

ON THRESHOLD MECHANISMS FOR ACHROMATIC AND CHROMATIC VISION

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ABSTRACT

On the basis of measurements of the achromatic zone for red light in the fovea and for green light in the periphery, a discussion is given on the possible difference in threshold mechanisms for the achromatic (scotopic) and chromatic (photopic) retinal systems. A specific suggestion for this distinction is given that not directly refers to the usual rod-cone concept but is based on the occurrence of multiple coincidence of quantum absorptions by multiple hits per receptor no matter rod or cone as photopic signals, versus multiple coincidences by single hits per receptor in a distinct ommatidium type group of receptors as scotopic signals.

INTRODUCTION

One of the pillars of our knowledge of the primate's visual system is the retina's duplicity: the existence of both a photopic and a scotopic system. This duplicity becomes apparent in fast and slow adaptation phenomena, in a shift of spectral sensitivity curve towards shorter wavelengths with decreasing illuminance and in chromatic and achromatic perception of stimuli. These well-established and experimentally frequently confirmed facts have settled this duplicity beyond any doubt. It has been widely accepted that the existence of two different classes of receptors, rods and cones explains this very fact of two types or categories of visual perception. This explanation, however, is theoretical and is morphologically not completely convincing (PEDLER, 1965).

SCOTOPIC AND PHOTOPIC CONE VISION

A well-known psychophysical phenomenon that contradicts the rod-cone idea as basis for the retina's duplicity are the achromatic perceptions of weak monochromatic stimuli that are presented foveally. In fact these foveal achromatic perceptions are – as introspection tells us – not

different from peripheral scotopic ones. Consequently in visual theory, scotopic perceptions mediated by foveal receptors have to be considered.

This naturally leads to the question of whether these receptors constitute a foveal scotopic system that is apart from the photopic system or whether the separation between these systems does occur at receptor level at all. If not, the same receptors can participate in photopic as well as scotopic perception.

This problem has been recognized as such earlier. We quote from GRAHAM et al. (1969): 'It was known to past researchers in vision (e.g., König, Nagel, von Kries: see discussion in PARSONS, 1924) that an achromatic threshold exists in the fovea at a lower value than applies to the chromatic threshold, although its basis was controversial. In particular, it was widely attributed to foveal rods. MONROE (1925) represented the contradictory, now accepted, position that there is a cone achromatic interval'.

Recently SPILLMAN et al. (1971) came to a conclusion in favour of this latter possibility as well. Our studies on threshold behaviour and its relation with the quantum statistics of the stimuli yielded relevant data on this achromatic zone or photochromatic interval. This zone or interval is the ratio between the chromatic threshold and the visual threshold. In the fovea it was found to be about 1.35 for monochromatic red circular flashes (BOUMAN and WALRAVEN, 1957). This value was confirmed by CONNORS (1970). There is surprisingly good agreement between most studies of various authors including ours (fig. 1) on the

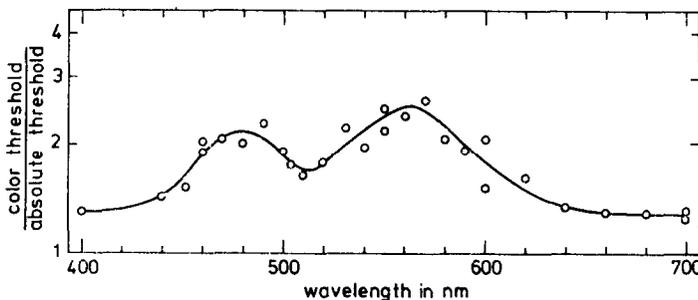


Fig. 1. The achromatic zone as a function of wavelength for a diameter of 60'.

