Tagungsband Luzern 1965

P. L. Walraven*, SOESTERBERG:

A Zone Theory of Colour Vision

DK 612.843.311.3

Es wird eine Zonentheorie zur Erklärung des Farbensehens aufgestellt, die die Theorien von Young-Helmholtz und Hering kombiniert. Die vorliegenden Daten über die Unterscheidung von Wellenlängen als Funktion der Leuchtdichte lassen zwei verschiedene Mechanismen für die Rot-Grün- und für die Gelb-Blau-Unterscheidung vermuten. Andererseits lassen einige psychophysische Erscheinungen wie die Stiles-Crawford-Effekte und die Farbumstimmung drei verschiedene Sehpigmente in den Rezeptoren annehmen, aus denen sich die spektralen Absorptionskurven und die Extinktion erklären lassen.

La vision des couleurs est expliquée par une théorie de zones combinant les théories Young-Helmholtz et de Hering. Les précisions données sur la discrimination des longueurs d'onde en fonction de la luminance, nous forcent à supposer deux mécanismes distincts pour le rouge/vert et le jaune/bleu. Quelques phénomènes psychophysiques, comme les effets Stiles-Crawford et l'adaptation chromatique, nous poussent d'autre part à admettre l'existence de trois pigments visuels différents dans les récepteurs ce qui expliquerait les courbes d'absorption spectrale et les densités.

Arguments are put forward to explain the basic facts about color vision in the frame work of a zone theory, a combination of the Young-Helmholtz and the Hering theory. Data on wavelength discrimination in particular as a function of luminance, necessitate to assume separate mechanisms for red-green and for yellow-blue discrimination (Hering). Some psychophysical data on the other hand, like the Stiles-Crawford effects and those on chromatic adaptation, give reason to assume three different visual pigments in the receptors, of which the spectral absorption curves and the densities can be derived.

During more than a century two theories of colour vision exist, the YOUNG-HELMHOLTZ theory and the HERING theory. In 1881 DONDERS [1] proposed that the solution might be that both theories are valid. Such a point of view, mostly called a *zone theory* — because both theories would apply to different zones in the transmission of the visual information — appeared several times in the literature. Especially the name of G. E. MÜLLER [2] is associated with it. The zone theory however did not get many adherents. In 1962 the author [3] proposed again a zone theory.

A row of arguments can be put forward to support the YOUNG-HELMHOLTZ theory. Already old data indicate that the fundamental response curves according to the YOUNG-HELMHOLTZ theory are peaked at about 450, 540 and 590 nm. We refer here to PITT [4], who based his determination on the properties of colour defective observers. New data on chromatic adaptation obtained by BRINDLEY [5] — although one can

* *Institute for Perception R. V. O. - T. N. O., Soesterberg (The Netherlands)*

differ in opinion about the interpretation (WALRAVEN [3; 6], WALRAVEN, VAN HOUT and LEEBEEK [7]) — are in agreement with that. Also the measurements by RUSHTON [8] and RIPPS-WEALE [9] on the reflection of light from the fundus after bleaching agree with these values. The recent analysis [10] of the chromatic STILES-CRAWFORD effect indicates, like RUSHTON's and WEALE's data, that the YOUNG-HELMHOLTZ character of colour vision is associated with three different cone pigments. The recent data obtained with microspectrophotometry of single cones do not leave any doubt about that [11; 12].

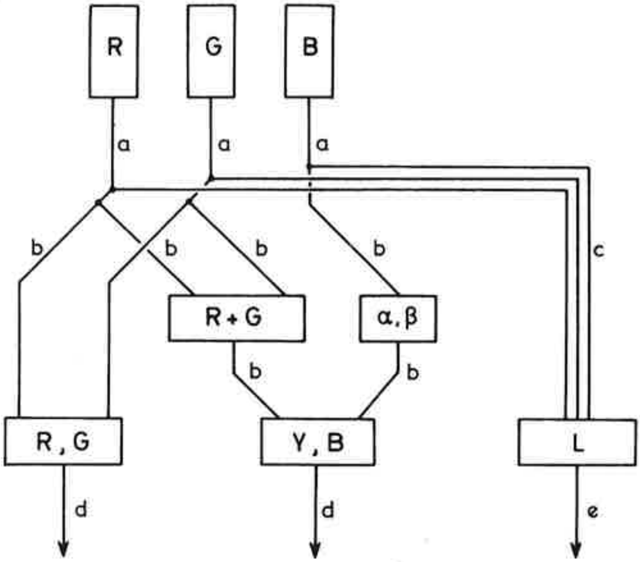

Fig. 1: Scheme of a zone theory of colour vision

On the other hand there are many arguments in favour of the HERING theory. In particular HURVICH-JAMESON [13] have defended this point of view based on the analysis of psychophysical data. In our opinion one of the strongest arguments to make a distinction between brightness and chromaticness channels is the fact that after moderate chromatic adaptation the colour impression changes while the luminosity curve keeps its shape according to PIÉRON [14]. Moreover the electrophysiological findings by SVAETICHIN et al. [15] in the fish retina, and by DEVALOIS et al. [16] in the lateral geniculate nucleus of the monkey do not leave any doubt that the HERING theory is valid somewhere in the nervous system.

