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Peripheral Colour Vision: Effects of Rod Intrusion at Different Eccentricities

BJØRN STABELL,*† ULF STABELL*

Chromaticities of monochromatic lights from different parts of the spectrum were measured both during the cone-plateau period of the long-term dark-adaptation curve and in a completely dark-adapted state. The measurements were obtained at 3, 8, 30 and 65 deg in the temporal field of view and at 1, 2, 3 and 4 log units above the cone-plateau level. The results show that cone-mediated colours obtained during the cone-plateau period in general are desaturated when rod signals intrude during long-term dark adaptation. The desaturation effect of rods obtained at high mesopic illumination levels was found to increase when the test field was moved from 3 to 30 deg but to reduce markedly between 30 and 65 deg. Surprisingly, the desaturation was clearly observable even at a retinal illumination of 20,000 ph td. The desaturation effect of rods is explained by the suggestion that differences in ongoing activity rates of the different types of spectrally opponent cells become levelled out to some extent when light signals from rods intrude during dark adaptation. Copyright © 1996 Elsevier Science Ltd.

Colour vision   Peripheral vision   Rods   Rod–cone interaction

INTRODUCTION

It is well known that the colour of a test light may desaturate and change qualitatively when the test light is moved outward from the rod-free area of the fovea into the far peripheral retina (Ferree & Rand, 1919; Moreland & Cruz, 1959; Boynton et al., 1964; Weitzman & Kinney, 1969; Gordon & Abramov, 1977; Van Esch et al., 1984; Stabell & Stabell, 1982, 1984; Abramov et al., 1991, 1992; Stromeyer et al., 1992; Nagy & Doyal, 1993). The most extensive quantitative study of this change in colour has been performed by Moreland & Cruz (1959). They introduced an ingenious asymmetric colour matching technique, whereby the colour appearance of monochromatic test lights viewed at different eccentricities could be matched by means of a foveal comparison field consisting of the Wright primaries 650, 530, and 460 nm. The asymmetric matches could then be plotted directly in the foveal WDW-system.

By this technique they measured the extrafoveal spectrum loci from 10 to 50 deg and found that colour vision tended to become dichromatic at 25–30 deg and monochromatic at 40–50 deg. Since the measurements were obtained in a dark-adapted eye at a moderate intensity level, they suggested that the rod receptor system might also be involved and contribute both to the

desaturation and the change in hue observed with eccentricity (Moreland & Cruz, 1959; Moreland, 1972).

Later on, psychophysical evidence has accumulated supporting this suggestion. Thus, in opposition to the Duplicity Theory of vision (Saugstad & Saugstad, 1959) it has been found that rod signals may change the chromaticities of cone-mediated colours over a long transitional intensity interval above the absolute dark-adapted cone threshold (v. Stabell & Stabell, 1975). In fact, at low mesopic illumination levels cone-mediated colours may be completely suppressed by light signals from rods (Lie, 1963; Spillmann & Conlon, 1972).

Hence, in order to unravel the underlying mechanisms of the deterioration of colour vision observed when a test field is moved outward from the fovea into the far peripheral retina, it appears necessary to analyse the relative contribution of the rod and cone components involved. To this end attempts have previously been made to isolate the contribution of the cone system by measuring wavelength discrimination and chromaticity coordinates of monochromatic lights during the cone-plateau period at different eccentricities (Stabell & Stabell, 1982, 1984). In the present study, on the other hand, we investigate the contribution of the rod system. The measurements were obtained at 3, 8, 30 and 65 deg. Since previous evidence strongly indicates that the effect of rod activity on colour vision decreases markedly with intensity (Wright, 1946; Lie, 1963; Stabell & Stabell, 1975), the measurements were obtained at different retinal illumination levels as well. Surprisingly, the

*Department of Psychology, University of Oslo, Box 1094, Blindern, N-0317, Oslo 3, Norway.
†To whom all correspondence should be addressed.

results show that in the far peripheral retina rods may affect cone-mediated colours, even at a retinal illumination of 20,000 ph td.

GENERAL METHODS

Well-founded evidence indicates that colour vision measured during the cone-plateau period of the long-term dark-adaptation curve is exclusively mediated by the dark-adapted cone system, while the change in colour observed during the further stay in the dark is an effect of rod intrusion (Stabell & Stabell, 1976a,b, 1980a,b). In the present study, therefore, chromaticities of monochromatic test lights were measured both during the cone-plateau period and in a completely dark-adapted eye. The chromaticity shift, computed from these two measurements, could then be ascribed to the effect of rod intrusion.