constancy of the achromatic zone for wavelengths longer than 640 nm (WALRAVEN, 1962; GRAHAM and YUN HSIA, 1969; NOVAKOVA, 1970). The fact that the visual and chromatic thresholds depend in the same

way upon wavelength suggests in that region of the spectrum equal action spectra of the receptors that contribute to these types of perception. In our experiments the photochromatic interval was also measured for various choices of stimulus area and duration. A striking and basic result proved to be the similar behaviour of both thresholds in their dependence on these spatial and temporal parameters of the stimuli (fig. 2). These findings confirmed by TITTARELLI (1967) compel us to consider the possibility that a particular receptor population, more particularly the 'red' cones, does indeed have a chromatic and an achromatic transmission system connected with it. Both systems should show threshold mechanisms that are in some aspects quite alike, but differ in others. In the long wavelength end of the spectrum the photopic responses are always red. This is understandable when we realise that for these wavelengths the absorption of the green system is negligible when compared to that of the red system, because the ratio of absorption of the two systems is about 1:25 according to VOS and WALRAVEN (1971).

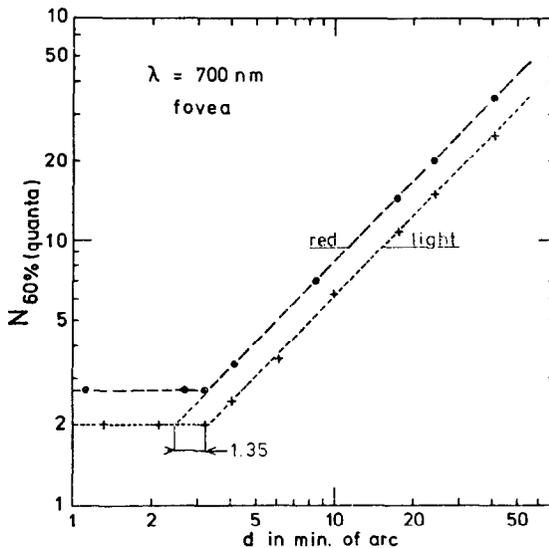


Fig. 2. Threshold energy (relative units) for the dark-adapted fovea as a function of diameter d of the circular testflashes, duration 0.02 sec. for 700 nm light. The lower curve represents the absolute threshold, the upper curve the colour threshold.

PHOTOPIC AND SCOTOPIC ROD VISION

Threshold measurements similar to those of fig. 2 were performed for

short test flashes 12 degrees temporal from the fovea in the dark adapted eye for 510 nm light. The results are represented in fig. 3.

Conclusions from such measurements are:

- (1) the photochromatic interval for large test areas is about a factor 8;
- (2) both the absolute achromatic or scotopic and the photopic (chromatic) threshold follow in their dependences on testfield diameter the same pattern as they do in the fovea for red light;
- (3) the photochromatic interval was found constant between 450 and 550 nm (450 nm: 7.1, 510 nm: 8.0, 550 nm: 7.8 for flashes 20 minutes diameter) so that both thresholds are mediated here by the rods;
- (4) the photopic perceptions that appear at about 8 times absolute threshold level are always white. In fig. 3 the detection threshold data are represented by the curve labelled 'light'. This curve separates invisible stimuli from visible ones. The curve for 'white' represents the photopic threshold which distincts stimuli whose intensity is too low for recognition of a specific colour in its perception (including white) from perceptions in which such recognition can be done. The first colour that under increase of luminance appears for the stimuli concerned turns out to be white.

Other receptors, particularly the green cones may be responsible for the greenish perceptions that occur at much higher intensity levels. Indeed the interval between the greenish and the absolute threshold depends on wavelength: for 510 nm: 200, for 480 nm: 14 and for 550 nm: 250 for 20 minutes of arc diameter flashes.

The above findings point to the possibility that the rods have a 'white' and an 'achromatic' transmission system connected with them. SPILLMAN and SENEFF (1971) distinguished only absolute threshold and 'correct' hue threshold. Their photochromatic interval is the relation between these two thresholds. Consequently their results can not directly be compared with ours.

The suggestions mentioned could be rather unacceptable if the scotopic cone and scotopic rod signals could not meet in a common system. From absolute threshold experiments with test flashes consisting either of monochromatic red, or of monochromatic green light or of mixtures of both, we know that subliminal effects in both receptor populations interact as if they were part of one system. The red and green lights that were used selectively stimulated the red cones and the rods in the dark adapted peripheral retina (BOUMAN and VAN DER VELDEN, 1948).

