and 12 in the latter. The choice of α was made so as to place the invariable hue at 476 nm, in accord with the experimental data of Purdy in 1931, which differ a little from his 1937 measurements as given in Fig. 16.

In the relation between stimulation and response the increase in response gradually drops off, asymptoting to an end value at very high levels of stimulation. A qualitatively similar relation to that given in Fig. 18 is the relation found in the lateral eye of *Limulus* between the input, illuminance on an ommatidium, and the output, frequency of nerve impulses in its optic nerve fiber. (Hartline 1940). A similar dependence between number of spikes and number of incident quanta has been assumed by Van der Velden (1944b) for the explanation of Weber's law in a quantum theory of brightness discrimination.

The theoretical hue shift as a function of wavelength for comparison of hues at 100 versus 1000 trolands is given as the solid curves in Fig. 15. The dotted curve represents the turnover of the tendency of the greens to shift towards yellow in the red-green region to the tendency of the greens to shift towards blue in the green-violet region, occurring at the sharp bend of the spectrum locus in the colour mixture diagram.

Using the relation shown in Fig. 18 theoretical curves are derived for the purple region. As already indicated in Fig. 17 the theoretical invariable hue is dependent upon the choice of α : 10 or 12 (see § 4a). The theoretical curves have their crossing points with the abscis at the invariable purple. As mentioned in § 4a the spread in the experimental determination of the invariable purple is too great to permit any choice between $\alpha = 10$ and $\alpha = 12$. To avoid complications in the graph only the theoretical curve derived with α taken as 12 is given in Fig. 17. The agreement with experiment is satisfactory.

d. *Conclusions*

The theory of Peirce (1877), in the framework of the Young-Helmholtz theory, is suitable to explain the facts of the Bezold-Brücke phenomenon, if there is taken into account

- (1) the large "chromaticness valence" of the blue system, and
- (2) the distinction between brightness- and chromaticness information channels.

5. **Discussion on the theories of colour vision; Young-Helmholtz, Hering or both?**

There are many arguments in favour of the distinction between a brightness information channel and a chromaticness information channel. Piéron (1939) was the first to emphasize this independence of brightness and chromaticness. He developed his tetrad theory to account for this independence. The theory states that a fourth cone exists, containing the three photochemical substances of the three known chromatic cones; this fourth cone then being the brightness cone. Walls (1955) raised objections to this theory, because he thought spatial resolution better than could be accounted for, if only about one of every four of the retinal cones could

contribute to brightness and could share in spatial vision. He assumes that there are three kinds of cones (in accordance with the Young-Helmholtz theory), but assumed that the signals from the cones were led separately to a brightness pool and to a colour centre. Walls was led to this idea especially to explain some of the facts related to colour blindness.

We will state some facts which impressed us as justifying the idea of separate channels for brightness and chromaticness.

a. The measurements by Piéron (1939), and earlier by Troland and Langford (1922) show that the luminosity curve changes only slightly after moderate chromatic adaptation. There is, however, an enormous difference in the colour impression of a coloured object seen before and after this adaptation. If chromatic adaptation can be described by a change in sensitivities of the three colour systems with respect to each other, one can calculate the influence on the luminosity curve from the observed colour changes. The underlying assumption is that the sum of the sensitivity curves of the three colour systems is the luminosity curve. No matter what sensitivity curves in Young-Helmholtz theory are chosen, if we exclude sets of curves for which the peaks are at nearly the same wavelengths, the experimental luminosity curve shows much less change than expected from the theoretical calculations. Therefore, it is necessary to assume two different adaptation mechanisms, one acting in the brightness channel, the other in the chromaticness channel.

b. If very strong chromatic adapting lights are used, one becomes monochromatic (Brindley 1953). The shape of the sensitivity curve after such an adaptation can be explained as suggested in Ch. IA § 5. In this theory the eye's sensitivity in that state of adaptation is not considered to be the sensitivity curve of one of the fundamental systems, but to be a combination of them. That, notwithstanding this, there is a state of monochromacy can easily be explained by the distinction between brightness and chromaticness channels. The chromaticness channel is fatigued, so that no information can be transmitted, while the brightness signal is still the sum of the signals from the red, green and blue receptors.

c. Svaetichin and MacNichol (1958) found laws governing chromatic adaptation in electrophysiological work in fish retina, analogous to those described under a. Using a micropipette electrode technique they could divide the electrical responses in the

retina to illumination into luminosity and chromaticity responses. Adaptation to spectral light changed the chromaticity, but not the luminosity responses. They concluded that the fishes studied have a luminosity mechanism which is separated from a chromaticity mechanism.

d. The measurements by Fincham (1953) showed that in cone-monochromatism the retina is probably intact. Although colour perception fails, the chromatic aberration reflex for the accommodation is as good as in normal colour vision. The accommodation information has thus been gathered in the retina, can be used for the accommodation reflex, but not for the perception. Because the brightness channel is quite intact, this is only possible if chromaticness and brightness are transmitted along different channels.

e. We mention here Hurvich and Jameson (1960) who gave a comment on Weale's (1953) remark, that the fact that the luminosity curve in cone-monochromates is substantially like that of normal, is hardly compatible with trichromatic theory, which postulates that the spectral sensitivity is the sum of the three colour mediating mechanisms. They write "It is, in fact, a further bit of evidence for a separate luminosity mechanism that is independent of the color mediating responses".

f. In the explanation of the BB-phenomenon this distinction was necessary (Ch. IB § 4).

In view of the previous arguments the distinction between brightness- and chromaticness information channels seems necessary. But is it necessary to assume a fourth receptor to account for this distinction, as proposed by Piéron (1939)? The close connection between the wavelength dependence of the Stiles-Crawford effect and the hue shift associated with it, points to the idea that the brightness- and the chromaticness information are obtained from the same receptors. This corresponds with the ideas of Walls (1955). That we are inclined to believe that Pitt's (1944) curves are a close approximation of the spectral sensitivity curves of these three kinds of receptors, is obvious from our treatment of the Stiles-Crawford effect and the Bezold-Brücke phenomenon.

Nevertheless in the attack on the Young-Helmholtz theory and the defense of the Hering principle by Hurvich (1960) on the Paris Symposium a substratum of truth of their reasoning hardly

can be denied. They put forward the following arguments. How f.i. can the Y-H-theory explain that the red and green hues in the spectrum predominate at low stimulus levels, and the yellow and blue components increase concomitantly as the spectrum is increased in luminance? Why, as stimulus size is greatly decreased, does discrimination between yellow and blue hues become progressively worse than that between red and green? Why do the hues drop out in pairs in instances of congenital colour defect, or when the visual system is impaired by disease? Moreover, since the sensation of white is granted no special physiological process in this parsimonious theory, but occurs as the fusion product of three equally large fundamental hue sensations, how account for the large degree of independence of white and chromatic qualities when the adaptation of the visual system is varied?

Moreover, the studies of DeValois (1960) show the existence of antagonistic red-green responses in the lateral geniculate body of the monkey.

To account for all the properties of the visual system mentioned, we propose the following concept: Fig. 20.

The retina is built up by red (R), green (G) and blue (B) cones in the ratio 7 : 9 : 1 (see Ch. IA § 4c). The absorption curves of the visual pigments are Pitt's curves, corrected for the absorption in the ocular media. The brightness signal is the sum of the brightness contributions of each of the cone systems. The brightness signal L is transmitted through channel c , the addition takes place before the transmittance through this channel. The chromaticness information is transmitted through the channels b . The information from the red and green cones goes to a red-green centre, from which the R,G-signal is transmitted to higher centres.

In the same way as the brightness is the sum of the brightness contributions of each of the cones, we think the yellow-signal as the addition of the red and green signals: $R + G$. The chromaticness contribution of the blue cone system is thought as its brightness contribution times the chromaticness valence factor a . The yellow and blue signals are led to the yellow-blue centre, from which the Y,B-information is transmitted to the higher centres.

The separation between brightness, yellow-blue and red-green channels is according to Hering's principle, while the receptor layer with its red, green and blue receptors is built up according to the principles of the Young-Helmholtz theory.

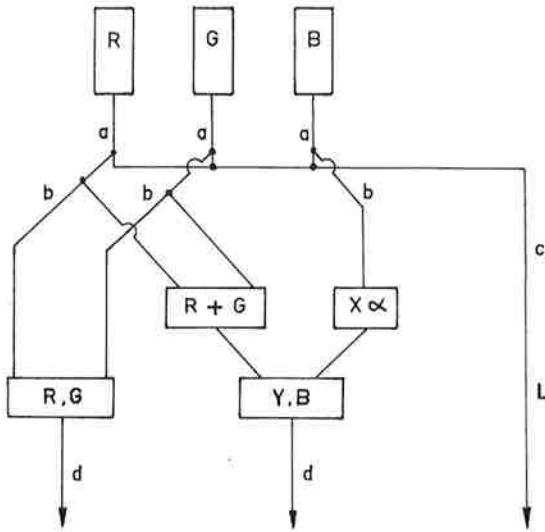


Fig. 20. Schema of the zone theory as explained in the text.

We have here to do with a zone-theory, like already proposed by Donders (1881), Von Kries (1929) and Muller (1930). Recently Müller-Limroth (1959) has pointed out, that the studies of the electroretinogram support the zone theory. It must be emphasized that no proposal is given by us about the nature of the antagonistic signal. This can be the ratio, the subtraction or something else of the original chromatic signals coming from the cones.

The choice of $R + G$ as the Yellow-signal is especially made, because, as will be pointed out in Ch. III, the properties of colour discrimination along the tritanopic confusion lines in the normal colour mixture diagram are the same for normals if colour perception along these lines is considered as the interaction of the $R + G$ -system and the blue system. As far as the determination of α from the experiments on the BB-phenomenon is concerned, it is possible that the non-linear relationship between stimulation and response has to be applied either on the total $R + G$ -signal, or on the separate R- and G-signals before the addition. In the former case $\alpha = 12$, in the latter 10. The uncertainty of the measurements in the purple region does not permit making a decision between these two possibilities.

It has to be emphasized, that the multiplication factor in the b-channel of the blue system is meant only to be a description of the large chromaticness valence of this blue system. It is, in general, not intended that the concept proposed is a description of actual nervous pathways. It only describes the properties of the visual system, in what we consider the simplest possible manner. It is obvious that the question of how this concept can be realised in actual nervous pathways is an interesting one.

CHAPTER II

COLOUR RECOGNITION

1. Introduction

Repeated weak flashes of light from a constant light source are variously seen and not seen. This is partly due to the statistical fluctuations of the number of quanta incident on the retina. Recently Bouman (1960a) gave a review of the development of quantum-statistical theories for visual functions, in which the influence of these fluctuations on the perception is described. Is this influence also apparent in colour perception?

It was found that repeated flashes frequently lead to contradictory indications of the same wavelength. For instance, a 550 nm flash, of which the intensity is a little above threshold, was sometimes called greenish, sometimes white or even reddish. The observer sometimes reported a highly saturated red appearance when "green wavelengths" were presented.

The variability in colour recognition near the threshold is well and already long known (Holmgren 1889, Hartridge 1947, Bouman and ten Doeschate, see Bouman 1950, Walraven and Leebeek 1960).

In view of the possibility to explain variability in the perception at the absolute threshold in the framework of a quantum-statistical theory, it is obvious to think also in these terms when variability in colour perception is involved. The statistical variations in the excitation of different colour mediating mechanisms with overlapping spectral sensitivity curves and the resulting statistical fluctuations in the ratio of excitation of these systems, might make this variability in colour perception understandable.

Colour recognition is highly dependent upon a great number of parameters, such as the spectral composition, the brightness, the angle subtended and the exposure time of the test stimulus, the location on the retina, preceding illumination of the eye, point of passage through the pupil and still other factors.

Our investigation however will be limited to the variation of some crucial parameters relative to the quantum-statistical theories mentioned. These are, because of reasons shown in subsection 2, the intensity, diameter and exposure time of a test stimulus of different wavelengths in darkness for the dark adapted fovea (Walraven 1959b).

It is considered as a basic point in our treatment that at very low illumination a very restricted number of quanta are sufficient for the achievement of perception. Van der Velden (1944a, 1946) has shown that for rod vision two quanta, if absorbed within a certain time, and within a certain area, are sufficient for perception. Bouman and Van der Velden (1948) have shown that this is also valid for cone vision. It might be worthwhile to mention that this conclusion does not mean the equality of the sensitivities of rods and cones. It only says that the number of effective absorbed quanta by the visual pigments is two at the threshold for both receptor systems.