Apparatus

The apparatus employed was a Wright colorimeter. For a detailed description of the colorimeter and its calibration procedures see Wright (1946 pp. 45–70).

Subjects

The two authors US and BS with normal colour vision served as observers during the experiments.

Procedure

The basic principles of the binocular matching technique pioneered by Wright (1946 pp. 209–219) and the asymmetric matching technique introduced by Moreland & Cruz (1959) were applied. The units of R (650 nm), G (530 nm), and B (460 nm) were first established in the R-channel system, and then transferred to the R2-channel system by way of radiometric measurements using an UDT-370 radiometer.

The matching stimulus, consisting of the three instrumental primaries, R, G, and B, was applied at the dark-adapted right eye fovea, while the monochromatic test light was applied nasally to the left eye fovea (i.e., in the temporal visual field of the left eye). Using two dental bites (one for the right and the other for the left eye) and successive stimulation, both stimuli could be directed through the centre of the pupil. An artificial pupil of 2 mm diameter was employed in front of each eye.

It should be noted that the asymmetric and the conventional, symmetric, foveal colour-matching technique differ in several important respects.

Firstly, the theoretical implications of the two techniques are quite different. Thus, it is generally assumed that symmetric, foveal colour matches are made by adjusting the light on the two halves of the colorimetric field to have equal quantum absorption in each of the photopigments of the three types of cone receptors. Consequently, nothing in the visual system can distinguish between the colours of the two halves. An asymmetric colour match, on the other hand, does not imply equal quantum absorption in the cone photopigments of the match and test fields. Hence, the two

indistinguishable colours of the test and matching fields may represent widely different physiological processes at the retinal level (cf. Stabell & Stabell, 1984; Abramov et al., 1992).

Secondly, the asymmetric-matching technique cannot generate negative coordinates for the matching light except when the extrafoveal test light can be matched by a monochromatic wavelength presented at the fovea. This limitation of the asymmetric technique does not represent any serious problem in the present study, however, since a good match could always be obtained between the extrafoveal test stimulus and the three instrumental primaries at the fovea.

Finally, the asymmetric technique can be applied to test fields at any retinal location, while the symmetric, foveal technique is restricted to test fields presented to the fovea.

The successive phases were as follows:

1. Both eyes were dark adapted for 40 min.
2. The *left* eye was then stimulated for 0.125 sec with the 1×2 deg test field of 650 nm applied 3 deg in the temporal field of view. The intensity was 1 log unit above the cone-plateau of the long-term dark-adaptation curve as measured for the test stimulus, representing a retinal illumination of about 2 ph td.
3. Dark adaptation 1 sec.
4. Stimulation of the *right* eye fovea for 0.125 sec with the 1×2 deg comparison field, consisting of the Wright primaries 650, 530 and 460 nm. The subject tried to establish a match by increasing or reducing the intensity of each of the three primaries. The match was established after four repetitions of phases 2–4. Only small adjustments were required since pre-experimentation had established an approximate match. The retinal illumination of the foveal match was about 30 ph td.
5. Repetitions of phases 2–4, except that the retinal illumination of the test light was varied between runs: 1, 2, 3 and 4 log units above the cone-plateau level were employed, representing retinal illuminations of about 2, 20, 200 and 2000 ph td at 3 deg.
6. Following 7 min in complete darkness, the left eye was light adapted with "white" light of 3200 K for 50 sec at a retinal illumination of 60,000 ph td. The size of the field was 30×30 deg and it was centred at 3 deg in the temporal field of view.
7. During the cone-plateau period between 5 and 8 min of dark adaptation phases 2–5 were repeated.
8. Repetitions of phases 1–7, except that the wavelength of the test stimulation was varied.
9. Repetitions of phases 1–8, except that the test field was located at 8, 30, and 65 deg in the temporal field of view of the left eye.