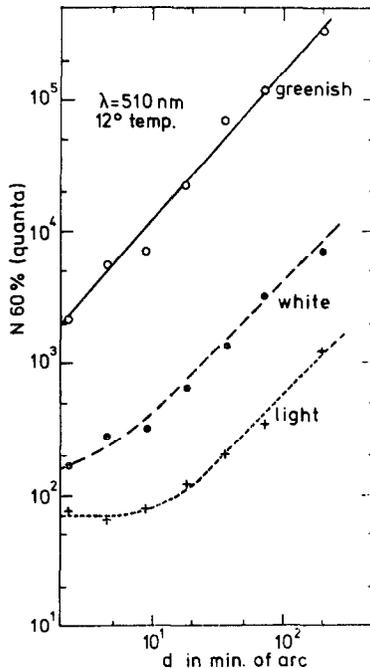


Fig. 3. Detection threshold (light), white and greenish photopic thresholds $N_{60\%}$ in quanta of 510μ light for dark-adapted peripheral vision, 12° temporal as a function of diameter d of circular testflashes, duration 0.02 sec.

PHOTOPIC AND SCOTOPIC THRESHOLD MECHANISMS

All four curves of figs. 2 and 3 show for large diameters threshold energy E_{th} to be proportional to testfield diameter: Piper's law. For small d -values Ricco's law $E_{th} = \text{constant}$ is valid over various ranges of d -values. This suggests that for all four threshold curves the same type of mechanism is responsible for triggering of the perception. This would mean that at a particular retinal location spatial and temporal conditions for reaching of the chromatic threshold are more severe than of the achromatic one. For instance the value 1.35 mentioned for the photochromatic interval for red flashes in the fovea could mean that Ricco's summation area for the photopic mechanism is about half ($1/1.35^2$) of this area for the scotopic one. Indeed for large test-field diameters the photopic threshold curve can be brought upon the scotopic one by a horizontal shift of a factor 1.35. Blur and imperfections of the eye optics unfortunately disallow the possibility that this difference could

manifest itself in different sizes of Ricco's region in the area-threshold relations for both thresholds. At 12° eccentricity the photopic summation area would be 1.5% ($1/8^2 = 1/64 = 0.016$) of this area for the scotopic system, because the achromatic zone here is 8. Here some of this large difference in Ricco's region does show up in the experimental results by the much smaller photochromatic interval for the smallest target areas studied.

In the fovea even for the scotopic signals Ricco's area is less than 2 min of arc in diameter, at 12° in the periphery the photopic system's summation area might also very well be less than this value of 2 min of arc. A very intriguing question is how many receptors are exactly covered by such photopic summation area of less than 2 min of arc diameter.

An extreme but very interesting possibility is that the individual receptor itself carries the summation mechanism by which photopic signals are triggered. This would mean that the scotopic mechanism for red light in the fovea is represented in a special type of interaction between pairs of red cones.

From absolute threshold experiments in the fovea with red and green light – similar to those mentioned for the study of interaction in the peripheral retina between red cones and rods – we found that subliminal effects in red and green cones interact also as if these two kind of cones were part of one system (BOUMAN and VAN DER VELDEN, 1948).

The photochromatic interval (fig. 1) reaches for foveal stimuli a maximum value of about 2.5 around 580 nm (WALRAVEN, 1962). Here the scotopic summation area should correspondingly be about 6 times as large as the photopic one. If the individual receptor represents the photopic Ricco area the scotopic system is then stimulated by interaction between subliminal effects in groups of receptors containing only a few red and a few green cones and an eccentricity dependent number of rods. Such a group would resemble the ommatidium of the insect eye (BOUMAN, 1969).

At 12° in the periphery the scotopic excitation unit should on the basis of the ideas given above contain about $8^2 = 64$ rods. Because for red light the photochromatic interval is at 12° eccentric almost as small as in the fovea, the ommatidium has in addition to these 64 rods the same numbers of the different types of cones as the ommatidium in the fovea has. This means that the ratio of rod and cone numbers pro unit area is here about 10 : 1. This is in agreement with the histological data for this retinal eccentricity.