If different numbers of quanta and different distributions of these over the retinal receptors are reflected as colours which can be perceived as different, any instability in colour recognition due to statistical fluctuations in the stream of quanta, will be in particular apparent in experiments near the threshold of vision, where the number of quanta involved is low.

In any experiment the desired goal is some predictability regarding the outcome of future experiments. In this study we hope to determine the predictability of the achievement of colour by observers using certain definite aspects of colour for flashes of various monochromatic lights: whether the perceived colour was reddish, yellowish, greenish, bluish, violet, white, colourless or absent. The term colourless is a description of an appearance of light, to which only the qualification of light can be applied, without any more specification.

We hope to determine the conditions in terms of numbers and distributions of quanta in the retinal receptor systems for the achievement of the defined colour perceptions as reddish, yellowish etc. Such combinations may be of the following patterns:

1. The stimulation of a particular receptor system by a certain number of quanta, with a minimum of two.
2. The combined stimulation of particular receptor systems by certain numbers of quanta, each number of each system being at

least one. The choice of these numbers is based on the two-quanta explanation of the visual threshold by van der Velden and Bouman as mentioned earlier.

In this chapter we will respectively discuss the methods used for the determination of numbers of quanta necessary for a certain perception, and the mathematics of these methods in order to apply this on colour perception. The experimental arrangement, the experimental results and the conclusions are given afterwards.

2. Methods used for the determination of the number of quanta necessary for a perception.

Following Van der Velden (1944a) we will define the threshold as the energy necessary for obtaining 60 % chance of perception. The threshold is up to a diameter of 3' in the fovea independent of the diameter (Ricco's law 1877) and up to 0.1 sec independent of the exposure time (Bloch's law 1885), according to the measurements by Bouman (1950).

We will call the area in which Ricco's law is valid Ricco-area, while the time to which Bloch's law applies is called Bloch-time. More quanta are needed to reach the threshold for large areas and long exposure times, the number gradually increasing with diameter from the mentioned integration area and integration time. Van der Velden assumed (1944a) that the threshold for a test stimulus of large diameter is reached whenever the threshold for an area as large as Ricco-area inside the stimulated area is attained. The number of quanta needed within an area as large as Ricco-area can be determined from the dependence of the threshold upon the area.

If this number of quanta k is equal to 1, the threshold energy is independent of the diameter, due to the simple fact that the chance of one quantum falling into an arbitrary region inside the area is as great as falling into the total area. If the number of quanta is larger than 1, the threshold is dependent upon the area, which is mathematically demonstrated in the following way (a more extensive derivation of the formulas can be found in Bouman and Van der Velden 1948):

Starting with the Poisson distribution of the incident light quanta,

demonstrated experimentally by Baumgardt (1957), the chance of perception $P(\bar{N}, k)$ as a function of the average number of quanta \bar{N} and k is given by

$$P(\bar{N}, k) = 1 - \sum_0^{k-1} \frac{(\bar{N})^s}{s!} e^{-\bar{N}} \quad (1)$$

The chance of no perception is thus

$$\sum_0^{k-1} \frac{(\bar{N})^s}{s!} e^{-\bar{N}}$$

If the area has a diameter d , and δ is the diameter of the Ricco-area, the average number of quanta falling into one Ricco-area is therefore $\bar{N}\delta^2/d^2$. The chance of no effective hit of quanta in a given Ricco-area is thus

$$\sum_0^{k-1} \frac{(\bar{N}\delta^2/d^2)^s}{s!} e^{-\bar{N}\delta^2/d^2}$$

and the chance of no effective hit in any area as large as Ricco-area, which is, as a matter of fact, equal to 1 minus the chance of perception, as a function of diameter $P(\bar{N}, d)$ is thus

$$1 - P(\bar{N}, d) = \left\{ \sum_0^{k-1} \frac{(\bar{N}\delta^2/d^2)^s}{s!} e^{-\bar{N}\delta^2/d^2} \right\}^{d^2/\delta^2} \quad (2)$$

Substituting x for $\bar{N}\delta^2/d^2$ and extending the exponential function into a series, we arrive at

$$1 - P(\bar{N}, d) = \left\{ \left(1 - \frac{x}{1!} + \frac{x^2}{2!} - \frac{x^3}{3!} + \dots \right) \left(1 + \frac{x}{1!} + \frac{x^2}{2!} + \dots + \frac{x^{k-1}}{(k-1)!} \right) \right\}^{d^2/\delta^2}$$

and (3)

$$1 - P(\bar{N}, d) = \left\{ 1 - \frac{x^k}{k!} + \frac{k}{(k+1)!} x^{k+1} - \frac{k(k+1)}{(k+2)! 2!} x^{k+2} + \dots \right\}^{d^2/\delta^2} \quad (4)$$

The next approximation can be used for values of $x \ll 1$:

$$1 - P(\bar{N}, d) = \left\{ e^{-\frac{x^k}{k!}} \right\}^{d^2/\delta^2} = e^{-\frac{(\bar{N})^k}{k!} \left(\frac{\delta^2}{d^2} \right)^{k-1}} \quad (5)$$

Recalling equation (2) we see, that the chance of an effective hit in an arbitrary Ricco-area, or according to the theory, the chance of seeing, P , is given by

$$P(\bar{N}, d) = 1 - e^{-\frac{(\bar{N})^k}{k} \left(\frac{\delta^2}{d^2} \right)^{k-1}} \quad (6)$$

A constant value of P for all values of d is attained when

$$\bar{N} \propto d^{2(k-1)/k} \quad (7)$$

This relation is for $k = 2$

$$\bar{N} \propto d \quad (d > \delta) \quad (8)$$

This relation has been found experimentally and is well known as Piper's law (Piper 1903). Van der Velden therefore deduced (1944a) that 2 quanta have to be absorbed within the distance δ to get a light perception. This conclusion referred only to rod vision, but Bouman and Van der Velden (1948) have shown that the same threshold conditions apply for cone vision.

The derivation of the equation relating threshold and exposure time is identical with the treatment relating threshold with area, if we replace d^2 by t and δ^2 by τ , in which t and τ are respectively the exposure time and the Bloch-time. This replacement leads to

$$\bar{N} \propto t^{k-1/k} \quad (9)$$

This relation is for $k = 2$

$$\bar{N} \propto t^{\frac{1}{2}} \quad (t > \tau) \quad (10)$$

This relation is also found experimentally and is known as Piéron's quadratic law (Piéron 1920). From this fact Van der Velden (1944) deduced that 2 quanta have to be absorbed within the time τ to get a light perception.

In order to refer to a more full account of the two-quanta explanation we mention Bouman and Van der Velden (1948) and Bouman (1950). The two-quanta explanation was still more supported by experiments with variation of other parameters. The absolute threshold conditions for line-shaped targets and moving point sources agreed with the two-quanta explanation (Bouman and Van den Brink 1953, Bouman 1953, Bouman 1955, and Van den Brink 1957).

The methods described in this section have been used for the determination of the numbers of quanta needed for colour perception. The determination by using the slope of the frequency of seeing curve, as proposed by Hecht (1942) and Van der Velden (1944a), is not used because Bouman (1960) pointed out that this method is not reliable.

3. Colournaming of monochromatic lights

a. *Experimental procedure and arrangement*

A tungsten filament lamp A is focused on the entrance slit of a monochromator containing a prism of constant deviation P_r (Fig. 21, in which, in order to save space, the filament is drawn close to the exit slit). The exit slit S_e is focused on the artificial pupil P_a , 2 mm in diameter, by the lens L . The flash time t is regulated through a sector opening of a rotating disc driven by a synchronous motor. Every three seconds a test flash was presented to the observer. Variations of the diafragma D , expressed in visual angle, covered a range from 1 to 50 min. of arc, while t was varied

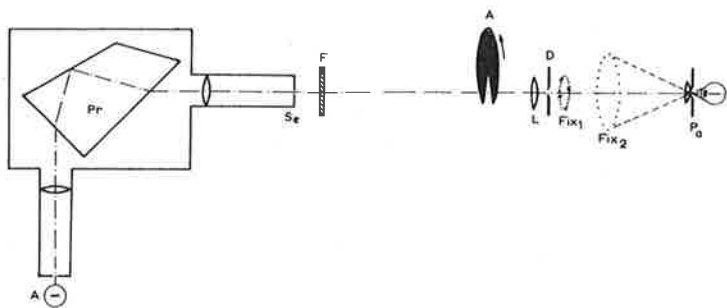


Fig. 21. Experimental arrangement as described in the text.

between 0.01 and 1.5 seconds. The intensity of the flash was changed by adjusting the current of the calibrated source A. In the range below 440 nm the filament lamp produced too little energy to allow measurements. In this case a Hg-spectral lamp was used. The intensity was regulated with a wedge.

Measurements were made in the fovea of the dark adapted eye of a normal trichromat (P.L.W.). Foveal fixation was maintained with the aid of four small lights, having the lowest intensity possible to be useful (Fix_1). The lights were situated at the corners of a square, measuring one degree of arc in diameter. The test flashes were presented in the center of the square. A comfortable chinrest and additional aids for the fixation of the head were used. In order to make allowance for the Stiles-Crawford effect, precautions were taken so that the light beam passed through the central area of the pupil. To accomplish this, a large ring of small lights Fix_2 was placed between the artificial pupil and the lens L, concentric with the optical axis, the eye being properly placed when the ring was just invisible. With improper alignment, light from some part of the ring falls on the retina. Hence the observer can correct his position.

At each particular combination of wavelength, intensity, flash time and visual angle 30 repetitions were made. Chromatic aberration of the eye was corrected for by a lens kindly made available by Van Heel (1946). In the red and blue ends of the spectrum, interference filters were added behind the exit slit in order to eliminate chromatic stray light.

b. *Results obtained with flashes of small visual angle and short duration*

The total chance P to perceive light within the range from 400 through 700 nm, and the chance p to perceive colour, subdivided into the chances of distinguishing a particular colour p_{red} , p_{green} etc., were determined as a function of the brightness of the flash. Our data pertaining the 530—700 nm region of the spectrum (Bouman and Walraven 1957a) are recently confirmed by Marriott (1959). They are given below together with the new data of the 400—530 nm region of the spectrum (Walraven 1960).

The diameter of the circular test stimulus was 2 minutes of arc, flash time 0.05 seconds, thus both were inside the limits of the

Ricco-area and the Bloch-time respectively. The results for some characteristic wavelengths are presented in Fig. 22, where brightness is plotted on a relative logarithmic scale. These graphs tell their own story. The important features of the data can be summarized as follows.

1. The existence of an achromatic zone is apparent at all wavelengths, even in the extreme red and violet. The ratio in brightness of the P- and p-curves is 1.30 at the ends of the spectrum, while it is 1.50 in its center.

2. The observer made a clear distinction between colourless and white. This differentiation is supported by a report of Arndt and Voit (1957), who also mention a colourless region.

3. In Fig. 23a the chances on a number of colours at the colour threshold are given, the maximum chance on colour being 60%, as a function of wavelength. The same is given at 4x absolute threshold in Fig. 23b. Starting at the red end of the spectrum the percentage of red decreases, reaching zero at 500 nm, and then increases again below 430 nm. The percentage of green reaches its maximum at 510 nm. Blue is only present below 490 nm and violet below 460 nm. The white sensations between 570 and 590 nm are in part replaced by yellow at higher intensities.