Colour vision in the far peripheral retina probably differs in important ways even between individuals with so-called normal colour vision. A pre-experiment was, therefore, designed to test whether the effect of rod intrusion on cone-mediated colours differs in any
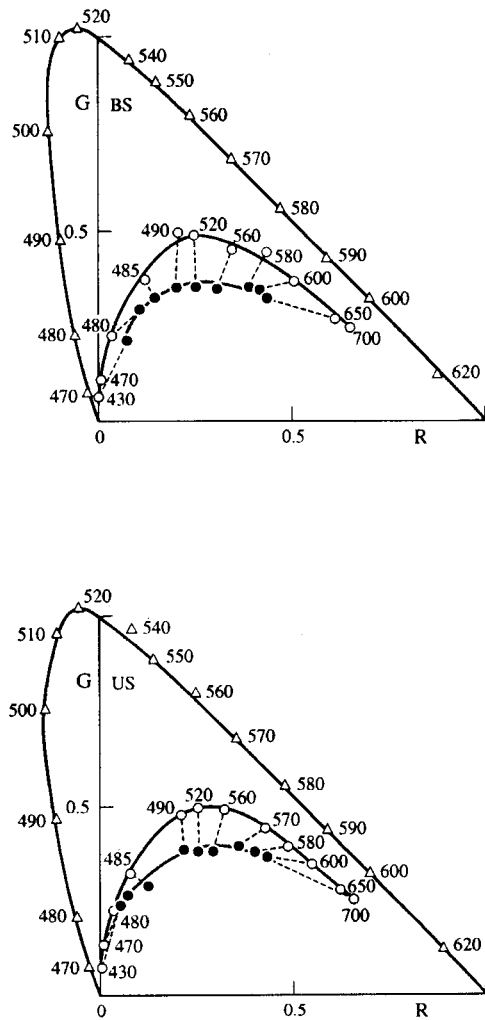
FIGURE 1. Chromaticity coordinates of monochromatic lights measured during the cone-plateau period (○), and in a completely dark-adapted state (●) for subjects BS and US at 27 deg in the nasal field of view. The size of the test field was 1 × 2 deg and it was exposed for 0.125 sec at a retinal illumination of 250 ph td. The results are expressed in the foveal WDW-diagram. As a reference framework, chromaticities of monochromatic lights obtained at the central fovea in a previous study (Stabell & Stabell, 1982) are given (△).
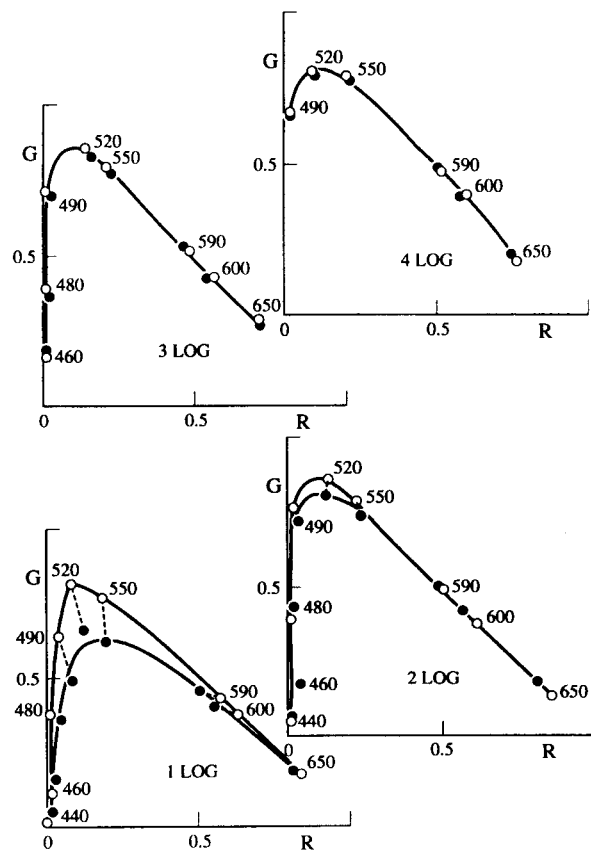

FIGURE 2. Conditions as in Fig. 1, except that the measurements were obtained at 3 deg in the temporal field of view and the intensity was 1, 2, 3, and 4 log units above the cone plateau level, representing retinal illumination levels of 2, 20, 200, and 2000 ph td. Due to the low energy output provided by the apparatus in the short-wave region, chromaticities for short wavelengths could not be obtained at the highest intensity levels. Only the results of US are shown.

essential way between the two observers of the present study. Chromaticity measurements of monochromatic test lights were obtained both during the cone-plateau period and in a dark-adapted state for both subjects.