The given suggestion for rods being part of the photopic system

and that white signals are generated in them must be considered with due reserve. However, it is worth to consider it just as the idea that cones are part of the scotopic system as well. None of these two ideas is new. Recently STABELL and STABELL (1969), McCANN et al. (1969) and TREZONA (1970) made suggestions concerning participation of rods in colour vision. Only the further specification of the difference in spatial and temporal requirements for the elicitation of photopic and scotopic signals from essentially the selfsame receptor population is the special issue of this paper.

If the validness of Piper's law is due to a two-fold quantum coincidence as threshold mechanism – as VAN DER VELDEN (1944) suggested – the following picture further emerges: two- and morefold coincidences of single hits in cones and/or rods within an ommatidium of these receptors produce achromatic or scotopic perceptions. Colour appears in the perception when cones and/or rods are individually hit by two and more quanta.

In this picture twofold quantum coincidence mechanisms mark the distinction between visible and invisible stimuli and between chromatic (photopic) and achromatic (scotopic) perceptions. Because of its surprising simplicity and intriguing precise and direct specification it is an elegant and interesting picture. However, its basis is controversial (PIRENNE, and MARRIOT, 1955; BARLOW, 1956; BRINDLEY, 1963). Elsewhere some comments are given on this controversy (BOUMAN and KOENDERINK, 1972).

Most of the direct arguments in favour of the two-quantum concept are psychophysical in nature. ZWAARDEMAKER's (1921) very first surmises of the significance of the concept were already based on critical evaluation of absolute energy values of psychophysical thresholds.

Only recently electrophysiology entered this problem area with experiments that are to our opinion very valuable and very adequate for testing such specific quantitative concepts.

In a way the study concerned is an extrapolation of KUFFLER's (1953) first approaches towards the functional meaning of action potential patterns in the retina. BARLOW and LEVICK (1969) estimated the intensities of brief test stimuli that are needed to produce an extra action potential in a retinal ganglion cell of the dark adapted cat retina. The test flashes were probably small enough in order to fill only the central excitatory zone of the cell's receptive field and not to extend onto the inhibitory surround. The authors loosely supposed a percentage as

large as 25 for the fraction of the 507 nm light incident upon the cornea that is effectively absorbed in the rods.

They arrived this way at an average number still as low as 2.7 quanta at the number needed for an extra spike under these conditions. In animal preparations of the same type LEVICK and SACKS (1970) demonstrated the restricted validness of Bloch's law for these threshold responses of the retinal ganglion cells. This excluded the possibility that actual threshold responses are elicited by single quantum absorptions. Indeed $I \times t = \text{constant}$ would then hold for indefinite long durations t . Consequently these electrophysiological studies make it realistic that the number 2 is the lowest number that succeeds in eliciting an action potential in the cat's retinal ganglion cell layer, even more because the 25% chosen by the authors for the cat's eye quantum efficiency seems more readily too high than too low a figure.

Elsewhere other more spurious indications from electrophysiological studies are reviewed (BOUMAN, 1969; BOUMAN and KOENDERINK, 1972). Altogether they provoked the idea that the two quantum concept has a significant general value for the dark-adapted duplex visual system not only of the vertebrates but the invertebrates as well.

So far about this paper's topic for dark-adapted conditions. What would happen to these photopic and scotopic two-quantum threshold mechanisms when the eye is light-adapted?