4. The shape and relative positions of the P- and p-curves show that colourless sensations occur most frequently — up to 50 % — when the total chance of seeing is 80 %.

c. *Results obtained with flashes of large visual angle and of long duration*

The absolute and the colour thresholds were measured as a function of diameter and time at a series of wavelengths. Some special cases are given in Fig. 24. It is apparent from these data that the achromatic zone, which is the region between the absolute threshold and the colour threshold curves, is independent of the size of the test stimulus at both ends of the spectrum. This zone increases with diameter, however, at wavelengths in the middle of the spectrum. Here the colour threshold is proportional to $d^{4/3}$ in a limited range of diameter values. The lower limit is the diameter of the Ricco-area, the upper limit is one dependent upon wavelength. Beyond the upper limit value the colour threshold curve

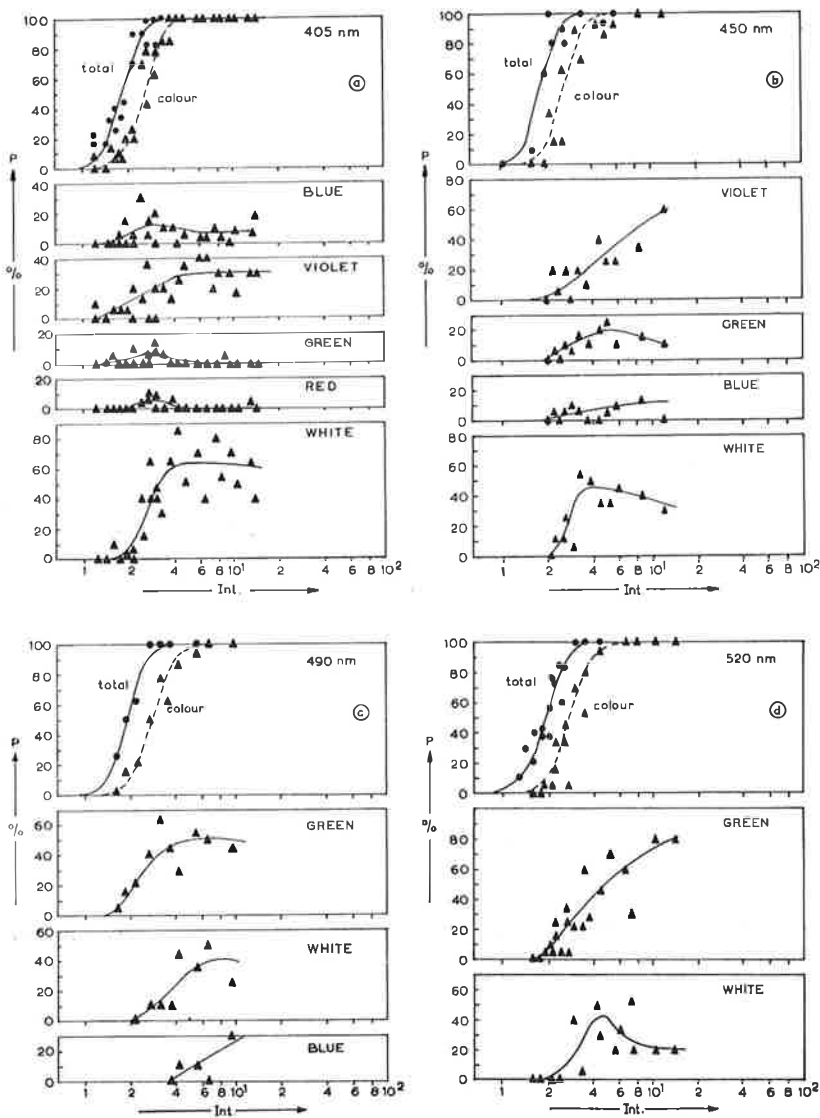
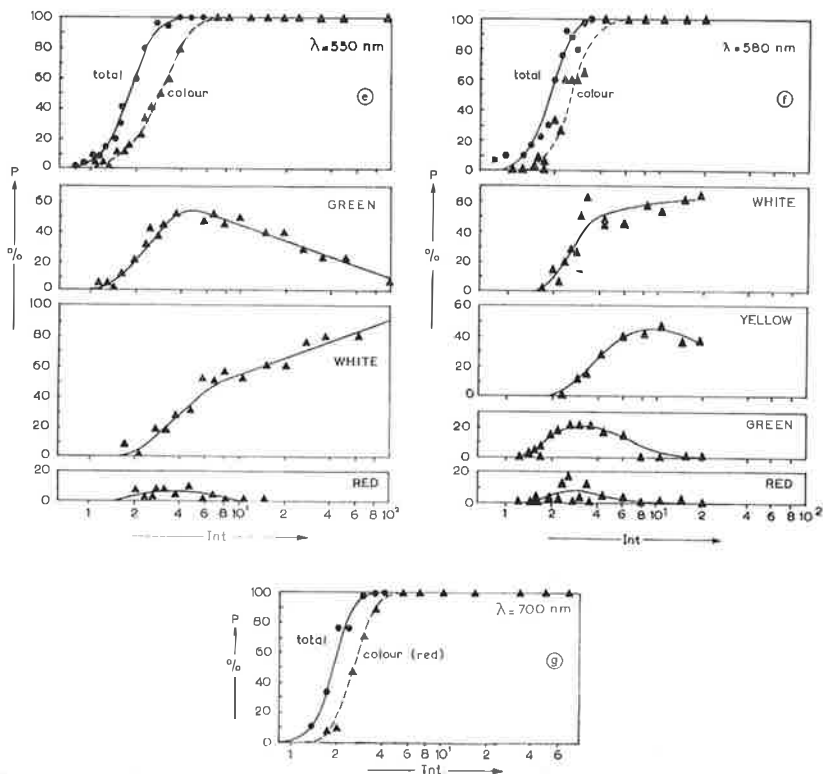


Fig. 22a, b, c, d, e, f, g. Frequency of seeing curves as a function of intensity at the indicated wavelengths, for flashes of small visual angle ($3'$) and short duration (0.05 sec.). The upper graph represents the frequency of seeing at all (total) and the frequency of seeing colour at all (colour). The other graphs represent the frequencies of seeing of the particular colours as indicated.



is again parallel with the absolute threshold curve. The size of the achromatic zone at which both threshold curves are parallel, is plotted as a function of wavelength in Fig. 25. This graph shows that the achromatic zone at large diameters is maximal at 570 nm and at 478 nm.

We measured the threshold energy as a function of exposure time only at 550 nm (Fig. 24). Measurements at other wavelengths were not performed because of the extreme difficulty to maintain alertness for a coloured appearance during a flash lasting one second or longer with constant fixation. The graph shows, however, an analogous dependence of threshold upon exposure time as that upon diameter, provided δ^2 is replaced by t . It has to be expected therefore that in the red end of the spectrum the achromatic zone is small even with long exposure times. Arndt and Voit (1957) did indeed find a much larger achromatic zone in the green than in the red.

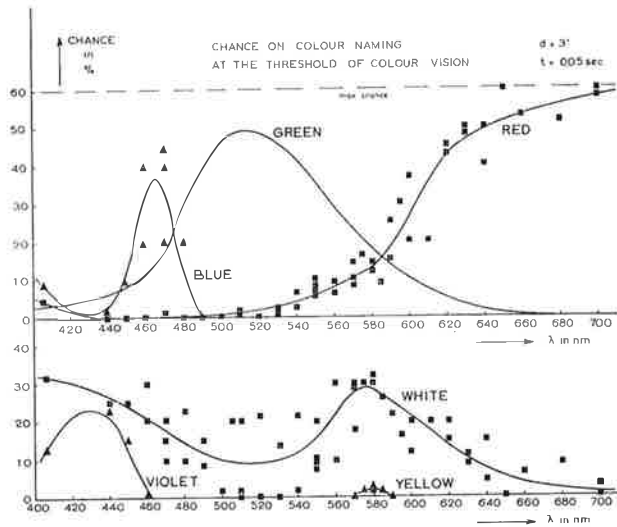


Fig. 23a. The frequencies of seeing particular colours as indicated, at the threshold of colour, as a function of wavelength.

The absolute threshold curves measured at 700 nm and 550 nm agree with the earlier results of Bouman and Van der Velden (1947). This means that the same conclusion can be drawn from these data: two quanta incident within the Ricco-area and within the Bloch-time are needed for perception.

The absolute threshold curve in the violet end (Fig. 24, 405 nm) shows some irregularity. This can be explained by inhomogeneity in sensitivity of the fovea at that wavelength. Threshold measurements for point sources show that the sensitivity at 405 nm at 30' extra foveal is about 20 % higher than in the very centre of the fovea. This is in accordance with measurements by Wright (1949) and Sperling and Yun Hsia (1957). Correction for this inhomogeneity smoothes out the irregularity in the threshold curve. It can thus be taken for granted that for the observer (P.L.W.) the two quanta behaviour holds all through the spectrum. We therefore measured at the other wavelengths only the size of the achromatic zone, and plotted the colour threshold curves by adding the achromatic zone to the absolute threshold curves, which were taken according to the ideal shape of Ricco's and Piper's laws.

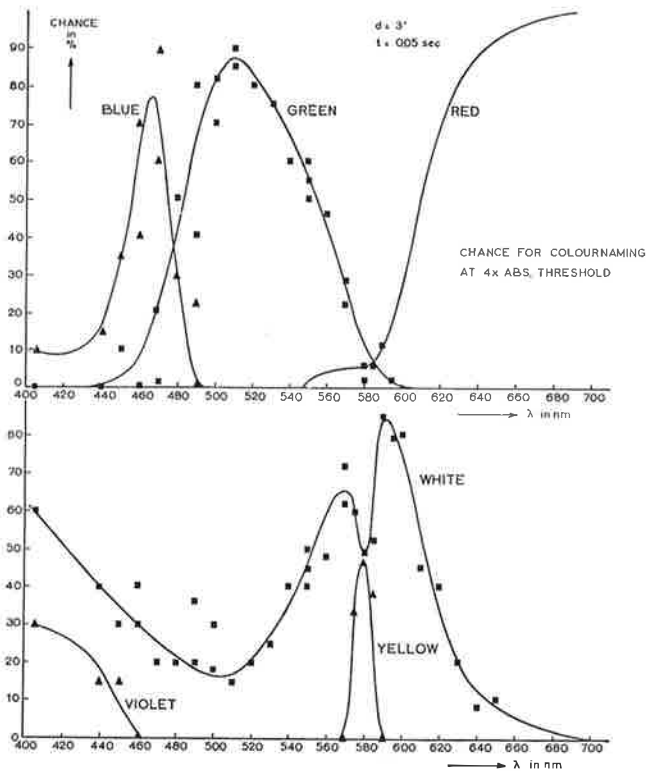


Fig. 23b. The frequencies of seeing particular colours as indicated at 4 x absolute threshold, as a function of wavelength.

As far as the colour naming of flashes of large visual angle is concerned, the results can be summarized as follows:

1. The 700 nm-flashes are either colourless or red,
2. The 405 nm-flashes are either colourless or violet at the largest diameters used (50'),
3. In the middle of the spectrum the amount of variation in colour-naming decreases with increasing diameter. E.g. the number of answers "green" decreases with increasing diameter at 590 nm (compare Fig. 23 with Fig. 26).

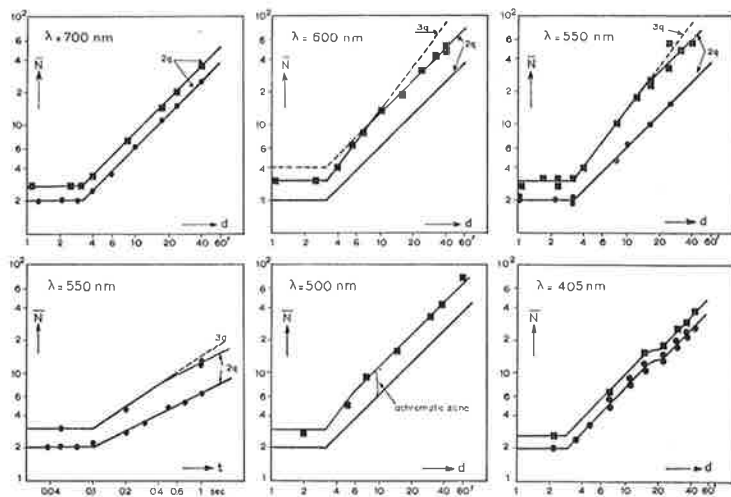


Fig. 24. Threshold as a function of diameter (d) and exposure time (t) of the test flash at the wavelengths as indicated. The lower curves represent absolute threshold, the upper curves colour threshold. The curves corresponding to a two-quanta mechanism are indicated by $2q$, those corresponding to a three-quanta mechanism by $3q$.

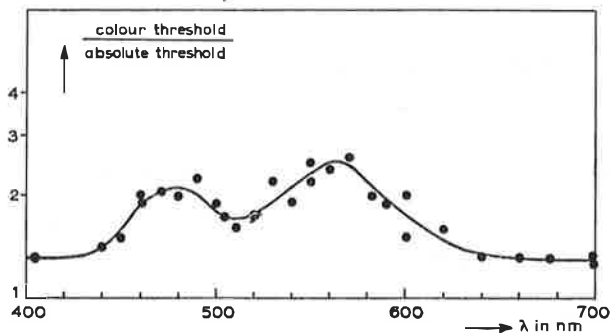


Fig. 25. The ratio of the colour and the absolute threshold at large diameter ($60'$) as a function of wavelength.