The results of the pre-experiment are shown in Fig. 1. The data points represent the means of four repetitions of the measurements of subjects US and BS and give the amount of the instrumental primaries of the foveal comparison field needed to match the spectral lights at 27 deg in the nasal field of view. The total scatter was about 0.04 in R and G for both subjects. As can be seen, the measurements obtained both during the cone-plateau period and in the dark-adapted state are closely similar for the two subjects. It was therefore decided to use subject US as the main observer and BS as a control, i.e., the measurements for BS were obtained only once for each condition. To increase the skill in making rapid and

reliable colour matches, the subjects underwent an extensive training period. Furthermore, in order to avoid long-lasting, artificial chromatic after-effects, pre-experimentation established an approximate match for both subjects before the actual experiments were performed. Thus, the laboratory work was very time-consuming, lasting nearly 1 yr.

RESULTS AND DISCUSSION

The results of the experiments are presented in Figs 2–5. The data points represent the means of four measurements of subject US and give the amount of the Wright primaries of the foveal comparison field needed to match the monochromatic lights of the extrafoveal test field. The total scatter in chromaticity was about 0.04 in R and G. The results of BS were the same in all essentials.

Figure 2 gives the R and G coordinates of the spectral lights obtained at 3 deg in the temporal field of view during the cone-plateau period and in a dark-adapted state. The results measured at the lowest intensity level at 1 log unit above the cone-plateau level, i.e., at a retinal illumination of about 2 ph td, show that all the spectral lights are more desaturated in the dark-adapted state than
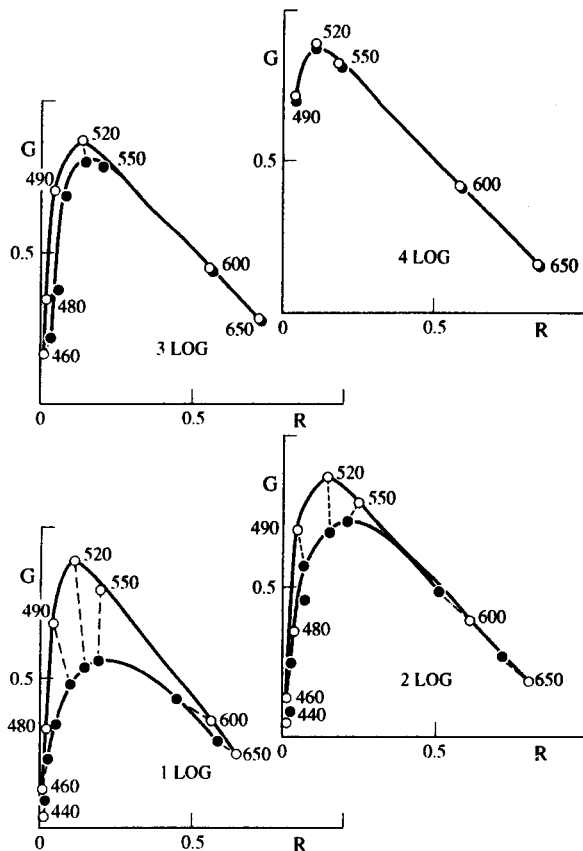
FIGURE 3. Conditions as in Fig. 2, except that the measurements were obtained at 8 deg in the temporal field of view.
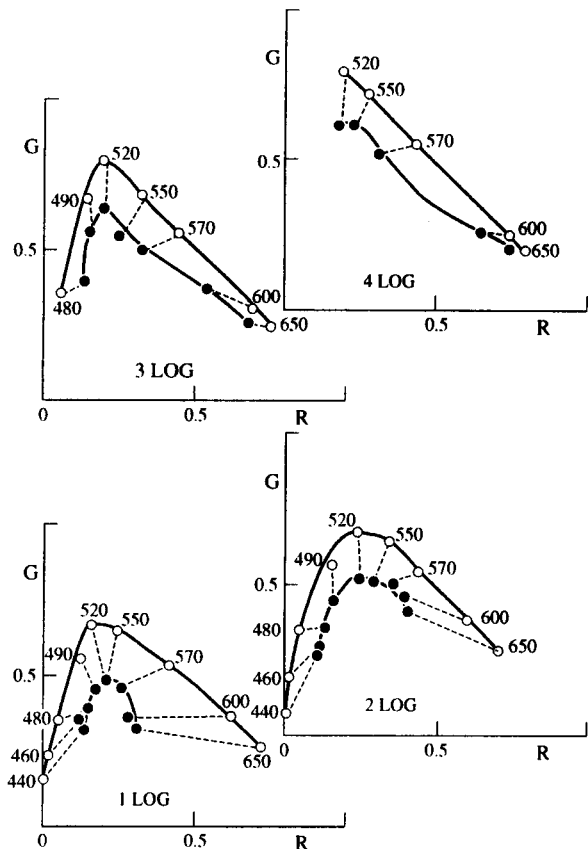

