

Proc. 2nd congress AIC "Colour 73", York, July 1973

THEORETICAL MODELS OF THE COLOUR VISION NETWORK

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I. INTRODUCTION

From the tremendous amount of literature available on colour vision it emerges that most researchers adhere to one kind or another of trichromatic opponent theory of colour vision. Present theoretical models of the colour vision network are all variations on this theme. One of these variations is the model proposed by Walraven (1962) and later amended by Vos and Walraven (1971). It would be appropriate to discuss in full detail every written variation. However, due to lack of space and time, I have chosen for description the amended Walraven model. Where appropriate, other thoughts are mentioned where they deviate from this model, or where they give more explicit form to certain parts of the model.

2. THE PRINCIPLE OF THE MODEL

A schematic representation of the model is given in Fig. 1. Essential characteristics are that the signals from a Helmholtz-type three receptor zone are converted to Hering-type antagonistic red-green and yellow-blue colour signals, and to a brightness signal which is the sum of the signals from the three receptor signals.

The sensitivity curves of the three systems, and thus the absorption spectra of the three different pigments in different cones, govern the colour mixture laws, the linear addition of the receptor signals takes care of Abney's law. Although the existence of three different pigments was hypothesized for a long time, the experimental evidence by microspectrophotometry (Brown and Wald, 1964; Marks *et al.*, 1964) made them a fact to be dealt with in any colour vision theory. The necessity to assume chromatic channels separate from a brightness channel in the information transport was already indicated by Piéron (1939), who showed that the luminosity curve changes only slightly after moderate chromatic adaptation. Without this assumption this experimental fact is deadly for the Helmholtz theory. In particular Hurvich and Jameson (1960) have stressed this point. They also have indicated, on the basis

that the luminosity curve of cone-monochromats is substantially like that of normal (Weale, 1953), that there must be a separate luminosity mechanism that is independent of the colour mediating responses. In addition to this separation, there is evidence to separate a red-green mechanism from a yellow-blue mechanism. Again it was Hurvich and Jameson (1960) who stressed this point, and so revived the Hering theory. The psychophysical evidence for this distinction that I find convincing is the different behaviour of red-green discrimination and yellow-blue discrimination as a function of luminance and diameter (Walraven and Bouman, 1966). Furthermore, the electrophysiological evidence for this distinction of two chromatic mechanisms by recording in the LGN of monkeys is overwhelming (De Valois *et al.*, 1966).

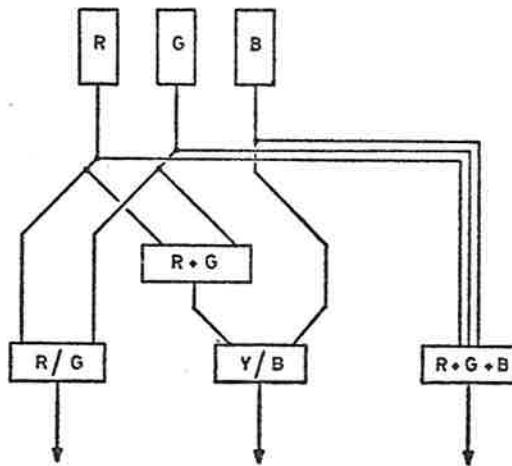


FIG. 1. Schematical representation of the described zone model of colour vision.

3. A MORE DETAILED PICTURE OF THE MODEL

The receptor level

In Fig. 2 the scheme of neural processing according to Vos and Walraven (1971) is given. The photopic retina is built up of red (R), green (G) and blue (B) cones. Of course colour names should not be given to these cones, but rather the indications, long wavelength, middle wavelength and short wavelength sensitive cones, e.g. indicated by a wavelength number for maximal sensitivity. However the indication of R-, G- and B-cones is used here as a sort of shorthand writing.

In accordance with general consensus it is assumed that the B-receptors are distinctly lower in population density. In general it is assumed that the R- and G-systems are more or less equivalent as to the number of receptors. In this model, however, it is assumed that there are twice as many R-receptors as G-receptors. The proportion of R-, G- and B-receptors is assumed to be 40:20:1. These data are average values. Depending upon the place in the retina the ratio might change. Thus, it is probable that the blue receptors in the centre of the fovea are even more scarce (Ruddock and Burton, 1972).