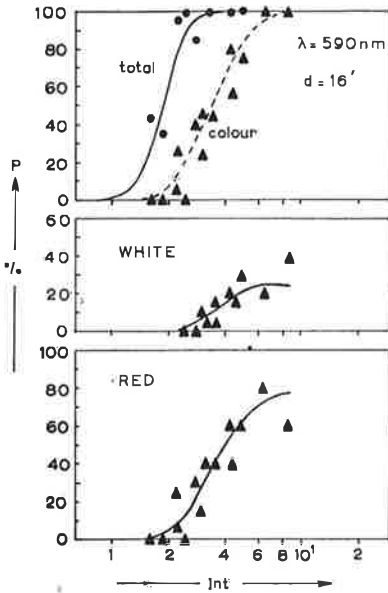


Fig. 26. Legend as Fig. 22, however at a diameter of 16'.

4. Interpretation

a. *The two quanta explanation of the colour threshold in the long wave and short wave portions of the spectrum.*

1. The red portion of the spectrum

The slope of the curve relating colour threshold and diameter is the same as the analogous relation of the absolute threshold. The conclusion is that two quanta have to be absorbed within the integration area and within the integration time in order to perceive colour (red). At the absolute threshold also two quanta are needed. This leaves two possibilities:

- (1) Two receptor systems are involved, stimulation of one receptor system with both quanta results in a colourless sensation; stimulation of the second one in a coloured appearance. The two receptor systems may have either the same or different sensitivity curves.
- (2) One receptor system is involved, excitation of which sometimes results in a coloured appearance, and sometimes not.

The existence of different sensitivity curves as mentioned under (1) seems improbable because this should introduce a fourth independent receptor system, which is contrary to the rules for colour mixture as expressed in the Young-Helmholtz theory.

In a previous study (Bouman and Walraven 1957a) it was stated that possibility (2) seems less probable because of the all or none law of nervous excitation. If we assume, however, different channels for chromaticness and brightness information (Ch. IB § 5), we cannot exclude this possibility.

2. The violet portion of the spectrum

The dependence of the colour threshold upon diameter is the same in the violet region as that found in the red region. This means that we have to draw the same conclusions as in the red region about the numbers of quanta needed for colourless and colour sensations.

We mentioned in the description of the results the difference between the appearance of flashes of large size and that of flashes of small size. In the former case the appearance was always violet, provided it was coloured, in the latter case there exists a large variation in naming possibilities (Fig. 22, 405 nm). In the red portion of the spectrum this difference between large and small size does not occur.

At 405 nm the sensitivity of the blue system is about equal the sum of the sensitivities of the red and green systems. The large variety in naming of light of this wavelength seems therefore not surprising, and can in a sense be compared with the large variety at 575 nm, where the sensitivities of the red and green systems are equal. Violet answers, however, always are given at large diameters, which can be compared with the long wave end of the spectrum, where only the answers "red" are given.

Apparently the blue system dominates now the other so far as colour is concerned. This is quite in accordance with the idea that the contribution of the blue system to chromaticness is much larger than its contribution to brightness. But what then about the small diameters, where a large variety in naming exists? This easily can be answered by considering that, where only a few quanta are involved, the chance is large, that the blue cones are not hit at all, and therefore in that case the large chromaticness valence

cannot play any role. Whether this answer is sufficient or that it is also necessary to hypothesize, that the large chromaticness valence of the blue system is dependent upon the number of blue cones stimulated, is difficult to analyse from the data. An illustration of the fact that conclusions of this kind are difficult, is that the number of violet answers does not increase with increasing intensity in the range measured for small areas, although the number of quanta involved is then also large (Fig. 22g). We have to keep in mind, however, that the subjective brightness of flashes of small area, if the same number of quanta is involved is higher than for large areas (Bouman 1950). It is thus possible that already the Bezold-Brücke phenomenon plays a role in the colour identification. We mention this possibility only to illustrate how speculative it is to incorporate the large chromaticness valence of the blue system in predicting the colour appearances at small diameter. In terms of hue experienced by an observer it would be better to speak about the violet system, but we are following the tradition of calling it a blue system.

We mention a private communication by Bouman and Ten Doesschate, that they stopped their colour naming experiments (see Bouman 1950), because of the appearance of distinctly different colours simultaneously, e.g. green in the one part and red in an other, in flashes larger than 15'. In our experiments we also met this phenomenon, but the percentage of occasions of this kind was so small, that the conclusions drawn in this section are not affected by it.

b. *The three-two quanta explanation of the colour threshold at wavelengths in the middle of the spectrum*

1. In the red-green region of the spectrum

The slopes of the curves relating colour threshold and diameter are in the middle of the spectrum according to a three quanta mechanism. This is valid, however, in a restricted range of diameters. The lower limit is the diameter of the Ricco-area, the upper limit is given by the diameter at which the three quanta mechanism shifts to a two-quanta mechanism. The ratio of colour threshold and absolute threshold at large diameters is larger than in the very ends of the spectrum (Fig. 25). Apparently the two-quanta mechanism is here less sensitive than at the ends of the spectrum. The

maximum size of the achromatic zone is at about 570 nm. This is at the intersection point of Pitt's red and green curves (Fig. 11). Apparently equal stimulation of the red and green systems is the least efficient combination in order to obtain colour perception. The three quanta slope at the smaller diameters, and the ratio 3:2 of colour threshold and absolute threshold proves that the excitation by 3 quanta always leads to colour perception. The two quanta mechanism at the large diameters means that, although a large number of 2-quanta excitations occur in an integration area, only one of them is the determining excitation for the colour perception.

Because the maximum achromatic zone is at the crossing point of the sensitivity curves of the red and green systems, the green system has the same properties as the red system as far as colour perception is concerned. This means that if the green system could be stimulated separate from the other, the achromatic zone will also be 1.30. As we did for the red system, we again can distinguish between two possibilities, a. the existence of an achromatic system, and b. only a part of the two-quanta excitations of the same system results in coloured appearances.

The decrease in variation of answers with increasing diameter proves that all absorbed quanta, provided the colour threshold is reached by the absorption of two or three quanta, determine the colour (compare Fig. 26 with 22). The variation in ratio of stimulations of the red and green systems is smaller when a large number of quanta, than when only a few quanta are involved.

2. In the green-violet region of the spectrum

The shape of the curves relating colour threshold and diameter are essentially the same as found in the red-green region: at small diameters a three quanta mechanism, which shifts to a two-quanta mechanism at larger diameters.

The maximum achromatic zone is at about 478 nm, which is at the crossing point of the blue and green fundamental curves, provided the blue one is multiplied by its chromaticness valence factor α (see Fig. 18). Equal stimulation of the green and blue system as far as their chromaticness is concerned, is the least efficient combination to obtain colour perception. Determination of α in this way gives the value $\alpha = 11$.

5. Discussion

The question whether two or more than two quanta are needed for the perception at the absolute threshold has already been a long time under discussion. Supporters (Hecht, Schlaer and Pirenne 1942) of seven or more quanta, base their reasoning on the slope of the curve relating chance on perception and intensity.

We want to emphasize here the large variety in colour naming. Even at 550 nm about 10 % of the flashes of small visual angle and short duration (Fig. 23a) are called red. If we suppose that indeed 7 quanta are needed at the absolute threshold, about 10 are needed at the colour threshold. It is difficult to imagine how at this wavelength where the green system is much more sensitive than the red, the red can so exclusively be stimulated that the sensation will be red. How lower the number of quanta involved, how greater the chance that the red system alone will be stimulated. Exact calculations about these chances are not made, because this should involve assumptions about the result of stimulation of one green and one red cone, 2 green and 1 red cone etc. Our point is only that any hypothesis about a large number of quanta is irreconcilably with the large variation in naming of colours. In other words, our measurements as regards the variation in colours observed support the hypothesis that only a few quanta are needed at the absolute threshold.

CHAPTER III

COLOUR DISCRIMINATION

§ 1. Introduction

There is an overwhelming literature concerning the experimental results on colour discrimination as well as on the description and interpretation of them. It is however generally assumed that the measurements on wavelength discrimination by Wright and Pitt (1935), and those on the sensitivities for colour differences through the whole colour mixture diagram by MacAdam (1942), are a fairly good approximation of the properties of the average normal human eye.

Among others, recent theoretical work has been done by Stiles (1946) (modification of Helmholtz' (1891) line-element), Le Grand (1950), Von Schelling (1955) and Hurvich and Jameson (1955). Although in a large part of the colour diagram a more or less fair approximation of the experimental data is given by these authors, all these theories fail markedly at the violet side of the spectrum.

The question arose whether the quanta statistical theory of de Vries (1943) and Rose (1948) on brightness discrimination could be applied to colour discrimination. De Vries and Rose correlated the statistical fluctuations in the stream of light quanta, which are proportional to $B^{\frac{1}{2}}$, for a given quantum flux B , with the experimental finding that for a large range of brightnesses the minimum visible contrast $\Delta B/B$ is proportional to $B^{-\frac{1}{2}}$. Their hypothesis states — recently it was reviewed by Bouman (1960) — that a brightness difference ΔB is just above threshold, when ΔB just exceeds the statistical fluctuations in background B . If we apply this idea to colour discrimination, this means in trichromatic theory that a colour difference required for threshold is also related to the statistical fluctuations in the rates of absorption of quanta by the three colour mediating systems. The development of such a theory is the purpose of this chapter.

In order to have any hope for a successful development of such a theory it is at least necessary to know whether the dependence of

colour discrimination upon brightness is governed by laws analogous to brightness discrimination. Some measurements, reported in § 3 of this chapter, indicate that this is indeed the case. Because the results seem to be influenced by the diameter of the test patch, some additional measurements on colour discrimination as a function of diameter are also reported.

An essential point in the theory is the choice regarding the sensitivity curves of the three colour components of the visual system. In view of the arguments put forward in Ch. IA, IB and II, we used Pitt's curves as governing the ratios of incident fluxes in the three systems at a given spectral distribution of the light.

It will be the most easy way to start the discussion with a less complex form of colour vision than normal trichromatic vision (Bouman and Walraven 1962). We find such less complex forms in those kinds of colour vision, where only two systems are involved: dichromatic vision. There are three kinds of it: tritanopia, protanopia and deuteranopia. In this treatment it is assumed that tritanopia is caused by lack of the blue receptor system, protanopia by lack of the red one, and that deuteranopia is caused by fusion of the red and green systems.

We will finish our treatment in § 2 with a discussion of normal trichromatic vision.

§ 2. Quantum theory of the colour difference threshold

a. *Red-green discrimination, tritanopia*

If we assume that tritanopia is caused by lack of the blue system, we can study discrimination involving only the red and green receptor systems by observing the properties of tritanopia.

Let us indicate the fluxes of light effectively absorbed in the red and green systems by \bar{n}_r and \bar{n}_g respectively, expressed in quanta per unit of time. The sizes of the statistical fluctuations in these fluxes are then given by $\bar{n}_r^{\frac{1}{2}}$ and $\bar{n}_g^{\frac{1}{2}}$. In departure from what is usual in colourimetry, we will indicate a certain colour by plotting the values of $\bar{n}_r^{\frac{1}{2}}$ and $\bar{n}_g^{\frac{1}{2}}$, rather than of \bar{n}_r and \bar{n}_g on the axes of a diagram. This is convenient for our purpose, because in such a scale the fluctuations cover a line element of constant length around the stimulus strength, regardless of the absolute value of \bar{n} . We owe this mode of plotting to a personal communication of Van

der Velden. The size of the statistical fluctuations in the \bar{n}_r , \bar{n}_g -combinations is given, according to the laws of statistics, for the absorptions in the red and green pigments are independent processes, by a circle around the colour point. The use of the $\bar{n}_r^{\frac{1}{2}}$, $\bar{n}_g^{\frac{1}{2}}$ -diagram is now shown to its full advantage, because at every place in this diagram the circles representing the statistical fluctuations are all equal in size.

Up to now only physical facts have been described. What we actually have in mind, is to consider whether the fluctuations are related with just perceptible differences. This means that we have to make assumptions regarding to the relation between physiological terms, as equal brightness etc., and the physical data (Bouman 1960b). Now we assume that equal brightness corresponds with $\bar{n}_r + \bar{n}_g = \text{constant}$. A treatment, in which the fluctuations in the nervous coding are considered, is given by Bouman, Vos and Walraven (1962).

If we plot the wavelengths in the $\bar{n}_r^{\frac{1}{2}}$, $\bar{n}_g^{\frac{1}{2}}$ -diagram, making use of Pitt's curves, on the line of equal brightness (a circle around the origin $(\bar{n}_r^{\frac{1}{2}})^2 + (\bar{n}_g^{\frac{1}{2}})^2 = \text{constant}$), we can read off the wavelength discrimination at constant brightness by drawing the same size circles around the colour points of the wavelengths involved. The radius of all these circles have to be chosen so as to give the best approximation of the experimental results. We will not go further into the absolute values of wavelength discrimination, but consider only the variation of it as a function of wavelength. If we choose a certain radius for the circles to fit it with the wavelength discrimination at one point in the spectrum, the whole wavelength discrimination curve is fixed. If we indicate the detectable differences in \bar{n}_r and \bar{n}_g by $k \cdot \bar{n}_r^{\frac{1}{2}}$ and $k \cdot \bar{n}_g^{\frac{1}{2}}$ respectively, k can be deduced from the experiments.