FIGURE 4. Conditions as in Fig. 2, except that the measurements were obtained at 30 deg in the temporal field of view.

during the cone-plateau period. The desaturation is most marked in the mid-spectral region (550–490 nm). Furthermore, colour sensation of 650, 600 and 590 nm test lights change slightly toward yellow, while 440 and 460 nm change toward blue. When the intensity of the test field increases to 2 log units above the cone-plateau level, the change toward yellow of the 650 and 600 nm lights becomes more pronounced, while there is a general reduction of the desaturation in the mid- and short-wave regions. The minute chromaticity shifts between the dark-adapted state and the cone-plateau period obtained at 3 and 4 log units above the cone-plateau level may be due to artifacts (e.g., uncontrolled chromatic adaptations).

The chromaticity shifts obtained between the dark-adapted state and the cone-plateau period measured at 8 deg are presented in Fig. 3. It can be seen that the chromaticity shifts at 8 deg are, in general, much more pronounced than at 3 deg. The chromaticity shifts with intensity, however, are quite similar at the two locations. Thus, when intensity is increased from 1 to the 2 log unit level, the chromaticity shift is reduced in the mid-spectral region, while 650 and 600 nm change toward yellow. At 3 log units above the cone-plateau level, only small desaturation effects remain in the short and mid-spectral regions and at 4 log there are no significant changes in colours between the two adaptational conditions.

Figure 4 gives the chromaticity shifts between the

dark-adapted state and the cone-plateau period at 30 deg. The desaturation effect in the long-wave region is very pronounced at the lowest intensity level but reduces somewhat as intensity increases. In the mid- and short-wave regions, the desaturation remains approximately independent of intensity.

At 65 deg the desaturation effect is relatively small at the two lowest intensity levels, increases somewhat at 3 log units above the cone-plateau level and then decreases slightly at the highest 4 log unit level (Fig. 5). Both at 30 and 65 deg the chromaticity shifts mainly represent reduction in saturation with no marked change in hue.

It is somewhat surprising that the rod and cone signals generally were perceived as a single event in spite of the well-known fact that the cone system has a shorter latency than the achromatic rod system. The recent results of Schneeweis & Schnapf (1995) indicate that the light response of the rods is much slower to develop in the long-wave than in the short-wave region for the same photopic troland values. They found that the time to the peak of the photovoltage response of the inner segments of rods and cones decreases with increasing flash strength above their absolute threshold levels–from 200 to about 35 msec in rods and from 35 to about 10 msec in cones. Since rods are much more sensitive than cones in the short-wave region (absolute thresholds differ about 3 log units), while the two receptor systems are about equally sensitive in the long-wave region, the rod and cone
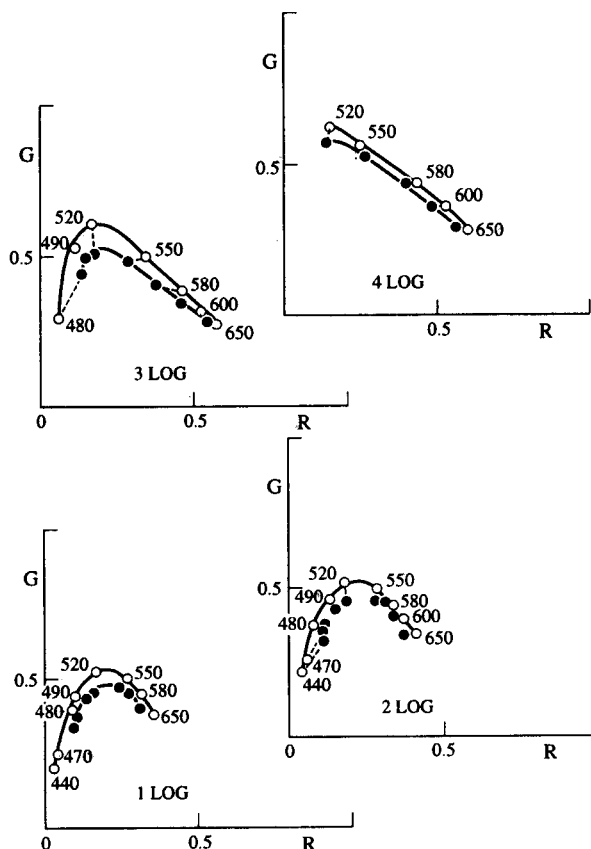
FIGURE 5. Conditions as in Fig. 2, except that the measurements were obtained at 65 deg in the temporal field of view.
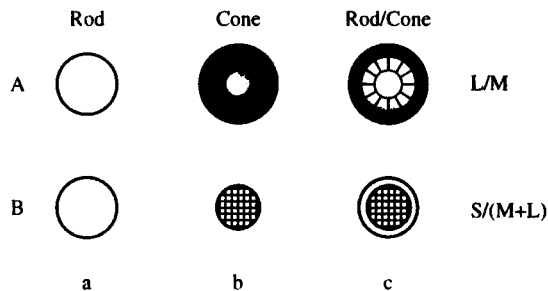