ADAPTING SCOTOPIC AND PHOTOPIC COINCIDENCE SCALERS

In the frame-work of a further study of possible roles of quantum coincidence mechanisms for visual discrimination, it has been suggested that the multiplicity of single hits per perceptive retinal unit needed from the test-stimulus in order to be seen is subject to adaptive changes (BOUMAN, 1952). Such suggestions initiated from studies of threshold dependences on stimulus parameters like area and duration that were similar to those studies from which for absolute thresholds the two-quantum concept was deduced. More specifically, such experiments firstly showed that threshold detection might rely on a coincidence mechanism whose multiplicity increases proportional to the square root of the average number of quantum absorptions from the background illumination (BOUMAN, 1961, 1964). This way the coincidence requirement goes parallel with the inherent quantum noise of the stimuli. This noise in itself has no significant value for visual perception and is by the adaptive effect mentioned eliminated to a certain degree from further pene-

tration into the visual system. It makes that under the simple conditions of small short testflashes on a large homogeneous background psychophysical contrast thresholds (fig. 4) run proportional to the square root of the illumination level: the DE VRIES-ROSE law (DE VRIES, 1943; ROSE, 1948). In the same pioneer work as referred to in the previous section BARLOW and LEVICK (1969) demonstrated the validness

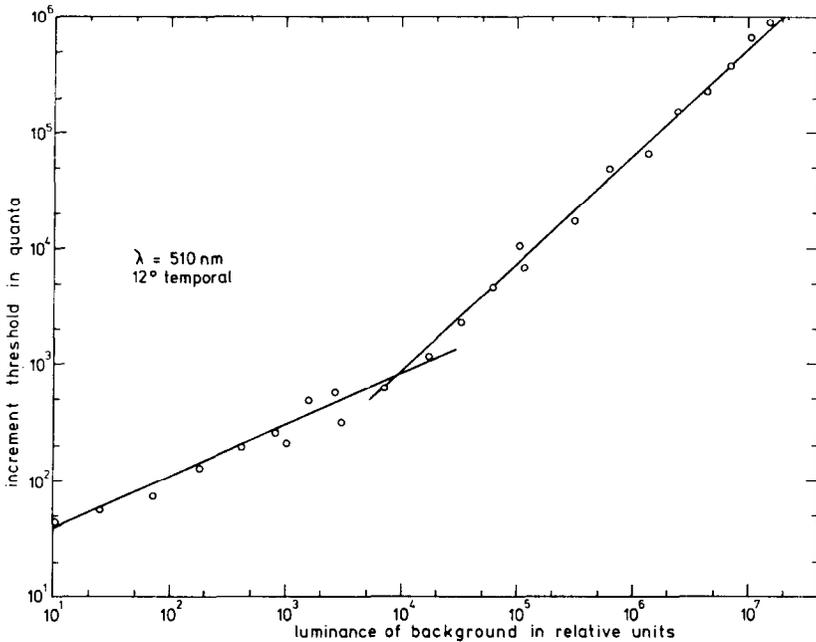


Fig. 4. Increment thresholds $N_{60\%}$ in quanta of 510 nm light for circular testflashes 20 min of arc diameter as a function of luminance of steady background 10° diameter and also 510 nm, for peripheral retina 12° temporal from fovea.

of this DE VRIES-ROSE law for the production of action-potentials in ganglion cells of the cat's retina: the number of quanta needed in a test flash in order to give an extra spike is proportional to the square root of background illuminance B over almost five log units of B . In connection with this result Barlow and Levick advocate the same type of ideas as mentioned above. For higher illuminance levels for both psychophysical and electrophysiological thresholds another law is valid. In fig. 4 this is demonstrated for the case of psychophysical thresholds. FISCHER and MAY (1970) found an analogous behaviour for the threshold

effect in the action potential production of the retinal ganglion cells. These results show the validness of Weber's law for these higher intensities: threshold energy is proportional to illuminance level. It means that the multiplicity of the quantum coincidence upon which the threshold mechanism is now operating is proportional to the average quantum catch per receptor at the transition luminance mentioned shows an absorption rate of about one quantum per few hundredths of a second per receptor. Consequently Weber's law becomes valid when almost all the photopic excitation units are almost continuously stimulated. This would mean that the intensity range over which DE VRIES-ROSE's law is valid is related to the achromatic zone in a very specific way (BOUMAN and KOENDERINK, 1972).

Elsewhere mechanistic models have been proposed for the strategy along which the scotopic and photopic systems are under variation of illumination levels brought to their appropriate coincidence scaling values (BOUMAN and AMPT, 1966; VAN DE GRIND et al., 1971; KOENDERINK et al., 1971).

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