In fig. 27 $\bar{n}_r^{\frac{1}{2}}$ and $\bar{n}_g^{\frac{1}{2}}$ are plotted for a number of wavelengths on the circle of constant brightness according to Pitt's fundamental curves. The wavelengths are indicated outside the circle. By drawing equal circles of the appropriate radius around each wavelength point we obtain the solid theoretical curve in Fig. 28. This curve is compared with a few experimental curves measured by Fischer, Bouman and Ten Doesschate (1951) and by Wright (1952). The correspondance between the theoretical and the experimental curves, especially between 470 and 650 nm, is satisfactory.

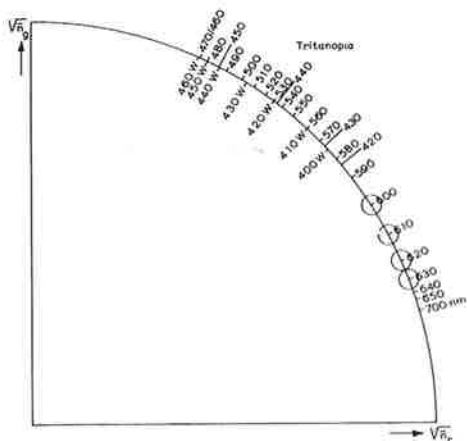


Fig. 27. The square root colour diagram of tritanopes. The circles represent the size of the statistical fluctuations, and according to the theory, equal discrimination steps.

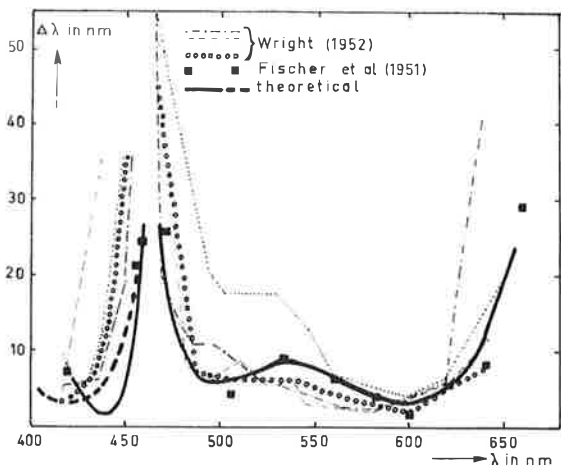


Fig. 28. Wavelength discrimination of tritanopes.

The theoretical curve shows a minimum at 440 nm. Unfortunately no measuring point is available in that region of the spectrum for Fischer's tritanope. The 440 nm-minimum is not found in the curves of Wright's tritanopes. Are Pitt's curves really applicable for tritanopes in that region of the spectrum? Fig. 29 shows the spectral mixture curves of the average of Wright's tritanopes, of the tritanope of Fischer et al, of the central fovea (Willmer and Wright 1945) and of the theoretical tritanope according tot Pitt's curves. All curves are transformed

to a mixture of 480 and 650 nm. This graph shows that Pitt's curves form an intermediate case. This is the reason, that we used for all the calculations in this thesis Pitt's original curves, instead of the curves derived by Thomson and Wright (1953), which are based on the data of Wright's tritanopes. If we assume that Pitt's curves are applicable for Wright's tritanopes for wavelengths longer than 470 nm, one can calculate the \bar{n}_r/\bar{n}_g values for them for the shorter wavelengths with use of their own spectral mixture functions. The colour points of the wavelengths below 470 nm according to this method are indicated (the W is added to the wavelengths number) inside the circle of equal brightness (Fig. 27). Calculations of the wavelength discrimination with these data give the dotted theoretical curve of Fig. 28.

This curve shows the typical shape of the experimental curves. In view of the spectral mixture curves of Fischer's tritanope a sharp minimum must be expected at about 440 nm for this tritanope. This shows how unfortunate it is that there is no experimental point available in that region of the spectrum.

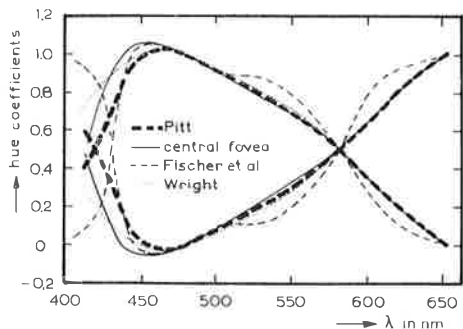


Fig. 29. The spectral mixture curves for 480 and 650 nm of the tritanopes indicated.

Wright (1952) remarks that colour discrimination for tritanopes seems to be better than for normals in the violet region. This is understandable by considering that colour discrimination in this region is due to the interaction of the red and green systems. As will be seen in the sections on protanopia and deuteranopia, the existence of the blue system does not contribute at all to colour discrimination in the violet region (see Fig. 31). This means that the existence of the blue system for normals only disturbs the colour discrimination there, and makes it inferior with respect to the tritanopes.

b. *Green-blue discrimination, protanopia*

If we assume that protanopia is caused by the absence of the red system, then colour discrimination by protanopes is due to the interaction of the green and the blue systems. Let us indicate as \bar{n}_g and \bar{n}_b the fluxes of light effectively absorbed by the green and blue systems respectively. We use again our quanta statistical approach as developed under (a) and plot now the wavelength points on a line of constant brightness in a $\bar{n}_g^{\frac{1}{2}}, \bar{n}_b^{\frac{1}{2}}$ -diagram. The values of \bar{n}_g/\bar{n}_b for each wavelength are chosen according to Pitt's curves. A line of constant brightness is the solid circle in Fig. 30. According to the theory, equal steps along this line are equal discriminable wavelength differences. The equal steps can be indicated in analogy as is done under (a) by $k \cdot \bar{n}_g^{\frac{1}{2}}$ and $k \cdot \bar{n}_b^{\frac{1}{2}}$. The theoretical wavelength discrimination curve, shows then the minimum at about 460 nm, as can directly be seen in Fig. 30 because of the wide spacing of the wavelength points in that region of the spectrum.

The experimental hue discrimination curve shows a minimum at 492 nm, so that the discrepancy between theory and experiment is enormous. In our opinion this discrepancy is of the same kind as found in the Bezold-Brücke phenomenon (Ch. IB § 4a). According to the theory of Peirce the theoretical invariable hue of the BB-phenomenon in the green-violet part of the spectrum is at about 445 nm, while the experimental value is 475 nm. We extended the

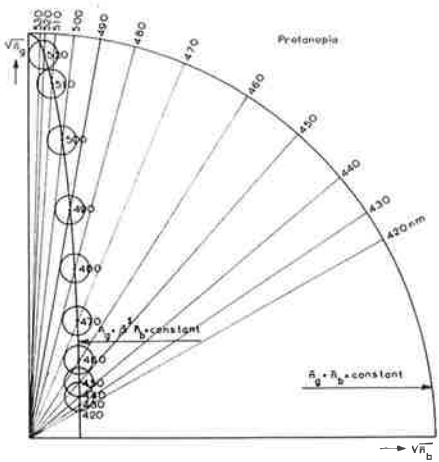


Fig. 30. The square root diagram of protanopes.

original theory of Peirce by assuming that so far as chromaticness is concerned, one has to reckon with the blue fundamental curve multiplied by the chromaticness valence factor α . We determined from the experimental invariable hue the value of this factor, which turned out to be about 10.

Because in hue discrimination we deal with the chromaticness contributions, rather than with the brightness contributions of the systems involved, it might be considered whether this difference is a reason of the inconsistency of the experiment (minimum in the wavelength discrimination curve at 492 nm) and theory (minimum at 460 nm). By proportional shortening of the line of equal brightness along the \bar{n}_b -axis by a factor β , a line is constructed which is given by $\bar{n}_g + \beta^2 \bar{n}_b = \text{constant}$. Taking the equal steps along this line rather than along the line of equal brightness $\bar{n}_g + \bar{n}_b = \text{constant}$, brings the minimum in the wavelength discrimination curve towards longer wavelengths, and the shape of the curve in good agreement with experiment. The choice β is equal to 8 brings the minimum in the curve at the experimental value. The theoretical curve obtained with this treatment is therefore indicated by $\beta = 8$ in Fig. 31.

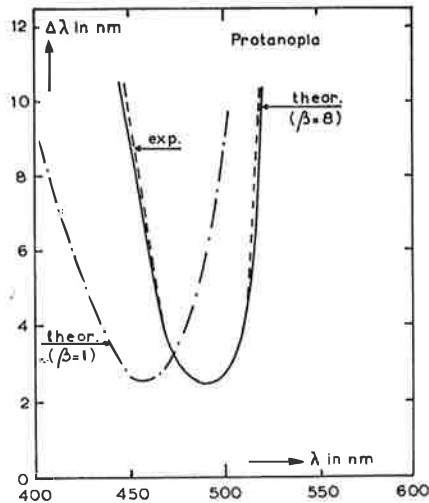


Fig. 31. Wavelength discrimination curve of protanopes, compared with some theoretical curves. The solid line represents the theoretical curve preferred.

It must be admitted, that beside the peculiar character of the blue system which is indicated by it, it is not yet clear what kind of physiological mechanisms are behind this factor β . The heart of the question is, in our opinion, whether the chromaticness valence factor a is so closely related with β , that a may be taken equal to β , for a turned out to be also about 10. We enter here a field, which is so large for speculations, that we will leave this point at the moment aside.

c. Red + green - blue discrimination, deuteranopia

It is generally thought that deuteranopia is caused by the fusion of the red and the green systems.

Colour discrimination by deuteranopes is thus due to the interaction of the combined red + green system and the blue system. Pitt (1944) has shown that the luminosity function of the deuteranopes better can be described by the sum of 0.75 times the green sensitivity curve + 1.30 times the red one. We will use this description in our treatment.

We use again our quanta statistical approach as developed under (a) and plot now the wavelength points on a line of constant brightness in a $(0.75\bar{n}_g + 1.30\bar{n}_r)^{\frac{1}{2}}, \bar{n}_b^{\frac{1}{2}}$ -diagram (Fig. 32).

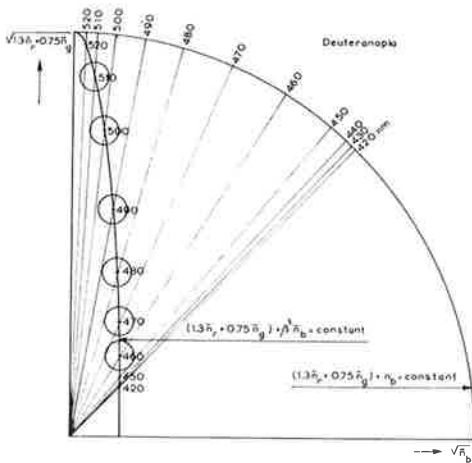


Fig. 32. The square root diagram of deuteranopes.

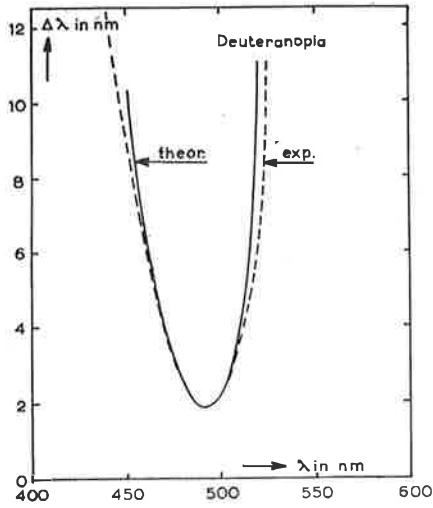


Fig. 33. Wavelength discrimination curve of deuteranopes.

The theoretical hue discrimination curve obtained in an analogous way as described in the previous subsections, shows a minimum at 465 nm. The discrepancy from experiment is of the same kind as found in protanopia.

Following the same treatment as in protanopia by taking the equal steps along the line $\bar{n}_g + \beta^2 \bar{n}_b = \text{constant}$, the theoretical curve can be brought in agreement with the experimental one (Fig. 33).

The β -factor turns out to be equal to 8 as in protanopia.

d. Normal trichromatism

Colour discrimination by normal trichromats is due to the interaction of the red, green and blue systems (Walraven and Bouman 1962).