FIGURE 6. A simplified, schematic illustration of the suggested organization of the receptive fields for an ON-centre ganglion cell of the L/M pathway (A), and a +S/ − (M + L) ganglion cell (B). Pure rod field (a), pure cone field (b), and combined rod and cone fields (c) are shown. Areas with antagonistic interaction are marked by straight lines.

responses at the cone plateau level will be approximately in phase at short wavelengths with a time to the peak of the photovoltage of about 35 msec, while in the long-wave region, the time to peak will be about 200 msec for rods and 35 msec for cones. At the ganglion cell level this difference in latency between the rod and cone receptor responses will be enhanced, since the rod signals, both through the primary and secondary pathways, have to pass through more synapses than the cone signals.

Nevertheless, the rod and cone responses were generally perceived as a single event even in the long-wave region of the spectrum. Hence, the temporal integration time for the rod and cone signals must be of very long duration (v. Andrews & Hammond, 1970). Yet, it might be expected that the different response latencies of rods and cones would tend to suppress the rod activity (v. Gouras & Link, 1966) and thus decrease the desaturation effect of the rods. Contrary to this expectation the desaturation effect of the rods in the long-wave region is seen to be very marked indeed at 30 deg (cf. Fig. 4). It should be noted, however, that the log difference between the dark-adapted rod and cone thresholds increases about 0.6 log unit when the test field is moved from 8 to 30 deg (Stabell & Stabell, 1981). The finding that the desaturation effect of the rods is relatively small in the long-wave region at 3 and 8 deg may, therefore, most easily be accounted for by the relatively small rod component of long wavelengths at these locations.

The results at 3 and 8 deg also show that, in addition to the desaturation effect generally obtained, rod intrusion may change the colour quality of the test stimulation somewhat: toward yellow in the long- and middle-wave parts of the spectrum and toward blue in the short-wave part. These results are in accordance with previous evidence (Stabell & Stabell, 1975, 1979) and show that rods do not contribute a constant achromatic or bluish component to visual sensation as generally assumed (e.g. Willmer, 1961; Trezona, 1970; Wyszecki & Stiles, 1967). Instead, it appears that the effect of rod intrusion may change qualitatively when the chromatic cone component changes. This change toward yellow or blue has previously been explained by the suggestion that cone signals at mesopic intensity levels may inhibit yellow- and blue-related scotopic activities to a lesser degree than red- and green-related activities (Stabell & Stabell, 1979).

GENERAL DISCUSSION

The present results show that there is a general tendency for all colours to become desaturated during the second phase of the long-term dark-adaptation process (Figs 1–5). Previous evidence strongly indicates that this desaturation is due to light signals initiated in rods that somehow suppress cone-mediated colours (Lie, 1963; Spillmann & Conlon, 1972; Peachey et al., 1990; Nagy & Doyal, 1993; Stabell & Stabell, 1976a, 1980a,b).

The suggestion that light signals from rods suppress cone-mediated colours implies that light signals from rods and cones converge into common pathways (Lie, 1963; Stabell & Stabell, 1976b). Accordingly, recent evidence on the mammalian retina indicates that light signals initiated in rods have inputs via gap junctions into cone pathways both through the so-called primary and secondary rod pathway (Daw et al., 1990; Strettoi et al., 1994; Schneeweis & Schnapf, 1995). Indeed, recent anatomical, pharmacological, and electrophysiological evidence strongly suggest that rod signals of the primate retina may feed *different types of midget* cone bipolar

cells via the primary rod pathway (Wässle et al., 1994, p. 576).

Since light responses of rods have inputs into cone pathways both through the primary and secondary rod pathway, the question arises as to the relative contribution of the two pathways to the desaturation effect of rods.