The scheme proposed in fig. 1 tries to combine the two features. There are three kinds of cones, the so called "red", "green", and "blue" cones, in a ratio of roughly 10:10:1 [3]. The absorption curves of the visual pigments in these cones are suggested to be a revision of the WRIGHT-THOMSON curves [17] corrected for the absorption in the eye media. The brightness signal L is the sum of the brightness contributions of the three different cone systems after going through the channels a and c and is transmitted through channel e.

The chromaticness information is transmitted through the channels b. The information from the red and green cone systems goes to a red-green centre, from which the R, G signal is transmitted along a channel d to higher centres. A yellow (Y) signal is thought as the addition of the red and green signals $R + G = Y$. It arrives in a yellow-blue centre, from which the Y, B signal is transmitted to the higher centres. The blue system does little contribute to brightness, but as far as chromaticness is concerned, it is of as much of value as the red and green systems. The chromaticness valence factor $\alpha \approx 10$ in channel b of the blue system takes care of that. The weighting factor β is a luminance-dependent variable to describe the behaviour of colour discrimination as a function of luminance [18].

The model explains the data as mentioned above, and the different kinds of colour defective vision.

References

[1] DONDERS, F. C., Über Farbensysteme. Graefes Arch. Ophthalm. **27** (1881), pp. 154-167
[2] MÜLLER, G. E., Über die Farbenempfindungen. Z. Psych., Erg. Bd. **17/18**, **46** (1930), pp. 508-541
[3] WALRAVEN, P. L., On the mechanisms of colour vision. Thesis Univ. of Utrecht 1962
[4] PITT, F. H. G., The nature of normal trichromatic and dichromatic vision. Proc. Roy. Soc. **B 132** (1944), pp. 101-117
[5] BRINDLEY, G. S., The effects on colour vision of adaptation to very bright lights. J. Physiol. **122** (1953), pp. 332-350
[6] WALRAVEN, P. L., Proc. Photobiology Congress Oxford (in press)
[7] WALRAVEN, P. L., A. VAN HOUT and H. J. LEEBEEK, Fundamental response curves of a normal and a deuteranomaleous observer derived from chromatic adaptation data. J. opt. Soc. Amer. **56** (1966), pp. 125-127
[8] RUSHTON, W. A. H., A foveal pigment in the deuteranope. J. Physiol. **176** (1965), pp. 24-45
[9] RIPPS, H., and R. A. WEALE, Photo-labile changes and the directional sensitivity of human fovea. J. Physiol. **173** (1964), pp. 57-64
[10] WALRAVEN, P. L., and M. A. BOUMAN, Relation between directional sensitivity and spectral response curves in human cone vision. J. opt. Soc. Amer. **50** (1960), pp. 780-784
[11] BROWN, P. K., and G. WALD, Visual pigments in human and monkey retinas. Nature **200** (1963), pp. 37-43
[12] MARKS, W. B., and E. F. MACNICHOL jr., Difference spectra of single goldfish cones. (Abstr. 2143). Fed. Proc. **22** (1963), S. 519

[13] HURVICH, L. M., and D. JAMESON, Color vision. Ann. Rev. Psychol. **11** (1960), pp. 99-121

[14] PIÉRON, H., La dissociation de l'adaptation lumineuse et de l'adaptation chromatique. L'Année psychol. **40** (1939), pp. 1-29

[15] SVAETICHIN, G., and E. F. MACNICHOL jr., Retinal mechanisms for chromatic and achromatic vision. Ann. N. Y. Acad. of Sciences **74** (1958), pp. 385-404

[16] DEVALOIS, R. L., G. H. JACOBS, and A. E. JONES, Responses of single cells in primate red-green color vision system. Optik *20* (1963), pp. 87-98

[17] WALRAVEN, P. L., and H. J. LEEBEEK, Phase shift of alternating coloured stimuli. Doc. Ophthalm. **18** (1964), pp. 56-71

[18] WALRAVEN, P. L., and M. A. BOUMAN, Quantum theory of color discrimination of normal trichromats. Vision Research (in press)

Anschrift des Verfassers:
Dr. P. L. Walraven
Institute for Perception R. V. O. - T. N. O.
Soesterberg (Niederl.)

Eingang des Manuskriptes:
1. Juni 1965