In order to make a long story short it turns out that we have again to handle with the blue system in the same way as in protanopia and deuteranopia. The β -factor has to be chosen again equal to 8 in order to bring the theoretical minimum in the hue discrimination curve at about 495 nm, according to the experimental value.

Following a replica of the treatment described for protanopia, applied to a three dimensional colour space $\bar{n}_r^{\frac{1}{2}}$, $\bar{n}_g^{\frac{1}{2}}$ and $\bar{n}_b^{\frac{1}{2}}$ are plotted on the axes of a three dimensional diagram (Fig. 34a),

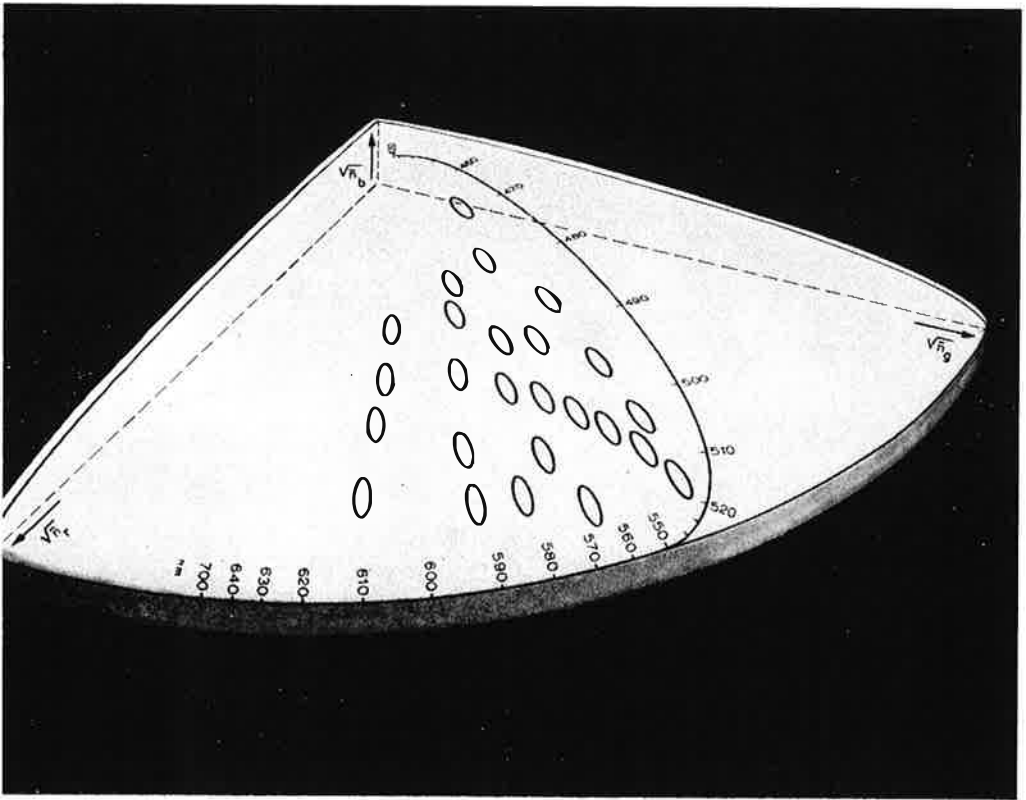


Fig. 34a. The square root space diagram of normals, in which the ellipses represent the theoretical MacAdam ellipses (Fig. 36).

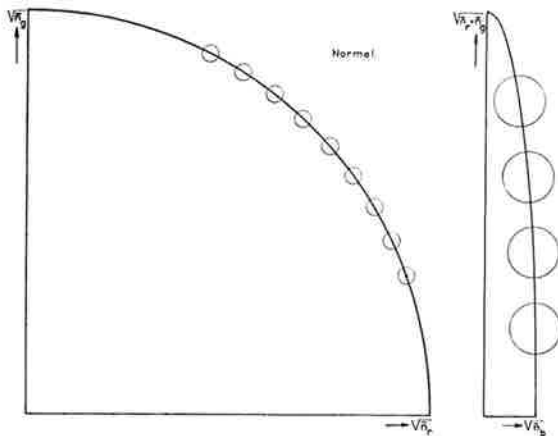


Fig. 34b. Left hand graph is the section of Fig. 34a through the $\bar{n}_r^{1/2}$ and $\bar{n}_g^{1/2}$ -axes. Right hand graph is a section through the $\bar{n}^{1/2}$ -axis. Note that the discrimination circles are in the latter section 3 x greater than in the former.



the latter in a β -shrunk scale. The spectrum locus and the wavelength points are indicated in the graph on the ellipsoid of $\bar{n}_r + \bar{n}_g + \beta^2 \bar{n}_b = \text{constant}$. Spheres in this space represent the statistical fluctuations. Nevertheless, these spheres do not represent the discrimination data. To clarify this statement, two sections through the colour space are made, one through the $\bar{n}_b^{\frac{1}{2}}$ -axis, and one through the $\bar{n}_r^{\frac{1}{2}}$ and $\bar{n}_g^{\frac{1}{2}}$ -axis (Fig. 34b). In the section through the $\bar{n}_b^{\frac{1}{2}}$ -axis, $\bar{n}_b^{\frac{1}{2}}$ and $(\bar{n}_r + \bar{n}_g)^{\frac{1}{2}}$ are plotted along the axes, because every point along the line of equal brightness in the $\bar{n}_r^{\frac{1}{2}}$, $\bar{n}_g^{\frac{1}{2}}$ -plane represents a constant value of $(\bar{n}_r + \bar{n}_g)^{\frac{1}{2}}$.

Agreement with experiment can be obtained by taking the circles, the sections of the spheres in the plane of drawing, in the $\bar{n}_b^{\frac{1}{2}}$, $(\bar{n}_r + \bar{n}_g)^{\frac{1}{2}}$ -diagram 3 times larger than in the $\bar{n}_r^{\frac{1}{2}}$, $\bar{n}_g^{\frac{1}{2}}$ -diagram. This is valid for every plane through the $\bar{n}_b^{\frac{1}{2}}$ -axis. If we represent the detectable differences in the $\bar{n}_r^{\frac{1}{2}}$, $\bar{n}_g^{\frac{1}{2}}$ -plane, by $k_1 \bar{n}_r^{\frac{1}{2}}$ and $k_1 \bar{n}_g^{\frac{1}{2}}$, and in the $\bar{n}_b^{\frac{1}{2}}$, $(\bar{n}_r + \bar{n}_g)^{\frac{1}{2}}$ -plane by $k_2 \bar{n}_b^{\frac{1}{2}}$ and $k_2 (\bar{n}_r + \bar{n}_g)^{\frac{1}{2}}$, the ratio k_2/k_1 is thus equal to 3. The agreement of experiment and theory is shown in Fig.'s 35 and 36, which represent the wavelength discrimination curve measured by Wright and Pitt (1935) and the colour discrimination ellipses through the whole mixture diagram measured by Mac Adam (1942), together with the theoretical curves.

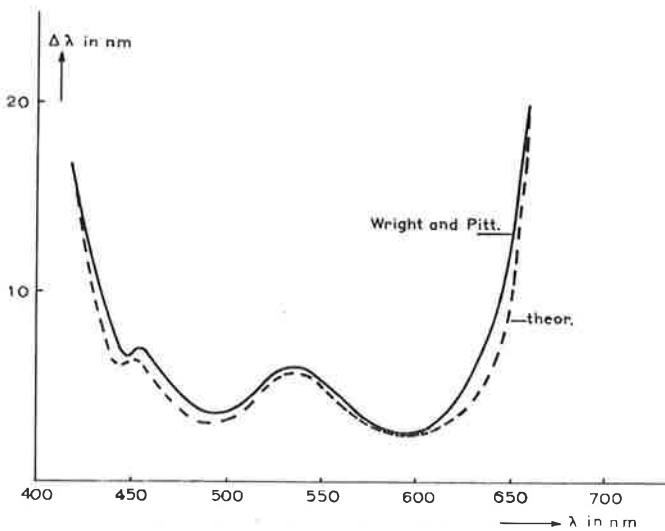


Fig. 35. Experimental wavelength discrimination curve measured by Wright and Pitt, and the theoretical one.

The fact that the criteria of discrimination, we might call it the safety factors, with respect to the statistical fluctuations are different between the interaction of the red and green systems, and the interaction of the sum of the red and green systems with the blue system is further evidence for the distinction of a red-green information channel and a yellow-blue information channel as proposed in Ch. IB § 5. The fact that the discrimination properties in every $\bar{n}_b^{\frac{1}{2}}$, $(\bar{n}_r + \bar{n}_g)^{\frac{1}{2}}$ -plane are identical, was the main reason of the hypothesis that the Y(ellow) signal is the addition of the R(ed) and G(reen) signals, as indicated in Fig. 20.

Note that according to this theory the minimum in the wavelength discrimination curve at 450 nm is due to interaction of the red and green systems.

Resuming it can be concluded that the quanta statistical discrimination theory of De Vries and Rose can be applied to colour discrimination of normal trichromats, if is taken into account:

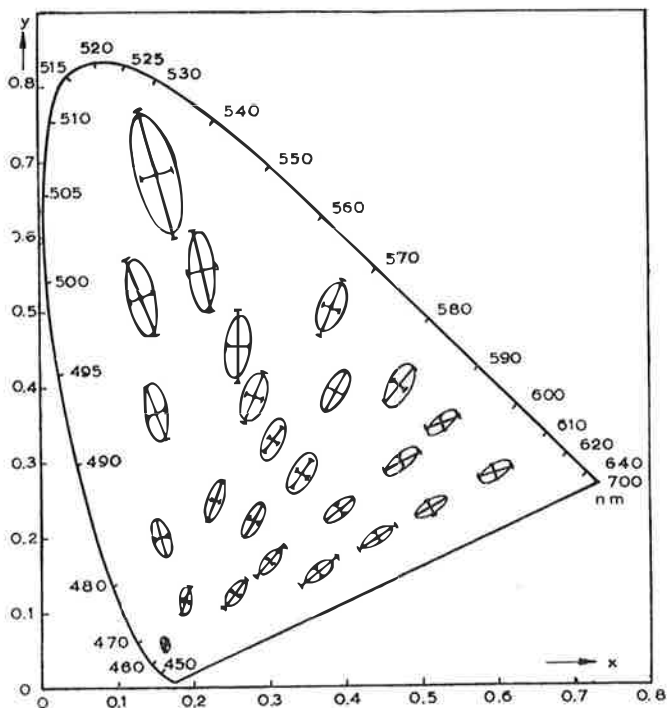


Fig. 36. The CIE-colour mixture diagram with the experimental and the theoretical MacAdams ellipses. The axes drawn belong to the experimental ellipses, the solid ellipses drawn are a transformation from those in Fig. 34a.

- a. the peculiar character of the blue system
- b. different safety factors of discrimination with respect to the statistical fluctuations in the red-green information channel and in the yellow-blue information channel.

3. Colour discrimination as a function of brightness and of area

a. *Experimental arrangement*

The colour discrimination measurements are performed by comparison of stimuli presented simultaneously in adjacent parts of the visual field. All data refer to monocular vision. The colorimeter used (extensively described by Bouman, Walraven and Leebeek 1956) consisted of two integrating spheres. Between the spheres is placed a plate, painted mat white, with a circular hole in its centre. Plates with holes of different size were available. The front side of the plate is illuminated by the light in the front sphere. The illumination was homogeneous, because the plate could be considered as a part of the wall of the integrating sphere. The light of the front sphere is adjustable in brightness B_1 and in colour C_1 . The plate is visible through a square window of 1° in diameter. The observer sees through the hole in the test plate the backwall of the second sphere. The illumination of the backwall is also adjustable in brightness B_2 and in colour C_2 . The observer sees therefore a round testfield of given diameter of brightness B_2 and colour C_2 , in a larger field of 1° of brightness B_1 and colour C_1 . The latter field is surrounded by a large white screen, illuminated with light of incandescent lamps, of the same brightness as the testfield.

White light and monochromatic light are mixed in the spheres. The white light is produced by headlight bulbs with colour temperature of 2848°K (standard white A). The monochromatic light was obtained by using interference filters, which filtered the light of projectors containing 750W lamps and special mirrors. The interference filters were air-cooled and placed behind heat absorbing water-cooled filters. In this way even at 650 nm a brightness of 30 cd/m^2 could be obtained in the spheres of 40 cm diameter. The brightness of the unfiltered white light could be 6000 cd/m^2 .