It is generally held that the primary pathway has a low threshold while the secondary pathway has a high threshold (Smith et al., 1986; Daw et al., 1990; Schneeweis & Schnapf, 1995). Indeed, the evidence suggests that the secondary pathway is functioning only when the test flash intensity reaches several log units above the absolute dark-adapted rod threshold. If so, the desaturation effect of the rods obtained in the long-wave region at the two lowest intensity levels used must exclusively be due to rod signals through the primary pathway, since the rod receptor system is only slightly more sensitive than the cone system in this region. Experiments performed by Alexander et al. (1988) support this conclusion. They found that in individuals where the transmission of rod signals through the primary pathway is blocked, there is no rise of the specific hue threshold of a green (525 nm) test light during the second phase of the long-term dark adaptation. This evidence, however, does not preclude the possibility that the secondary pathway may contribute to the desaturation effect observed at high mesopic intensity levels.

Rod signals, both through the primary and secondary pathway, are transferred to the cone pathway via gap junctions. Functions mediated by gap junctions often occur in an all-or-non manner (Kandel et al., 1991). Hence, one might expect that when rods increase their sensitivity rapidly during dark adaptation, the desaturation process would start suddenly and reach its maximal response in a short time. Previous psychophysical data are in agreement with this expectation (Lie, 1963; Spillmann & Conlon, 1972; Stabell & Stabell, 1976a). Thus, a major finding of these studies cited is that the desaturation process obtained in the short- and middle-wave regions is completed within a surprisingly short time, so that the last part of the dark-adaptation process has little or no effect.

The desaturation effect of the rods has previously been explained by the suggestion that rod and cone signals are mutually exclusive in single optic nerve fibres (for a review of this classical hypothesis see Lie, 1963, pp. 482–484). Contrary to this suggestion, however, gap junctions are sign-conserving synapses so that a light response in the rods will tend to depolarize cone ON-bipolar cells both through the primary and secondary rod pathway (Daw et al., 1990). An explanation of the desaturation effect must, therefore, be based on the fact that rods and cones add their responses of the same polarity (cf. Andrews & Hammond, 1970).

The apparent paradox may be resolved by assuming that rods in a dark-adapted state excite different types of spectrally opponent cells to approximately the same degree (Stabell & Stabell, 1976b, 1994). Thus, assuming

that the rod system utilizes the circuitry of the different types of cone receptor systems at the inner plexiform layer (Wässle et al., 1991), and that this circuitry plays a major role in forming colour-opponent surrounds of ganglion cell receptive fields in the human retina (Kolb, 1991; Kolb & Lipetz, 1991), one might suggest that the rod input into the different types of spectrally opponent cells mimics the inputs of the three cone receptor systems activated to about the same degree (cf. Lie, 1963; Spillmann & Conlon, 1972). The desaturation effect of the rods might then be explained by the suggestion that differences in ongoing activity rates of the different types of spectrally opponent cells become levelled down to some extent when light signals from rods intrude during dark adaptation.

However, two further assumptions should be taken into account in order to explain the desaturation effect of the rods:

1. The centre of the receptive fields probably becomes enlarged with the changeover from cone to rod vision, in that the field centre for rods substantially overlies the cone surround (for an analysis of such complex rod–cone interactions see Andrews & Hammond, 1970). Supporting evidence has recently been given by Abramov et al. (1992). They found a reduction in the sizes of the local perceptive fields when the surrounding retina was light-adapted.
2. The antagonistic surround of the rod receptive field tends to disappear in a completely dark-adapted state (Barlow et al., 1957; Daw et al., 1990). (A simplified, schematic illustration of the suggested changes in the receptive field organization for an ON-centre ganglion cell of the L/M pathway and a $+S/-(M + L)$ ganglion cell when rod signals intrude are shown in Fig. 6.)

Although it would be mere speculation to press the analysis in any detail, it appears reasonable to suggest that rod intrusion would tend to increase the ON-centre ganglion cell activity in both the L/M and S/(M+L) pathways and to inhibit OFF-centre cell activity. Accordingly, it has long been known that rods in a dark-adapted state under scotopic conditions may activate spectrally opponent cells at the LGN level (De Valois, 1965; Wiesel & Hubel, 1966). Obviously, these opponent cell activities must be antagonized centrally to the LGN level, since scotopic vision is essentially achromatic vision (see Hering, 1878).

When the retinal illumination level in a dark-adapted state increases above the cone-plateau level, however, the cone-mediated opponent cell activity may be assumed to increase and as a consequence become progressively more effective in suppressing the opponent cell activity of rods for a long transitional intensity interval (for a more detailed discussion of this point see Stabell & Stabell, 1973, 1976b). Accordingly, the results obtained at 3 and 8 deg show a pronounced reduction of the desaturation effect of the rods when the intensity increases. In fact, at 3 deg there is no measurable effect

of the rod intrusion at the two highest intensity levels, indicating that the desaturation effect of the rods is completely suppressed by cone activity at these levels.