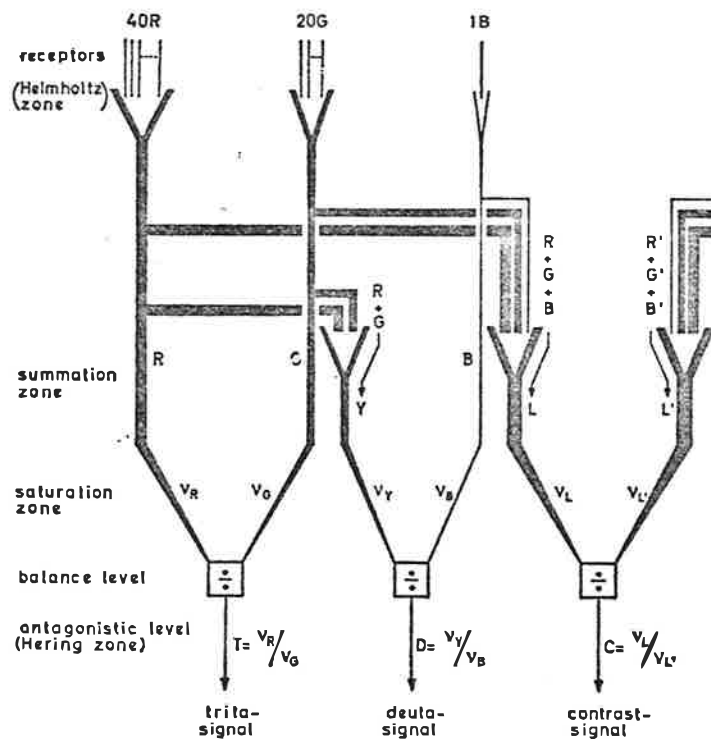


FIG. 2. Scheme of neural colour processing.

The derivation of the numbers of receptors and their spectral absorption curves is mostly based upon the observation that dichromatic vision can be conceived as a reduced form of normal trichromatic vision, plus a number of additional data.

In the model two main types of colour defectiveness are easily placed:

red-green defectiveness by inadequate function of the R/G channel; and yellow-blue defectiveness by failure of the Y/B channel. Such a failure may find its origin in the absence of one receptor system. In this scheme it is assumed that protanopia is due to loss of the R-receptors, deuteranopia to loss of the G-receptors and tritanopia to

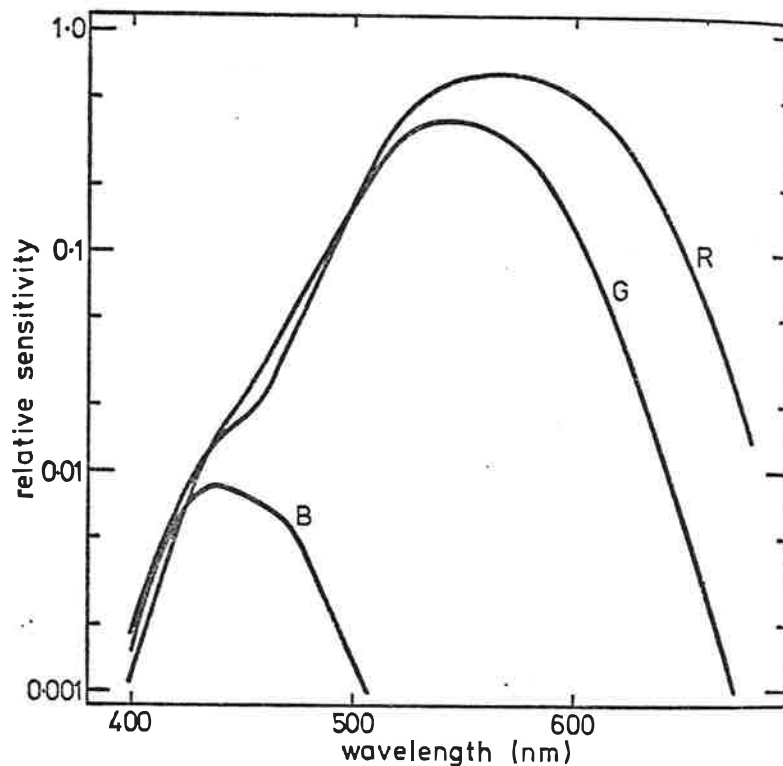


FIG. 3. The used set of spectral sensitivity functions for the foveal receptor systems.

loss of the B-receptors. The location of the dichromatic confusion centres are in the x_1, y_1 -diagram (revised CIE diagram according to Judd, 1951).

protanopic centre	$x = 0.7465$	$y = 0.02535$
deuteranopic centre	$x = 1.40$	$y = -0.40$
tritanopic centre	$x = 0.1748$	$y = 0.0044$

The corresponding fundamental response curves are given in Fig. 3.