It was sometimes suitable to make use of test patches built up by a great number of holes, placed so close to each other that observed at a distance of 3 metres the holes cannot be distinguished

separately. The colour of the test patch is then the mixture of the colour of the light of the second sphere coming through the holes, and of the colour of the light reflected by the remaining part of the plate between the holes.

The method of making series of colours by the choice of a series of diameters of such holes has been described by Bouman et al (1956).

b. Procedure

Two methods were used:

1. Both spheres were made white (2848° K) of equal brightness. The hole in the test plate, the test field, is therefore invisible. Next the brightness of the white of the second sphere is decreased. The subject sees a dark test field in a brighter surround. The subject is asked to increase the brightness of a spectral light in the second sphere, until the test patch is again invisible. If this is possible, the brightness of the white of the testfield is decreased again, and the procedure has to be repeated. If the test patch remains visible, the brightness of the white is increased, and the procedure has to be repeated. Summarizing: the brightness of the white in the second sphere has to be changed until it turns out that addition of spectral light can bring the test patch at the threshold of discrimination.

2. In the second sphere a certain amount of spectral light is added to the white. The subject is now asked, again by the method of trial and error, as described under 1), to bring the test patch at the threshold of discrimination by changing the brightness of the white of the test patch.

The actual difference between the two methods is illustrated in Fig. 37. In this graph brightness is plotted vertically and saturation degree ΔC of mixtures of white A and 525 nm horizontally. The vertical axis represents white A, and the horizontal axis the line of constant brightness, arbitrarily chosen 100.

The chromaticity point of the front sphere is the intersection point of the axes. By using method 1 the chromaticity point of the second sphere moves along a line parallel with the line indicated by "method 1". By using method 2 this is a line parallel to the vertical axis, because the change in saturation-degree by a small variation of white is negligible. The experimental points in the

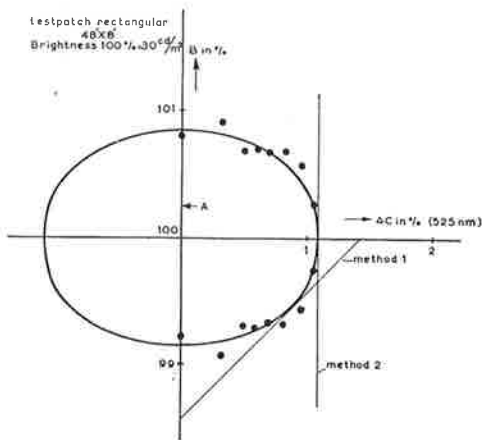


Fig. 37. Measurements of just noticeable combined brightness and chromaticness differences to illustrate the difference of the experimental methods of measuring just noticeable saturation degree as described in the text.

diagram represent just noticeable differences measured by using method 2. The upper and lower thresholds are averaged. The upper and lower thresholds coincide at that value of ΔC , which is the just noticeable saturation-degree difference at equal brightness. A priori this is not necessarily true, but the measurements by Brown and MacAdam (1949) show that the axis of the discrimination ellipses, especially in the white region, are oriented as shown in Fig. 37. Method 2 is therefore the accurate one, is however, less convenient because the variation in brightness has to be done by variation of the distance of the lamp to a diaphragm, in order to avoid changes in colour temperature. With method 1 only current regulation of the lamp is needed, because by using an interference filter the wavelength does not change. Fig. 37 shows clearly why method 1 fails. The actual setting by the subject will be at the place where the line indicated by "method 1" touches the discrimination ellips. If the discrimination ellips is more elongated along the horizontal axis, the error made by using method 1 becomes small.

All measurements reported in this section are done by using method 1 provided it was justified by the relation between brightness discrimination and colour discrimination. Method 2 was used in all other cases.

c. Colour discrimination as a function of brightness

The experimental results of the determination of just noticeable saturation degrees are given in the right hand part of Fig. 38. Two different diameters were used: 6' and 23', and five different wavelengths, as indicated in the graph.

The main conclusion from these experiments is, that over a rather extensive region of brightnesses, from 1 to 1000 trolands, the just noticeable saturation degree is inversely proportional to the square root of the brightness. This is the experimental evidence (see the introduction of Ch. III) which justifies our quanta statistical theory of the colour difference threshold as described in the first part of this chapter.

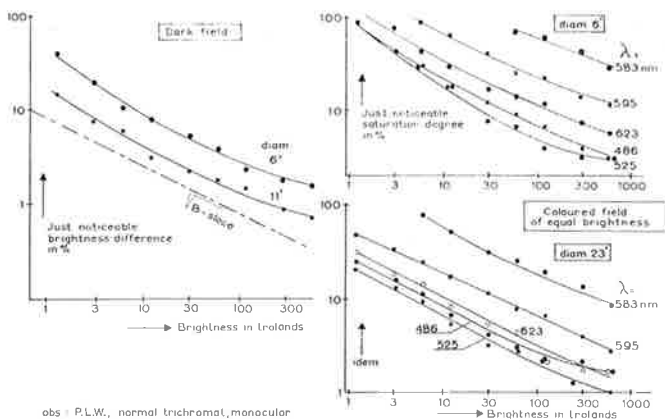


Fig. 38. Right hand graphs represent just noticeable saturation degrees as a function of brightness for the wavelengths and diameters indicated. Left hand graph represents just noticeable brightness differences as a function of brightness.

At the left hand side of the graph some results of measurements of just noticeable brightness differences are plotted. These measurements refer to a dark test field in a brighter surround, under the same circumstances as the colour difference measurements. The experimental points cannot be fitted exactly by a straight line, but the approximation by a square root line is fair.

There are a few differences between the experimental results at 6', and those at 23' as regards the just noticeable saturation degree measurements. In general the saturation degree must be larger at the small diameters than at the large diameters. This change is,

however, less at 486 and 525 nm than at the other wavelengths. It seemed therefore worthwhile to investigate the relation of the just noticeable saturation degree with diameter. The results are given in the next subsection.

d. *Colour discrimination as a function of diameter*

The relation between just noticeable saturation degree and diameter at several brightness levels is given for 623 nm and 525 nm in Fig. 39. In this graph, however, the saturation degree is multiplied by a factor d^2 , proportional to the area of the test patch. This way of plotting gives the relation between the amount of energy of the spectral light in the test patch, and the diameter. This has the advantage that one easily can see in the graph that up to about 3' to 4' only the total amount of spectral light in the test patch is the determining factor for visibility (Ricco's law). This way of plotting provides also easy comparison with the data reported in Ch. II as regards dependence of the colour threshold upon diameter. The peculiar difference between the left hand and the right hand curves is, that the latter are steeper for values larger than the Ricco-area. The curves relating colour threshold and diameter, as reported in Ch. II, are at the wavelengths in the middle of the spectrum also steeper than for red (Fig. 24). We do not want to emphasize this correspondence, nor state that the origin will be the same. Nevertheless the correspondence may be

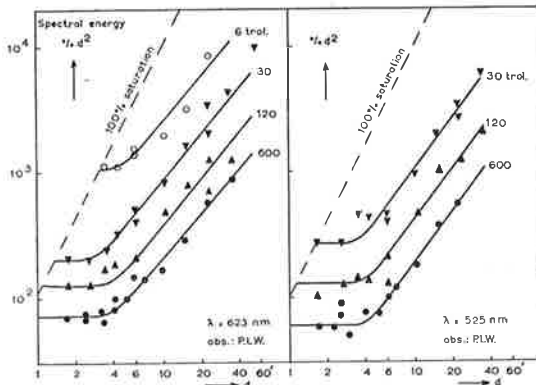


Fig. 39. Dependence of amount of spectral energy in a test patch needed in order to be seen as a function of diameter at the wavelengths indicated for a few brightness levels. Note the curves are steeper for green than for red.

the key to a better understanding of the behaviour of the colour difference threshold as a function of diameter.

The measurements using 590 nm (Fig. 40) as the spectral light show an other peculiarity. The curves show a marked inflection at about 20' to 30'. This means that the colour discrimination is relatively worse at the small diameters than at the large diameters, compared with the relation found with 525 nm and 623 nm. This is exactly what small-field tritanopia amounts to: the discrimination in the yellow-blue direction of the colour mixture diagram becomes progressively worse with decreasing diameter than in the red-green direction (Farnsworth 1955). Because of the existence of small-field tritanopia the inflections of the curves were expected. (Boumand and Walraven 1957b). This graph shows moreover that the place of the inflection is independent of the brightness level. This can be explained by assuming that the blue system is less sensitive in an area of 20' diameter in the centre of the fovea than in the next surrounding part. This is in accordance with the threshold measurements reported in Ch. II § 3c.

The measurements reported in this section support on the one hand the soundness of the quanta statistical theory of colour discrimination (the just noticeable colour difference is inversely proportional to the square root of brightness), indicate on the other hand that the theory developed has to be refined in order to cover the complex behaviour of colour discrimination as a function of diameter.

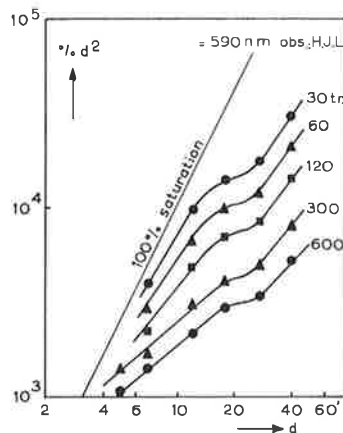


Fig. 40. As Fig. 39. Note the inflections at about 25', as a result of small field tritanopia.

SUMMARY

The psycho physical studies, reported in this thesis, give on the one hand connections to some objective data, the absorption spectra of the visual pigments and saturation effects in nerve transmission. They deal on the other hand with the influence of the quantum nature of light.

Chapter IA deals with the chromatic Stiles-Crawford effect, the hue shift of light, when the point of entry of it moves over the pupil. The experimental data obtained are in accordance with those reported in the literature. An explanation of this effect is put forward in which it is considered that the light coming from the edge of the pupil, falls obliquely at the retina, and therefore has a smaller pathway through the visual pigment. A smaller pathway through a dense solution of pigment corresponds with a narrowing of the absorption curves. Assuming Pitt's curves, after correction for the absorption in the ocular media, as the absorption curves of the visual pigments, this gives a quantitative description of the chromatic Stiles-Crawford effect. This theory strongly points to high densities of the photopigments (absorption in the peak of the absorption curves about 80%). The theory explains in the same way the wavelength dependence of the Stiles-Crawford effect proper and the breakdown of the colour matches for oblique light. The agreement of different experimental data with this theory gives a strong support for the Young-Helmholtz theory so far as the receptor layer is concerned, and secondly for the fair approximation of the absorption curves as derived by Pitt.

The disagreement of theory and experiment when the absorption curves according to the determination by Brindley were used, originated a discussion on the merits of this determination using strong chromatic adaptation. The discussion shows that Pitt's curves are even a better base for explaining the experimental chromatic adaptation data.

The Bezold-Brücke phenomenon, the hue shift of light with increasing brightness, is also explained in the framework of the Young-Helmholtz theory (Ch. IB). It is assumed, that the responses of the three independent receptor systems gradually increase to

an end value with increasing stimulation, such as is well known in nerve transmission, making use of Pitt's curves again. To account for the law of additivity of brightness it is necessary to make a distinction between a brightness and a colour information channel. No hue change can be expected at the intersection points of Pitt's curves. The invariable hue at 570 nm is thus explained, but in order to account for the invariable hue at 476 nm it is necessary to assume that the contribution of the blue system to chromaticness, its "chromaticness valence" is about 10 times its contribution to brightness.

The theory is in accordance with data obtained in the purple region of the colour diagram, where an invariable hue was also found.

More evidence is gathered from the literature for the separate transmission of chromaticness and brightness. Anticipating the next chapters and together with other reasons, evidence is indicated for the separation in red-green and yellow-blue channels. This separation in brightness and two chromaticness channels is in fact the Hering theory. It is therefore proposed that the Young-Helmholtz scheme is valid at the receptor level, and that the Hering scheme is valid at a higher stage in the transmission of the information to the visual centres.

Chapter II deals with the influence of the quantum nature of light on the variability in the colour appreciation of monochromatic light by a normal trichromat. The frequencies of reddish, yellowish, greenish, blueish, violet, colourless and white appearances in the perception were determined under variation of brightness, wavelength, exposure time and visual angle of the teststimulus.

The mathematics of the determination of the number of quanta necessary for a certain perception from the dependence of the energy at the threshold for this perception and the exposure time or the area of the teststimulus is repeated and applied to the colour threshold. In order to perceive red at least two quanta are needed within the integration area and the integration time.