As opposed to the increase of the cone-mediated opponent cell activity with intensity, well-founded evidence indicates that it decreases with eccentricity (Stabell & Stabell, 1982, 1984). The present results are consistent with this suggestion and clearly show that the chromatic responses of the cones measured during the cone-plateau period desaturate when the test field moves from 3 to 65 deg (Figs 2–5). As a consequence, one would expect a reduction of the cone-mediated suppression of the rod activity with eccentricity. Confirmatory evidence is found in that the desaturation effect of the rods at high mesopic intensity levels increases markedly when the test field is moved from 3 to 30 deg (Figs 2–4). Surprisingly, the desaturation effect of the rods could be observed even at a retinal illumination of 20,000 ph td (the maximal retinal illumination provided by the apparatus for a 550 nm test light). This finding is in sharp contrast to the basic assumptions of the Duplicity Theory of vision that cones and rods respond at high and low intensity levels, respectively, and that for each wavelength there exists only a small transitional intensity interval where both receptor types may influence vision (for an evaluation of the Duplicity Theory see Saugstad & Saugstad, 1959). It should be noted that the pronounced increase of the desaturation effect of the rods between 8 and 30 deg cannot be due to an increase of the number of rod receptors per unit retinal area since the number is approximately the same at the two locations (v. Rowe, 1991).

When the test field is moved further outward from 30 to 65 deg, the cone-mediated colours deteriorate further (Fig. 5). Hence, one would expect a further reduction of the cone-mediated suppression. The present results appear to be in agreement with this prediction since the results show no significant progression of cone suppression with intensity. However, the most outstanding feature of the 65 deg data is that *the desaturation effect of the rods* is greatly reduced at all intensity levels investigated. In fact, the desaturation effect of the rods is barely measurable.

Hence, one may conclude that both the suppression of cone-mediated colours by rod signals and the progressive cone suppression of these rod signals with intensity are markedly reduced in the extreme peripheral retina. This conclusion may be reconciled with the suggestion that the rod and cone suppressions both are mediated through opponent pathways which obviously are poorly developed in the extreme peripheral retina (cf. Wässle et al., 1994).

On the other hand, it has previously been suggested that the desaturation effect of the rods may partly be due to rod impulses acting through non-opponent pathways (Stabell & Stabell, 1976b). A complication is introduced, however, since non-opponent cells are found both in the parvo- and magnocellular layers. Although it seems reasonable to suppose that the non-opponent parvocel-

lular system is in a better position to interact with the opponent cell activity than the faster magnocellular system, there is no obvious locus for such an interaction, and the underlying mechanism remains elusive. Furthermore, the results obtained at 65 deg are not easily reconciled with the suggestion that the desaturation effect of the rods is due to rod signals feeding into non-opponent cells, as suggested by Stabell & Stabell (1976b) since one would expect non-opponent rod activity, as compared with cone-mediated opponent activities, to be relatively high at 65 deg. At present, there is no obvious explanation of this inconsistency.

It should also be noted that the reduction in number of rod receptors per unit retinal area between 30 and 65 deg (Rowe, 1991) does not provide a very likely explanation of the decrease of the rod desaturation effect at 65 deg, since the rod system is still several log units more sensitive than the cone system at this extreme location (Stabell & Stabell, 1981). Furthermore, the results obtained at 30 deg reveal that the desaturation effect of the rods is pronounced even in the long-wave region where the rod component is relatively small.

It is well known that the rod and cone systems differ with regard to spatial summation and temporal integration properties. It therefore appears reasonable to suggest that the desaturation effect of rod intrusion may change significantly when the size or exposure time of the test stimulation are varied. A discussion of such effects may, however, await further experimentation, since both the size and exposure time of the test field were held constant in the present study.

Even so, the work of Abramov et al. (1991, 1992) should be mentioned since their results are directly relevant to such an analysis. They showed that the saturation of extrafoveal test fields increases asymptotically with the size of the field when the surrounding retina is dark-adapted and that the stimulus size that elicits the asymptotic values becomes smaller when the surrounding retina is light-adapted. These results seem to indicate that the desaturation effect of rod intrusion is a complex function of the size of the test field (Abramov et al., 1992).

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