According to Pokorny and Smith (1972) these curves are in excellent agreement with the luminosity curves of protanopes and deuteranopes. The hypothesis that deuteranopes have both the normal red and the normal green pigment, and that the nerves from the two kinds of cones are 'fused' is in this scheme rejected. That hypothesis has been very popular because the confusion lines of deuteranopes at the CIE diagram seemed to converge very near $x = 1.0$, $y = 0.00$. This point is the theoretical convergence point for such a fusion deuteranope. But Nimeroff (1970) cleared up a longstanding error. He has shown from the literature, including some from Russian sources, and from his own measurements that although there is a considerable spread, the convergence points have a weighted mean of $x = 1.54$ and $y = -0.54$. The chosen x_1 - and y_1 -values in our scheme are in the permissible range of Nimeroff's data. It is also in accordance with Alpern *et al.* (1968) and Richards and Luria (1968), who conclude that all the deuteranopes they studied were completely lacking the green pigment. And it is also in line with Rushton's view that in addition to cyanolabe the protanope has only the pigment chlorolabe (1963) and the deuteranope only the pigment erythrolabe (1965).

The densities of these pigments has been a matter of dispute in recent years. Although the common view was that these densities in cones were pretty low, the report by Dobelle *et al.* (1969) suggests high values (>0.7). This finding gives more basis to the so-called self-screening hypothesis, which explains the deviations in colour matching after bleaching (Brindley, 1955; Terstiege, 1966), changes in the Stiles-Crawford effect after bleaching (Walraven, 1966) and the second Stiles-Crawford effect (Walraven and Bouman, 1960). A tetrachromatic hypothesis, where a fourth receptor system is introduced, like that suggested by Ingling (1969), is then not necessary.

The determination of the ratio of number of receptors will be treated in the next section on the nervous processing.

The nervous processing

The Bezold-Brücke effect is the change in hue when coloured light is changed in intensity. The classical measurements were made by Purdy (1931, 1937), confirmed by Van der Wildt and Bouman (1968) and Boynton and Gordon (1965), and extended to the purple region of the spectrum by Walraven (1961).

Light of the wavelengths 570 nm and 476 nm does not change, these are invariant hues. Walraven (1961) has shown that the effect can be explained quantitatively in terms of saturation of nervous processing in the separate chromatic mechanisms. The neutral wavelengths are those at which the antagonistic R-G and Y-B nervous processes are in balance, so that they saturate at the same rate, and so that the ratio of

their load levels remains equal to one, from low to high stimulation levels.

As a matter of fact, we find here another argument for separation of chromatic and brightness channels. Non-linear processes of the kind to explain the Bezold-Brücke effect quantitatively, when apparent also in the brightness channel, would be contrary to Abney's law. So these non-linear processes must occur in separate chromatic channels.

Coming back to the condition for the neutral wavelengths, this amounts to

$$\nu_R/\nu_G = \text{constant} \quad \text{and} \quad \nu_Y/\nu_B = \text{constant}$$

ν being the neural activity instead of the physical stimulation (see Fig. 2). Leaving aside by which actual process and in which way this nervous saturation occurs, this condition means, e.g. for 570 nm, that the R- and G-receptors should have equal input. With N_R and N_G the number of R- and G-receptors in the retinal area under consideration, and with R_{570} and G_{570} for the systemloads, the mathematical expression for equal receptor load is

$$\frac{R_{570}}{N_R} = \frac{G_{570}}{N_G}$$

Similarly for 476 nm we get,

$$\frac{(R+G)_{476}}{N_{R+G}} = \frac{B_{476}}{N_B}$$

in which we have to consider N_{R+G} as the number of receptors feeding into the (R+G)-channel, assuming that the Y-signal = R+G. The spectral sensitivities at the indicated wavelengths (see Fig. 3) give then the answer:

$$N_R:N_G = 2:1 \quad \text{and} \quad N_B:N_{R+G} = 1:20.$$

REVIEW OF ALTERNATIVE MODELS

In the scheme of Fig. 2 it is left open how at the balance level the messages from the receptors are recoded into opponent responses in the two chromatic channels and the brightness channel.