The existence of an achromatic zone, together with the fact that at the absolute threshold also two quanta are needed leaves two possibilities: either two receptor systems are involved, stimulation of the one resulting in a colourless sensation, and of the second in a red appearance; or one receptor system is involved, excitation of which sometime results in a coloured appearance and sometimes

not. In the violet region of the spectrum the same conclusions can be drawn for the blue receptor system, if we speak about the red, green and blue receptor systems in terms of the Young-Helmholtz theory.

It is further necessary to attribute to the blue system a larger contribution to chromaticness than to brightness to account for the differences in colour naming at large and at small areas.

In the middle portion of the spectrum three quanta are needed to reach the colour threshold. When the green system separately could be stimulated, the same threshold conditions apply for it as for the red system, so that combined stimulation of different receptor systems apparently is less effective for a coloured appearance. It is therefore expected that the maximal values of the achromatic zone, in particular at large areas, are found at the intersection points of the fundamental response curves. This leads to a determination of the chromaticness valence factor of the blue system of about 10.

In chapter III the hypothesis of de Vries and Rose has been applied to colour discrimination of dichromats and normal trichromats.

The hypothesis states that a brightness difference ΔB is just beyond threshold, when ΔB just exceeds the statistical fluctuations in background brightness B , which are proportional to $B^{\frac{1}{2}}$. The colour difference, required for the threshold is related to the statistical fluctuations in the rates of absorption of quanta by the colour components in the visual system.

The sensitivity curves derived by Pitt have been used to represent the three systems of the Young-Helmholtz theory.

This treatment describes the wavelength discrimination in tritanopia by assuming the lack of the blue system. By assuming the lack of the red system in protanopia, and fusion of the red and green systems in deuteranopia, this theory is in satisfactory agreement with experiment, provided the blue system is given a larger weight regarding a decision about an apparent hue difference. This implies separate transmission mechanisms in the visual system for the brightness- and for the hue aspect of a stimulus.

The theory describes for normal trichromats the wavelength discrimination curve as measured by Wright and Pitt, and the just perceptible colour differences in the colour mixture diagram as measured by Mac Adam, when normal colour vision is treated as a combination of deuteranopic and tritanopic vision. The just per-

ceptible difference in the tritanopic component must be taken three times larger with respect to the statistical fluctuations than in the deuteranopic component. This gives further evidence for the separation of yellow-blue and red-green channels as proposed in the Hering theory.

A number of experiments on just perceptible saturation differences are reported, using the double-sphere-colourimeter. They show that over about three log-units of brightness the just perceptible colour difference is proportional to $B^{\frac{1}{2}}$.

The relation between just noticeable saturation degree and diameter is established for different wavelengths. This relation is different for red and green as the spectral lights, and shows for yellow light the influence of small-field tritanopia.

SAMENVATTING

Enige objectieve gegevens, zoals de absorptie spectra van de visuele pigmenten en verzadigingsverschijnselen in zenuwgeleiding zijn in hoofdstuk I verbonden met psycho-fysische gegevens van het kleurenzien. In de hoofdstukken II en III ligt de nadruk op de relatie tussen zulke gegevens en de quanteuze structuur van het licht.

Hoofdstuk IA behandelt het chromatische Stiles-Crawford effect. Dit effect is de kleurverschuiving die optreedt, wanneer de plaats, waar het licht de pupil binnentreedt, verplaatst wordt over de pupil. Enige metingen die hierover zijn gedaan zijn in overeenstemming met de schaarse gegevens hierover in de literatuur. Een verklaring voor dit verschijnsel is gegeven door er zich rekenschap van te geven, dat licht, dat scheef op de receptoren invalt, een kortere weglengte door het visuele pigment aflegt. Bij een sterk absorberende pigmentlaag betekent dit een versmalling van de absorptiekromme bij scheef invallend licht.

Veronderstellend dat de Pitt'se krommen, na correctie voor de absorptie in de oogmedia, de absorptiekrommen van de visuele pigmenten voorstellen, dan is hiermede een kwantitatieve beschrijving van het chromatische Stiles-Crawford effect te geven. De absorptie door de pigmenten blijkt vrij sterk te moeten zijn, nl. ongeveer 80% in de top van de absorptiekrommen. Deze theorie verklaart eveneens de golflengte afhankelijkheid van het gewone Stiles-Crawford effect, en tevens de verandering die optreedt in de kleurvergelijkingen.

De overeenstemming, die tussen theorie en experimenten wordt gevonden is een steun voor de Young-Helmholtz theorie van het kleurenzien althans voorzover het de receptoren betreft. Tevens dient het als bevestiging van de absorptiekrommen, zoals deze door Pitt zijn voorgesteld.

Het Bezold-Brücke phenomeen, de kleurverschuiving bij toenemende helderheid, is eveneens verklaard in het kader van de Young-Helmholtz theorie (Hoofdstuk IB). In deze theorie wordt aangenomen, zoals bekend is uit de zenuwgeleiding, dat de responsies van de drie onafhankelijke receptorsystemen geleidelijk tot een vaste eindwaarde toenemen. Hierbij is weer gebruik gemaakt van

de Pitt'se krommen. Om met de additiviteits wet niet in tegenspraak te komen, is het nodig om een onderscheid te maken tussen een helderheids- en een kleurinformatie-kanaal. Op de snijpunten van de Pitt'se krommen moeten volgens de theorie de invariante kleuren liggen. Dit klopt wel met de kleur bij 570 nm, doch niet bij die van 476 nm.

Om toch overeenstemming te verkrijgen is het noodzakelijk aan te nemen, dat de bijdrage van het blauwe systeem tot de kleur, zijn kleurkracht, ongeveer 10 maal zo groot is als zijn bijdrage tot de helderheid.

De theorie is in overeenstemming met de metingen, die in het purper gedeelte van de kleurendriehoek zijn uitgevoerd. Hier werd een invariante kleur, zoals door de theorie voorspeld, eveneens gevonden.

In de literatuur werd nagegaan in hoeverre meer gegevens te verkrijgen waren, die wezen in de richting van een gescheiden transmissie van kleur en van helderheid. Mede vooruitlopend op de gegevens van de volgende hoofdstukken werden tevens aanwijzingen verzameld voor de scheiding in een rood-groen kanaal en een geel-blauw kanaal. Een dergelijke opzet is in feite de Hering-theorie. In de discussie wordt gesuggereerd dat de Young-Helmholtz theorie geldt in de receptorlaag, maar dat een transformatie optreedt naar een Hering's schema tijdens het transport van de informatie naar de visuele centra.

Hoofdstuk II houdt zich bezig met de invloed van de quanteuze natuur van het licht op de variabiliteit in de kleurbenoeming van monochromatisch licht door een normale trichromaat. De percentages, dat gegeven licht rood-, geel-, groen-, blauw- of violetachtig werd genoemd en tevens van de kleurloze en de witte gewaarwordingen werden bepaald als een functie van de helderheid, golflengte, flitstijd en visuele hoek van de teststimulus.

De wiskundige behandeling van de bepaling van het aantal quanten dat nodig is voor een bepaalde waarneming uit de relatie tussen de drempelenergie en de diameter van de stimulus, wordt uiteengezet en toegepast op de kleurwaarneming. Om rood te zien zijn minstens twee quanten nodig binnen de integratietijd en het integratieoppervlak. Ook bij de absolute drempel geldt dit, en daar er een achromatische zone bestaat, zijn er twee mogelijkheden: of er zijn twee receptorsystemen betrokken in de perceptie, waarvan de een bij stimulering met twee quanten een rode indruk veroorzaakt, terwijl

bij de ander deze kleurloos is, of slechts één receptorsysteem is erin betrokken, die bij stimulering de ene keer een rode, de andere keer een kleurloze indruk veroorzaakt.

In het violette deel van het spectrum gelden dezelfde regels als in het rood, doch dan betrokken op het blauwe systeem, wanneer we spreken over het rode, groene en blauwe systeem volgens de Young-Helmholtz theorie.

Tevens is het nodig om aan het blauwe systeem een grote kleurkracht toe te kennen om het verschil in de kleurbenoeming bij grote en bij kleine gezichtshoeken te kunnen verklaren.

In het middengedeelte van het spectrum zijn drie quanta nodig om een kleurgewaarwording te verkrijgen. Wanneer het groene systeem apart gestimuleerd zou kunnen worden, gelden de zelfde drempel voorwaarden als voor het rode systeem, zodat stimulering van twee systemen tegelijk minder effectief is voor een kleurgewaarwording.

De golflengten, waarbij de achromatische zone maximale waarden aanneemt, deze zijn meer uitgesproken bij grote diameters, moeten dan op de snijpunten liggen van de fundamentele gevoeligheidskrommen. Op deze wijze bepaald, moet de kleurkracht factor van het blauwe systeem ongeveer 10 bedragen.

In hoofdstuk III is de hypothese van de Vries en Rose toegepast op het kleuronderscheidingsvermogen van dichromaten en normale trichromaten. De hypothese stelt, dat een helderheidsverschil ΔB juist boven de drempel is, wanneer ΔB net groter is dan de statistische fluctuaties in de achtergrondshelderheid B , en dus evenredig met $B^{\frac{1}{2}}$. Ook het kleurverschil dat net waargenomen zou kunnen worden zou zo samen kunnen hangen met de fluctuaties in de aantallen invallende quanten in de verschillende receptor systemen.

De drie gevoeligheidskrommen volgens Pitt zijn aangenomen als die van de receptoren systemen volgens de Young-Helmholtz theorie.

Het golflengte onderscheidingsvermogen van tritanopen wordt op deze wijze beschreven, als wordt aangenomen dat deze het blauwe systeem missen. De theorie is eveneens goed in overeenstemming met de gegevens van protanopen, veronderstellende dat deze het rode systeem missen, en van deuteranopen, aannemend dat bij hen fusie van het rode en groene systeem optreedt. Dit is echter alleen juist als aan het blauwe systeem een groter gewicht wordt toegekend in de beslissing over het zien van kleurverschillen.

Dit geeft een aanwijzing dat de transmissie van kleur en van helderheid door verschillende mechanismen in het visuele systeem wordt verzorgd.

De theorie geeft een voldoende beschrijving van het golflengte onderscheidingsvermogen van normale trichromaten, zoals gemeten door Wright en Pitt, en van de juist waarneembare kleurverschillen in de kleurendriehoek, zoals gemeten door MacAdam. Het normale kleurenzien moet dan gezien worden als een combinatie van deuteranopisch en tritanopisch zien.

Het net waarneembare verschil in de tritanopische component moet drie keer zo groot gekozen worden t.o.v. de optredende fluctuaties als in de deuteranopische component. Dit verschijnsel is een steun voor de opvatting, dat er aparte rood-groen en geel-blauw kanalen bestaan, zoals dat in de Hering theorie wordt uitgedrukt.

Enige experimenten over net waarneembare verzadigingsverschillen, die uitgevoerd zijn met de twee-bollen-colorimeter, zijn beschreven. Eén van de conclusies hieruit is, dat net waarneembare kleurverschillen evenredig zijn met $B^{-\frac{1}{2}}$ over een helderheidsgebied van ongeveer 3 log-eenheden.

Het verband tussen de juist waarneembare verzadigingsgraad en de diameter werd bepaald van een aantal golflengten. Voor rood en groen verschillen deze relaties enigszins, terwijl bij gebruik van geel licht als het spectrale licht het verschijnsel van de tritanopie van de kleine velden optreedt.

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J. Opt. Soc., **43**, 890-894.

CONTENTS

	Page
Introduction	1
I. Hue shift	3
A. The hue shift associated with the Stiles-Crawford effect	3
1. Introduction	3
2. Literature review about the directional sensitivity of the retina and associated phenomena	4
3. Drawing in outline of the theory	10
4. Quantitative development of the theory	13
5. Critical consideration of other hypotheses	21
B. The Bezold-Brücke phenomenon	27
1. Introduction	27
2. Experimental data	28
3. Review of theories	30
4. Refinement of Peirce's theory, an explanation in the framework of the Young-Helmholtz theory	31
5. Discussion on the theories of colour vision, Young-Helmholtz, Hering or both?	36
II. Colour recognition	42
1. Introduction	42
2. Methods used for the determination of the number of quanta necessary for a perception	44
3. Colour naming of monochromatic lights	47
4. Interpretation	55
5. Discussion	59

	Page
III. Colour discrimination	60
1. Introduction	60
2. Quantum theory of the colour difference threshold .	61
a. tritanopia	61
b. protanopia	65
c. deuteranopia	67
d. normal trichromatism	68
3. Colour discrimination as a function of brightness and of area	71
Summary	77
Samenvatting	81
References	85