Jameson and Hurvich (1968) and Richter (1969) derive opponent responses as linear relations with the absorption curves of the photopigments. Some authors like Bouman (1969) and Sperling (1971) think of these responses as differences between outputs of receptors; others such as Shklover (1969), Matveev (1969) and Meessen (1968) assume logarithmic or other non-linear transformations before recording takes place.

The processes depend also on the state of adaptation. Koenderink

et al. (1972) worked out a Weber-adaptation model. Other refinements are possible for certain cases where Abney's law apparently does not hold, as for instance, at the absolute threshold. Guth (1971) considers vector addition then as a useful alternative to Abney's law.

As indicated by the use of the terms trita-signal and deuta-signal in Fig. 2 the scheme supposes in fact that normal colour vision is a combination of tritanopic (interaction of the R- and G-system) and deuteranopic (interaction of the Y- and B-system) vision. The term deuteranopia is based on the 'old' notion that deuteranopia is due to fusion of the red and green systems. Judd and Yonemura (1969) suggest, following the Müller theory, that it is a combination of tritanopic and protanopic vision. Hassenstein (1967) presents another variation by assuming that the green system is antagonistic to a combined action of blue and yellow systems. Abranov (1968) rejects the G-input in the Y-B channel, Guth *et al.* (1968) the B-input to the brightness channel as well. Wiesel and Hubel (1966) raised doubts as to the presence of the G-input into the Y-B system.

At present there is not enough evidence to make a choice between all the mentioned variations. With this in mind, I still prefer the hypothesis that $Y = R + G$, because the properties of colour discrimination along the tritanopic confusion lines in the normal colour mixture diagram are the same for normals, if colour discrimination along these lines is considered as the interaction of the (R+G)-system and the B-system (Walraven and Bouman, 1966). But even this is loaded with doubts now, because one of the facts emerging from the discussions at the Helmholtz Memorial Symposium on Color Metrics (1972) is that the variability in colour discrimination data does not yet permit definite conclusions as to the model used for predicting colour discrimination and the formulation of the line-element. Nevertheless, the choice of $Y = R + G$ seems to my mind the most simple and therefore obvious choice.

In this way groups of receptors are linked. This fits in with a suggestion by Bouman (1969) that the cones of the human retina are organized in distinct units which he calls 'human ommatidia'. Such an ommatidium contains red, green and blue cones in certain proportions, and also rods in a number dependent upon eccentricity. This brings in an element which has to be added in a way that they act as white signals which inundate the red-green and yellow-blue channels more and more as eccentricity increases. This would explain the tendency towards dichromacy and monochromacy with increasing eccentricity.

Hough (1968) and Ruddock (1971) think along the same line that rod signals are colorimetrically neutral but suppose more specifically, supported by Trezona (1970), that the rods and blue cones share their input before recording takes place.

6. NECESSARY FURTHER DEVELOPMENTS

An essential extension of Fig. 1 as depicted in Fig. 2 is that the brightness signal is not just an addition of R, G and B, but is also compared with signals from neighbouring receptors or groups of receptors at the balance level. This makes it a real Hering-scheme as compared with Fig. 1, so that by contrast the colour black also finds its place in the model.

Spatial colour transfer functions show that the spatial pass band for yellow-blue is smaller than for red-green (Horst, 1969). Moreover, those inhibitory effects as occur in brightness vision, which are the sources of Mach bands, are very weak or missing in the mechanisms of colour vision. Colour Mach bands do not occur. All these lateral interactions, different for each of the chromatic channels and for the brightness channel, must be taken into account in order to complete the model. A first attempt of such kind has been made by Koenderink *et al.* (1972).

Reviewing the last ten years, the controversies changed from Helmholtz versus Hering to alternatives of the trichromatic opponent scheme. The first controversy was finally solved by objective measurements in the receptors and in the nervous system. However, there is still a need for psychophysical and electrophysiological data in order to improve our insight in the mechanisms of colour vision.

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