Spatial and temporal properties of light adaptation in the rod system

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Abstract

Little is known about the mechanism that regulates the sensitivity of rod system at its normal operating light levels. Two experiments are reported in this paper. First, we searched for nonlinear distortion products in rod vision that could be generated from any local adaptation process, using a sensitive experimental procedure that has demonstrated local adaptation in cone vision. No local adaptation was evident in the rod system, even at near saturating light levels. Second, to investigate the dynamics of light adaptation in the rod system we presented a uniform flickering background, sinusoidally modulated in time, and measured increment thresholds for brief test flashes that were superimposed on this background at different times during the sinusoidal flicker cycle. At frequencies less than 5–6 Hz, the rod increment threshold follows the background modulation, with a slight phase advance. When the background is modulated faster than 5–6 Hz, the increment threshold remains the same regardless of when the test flash occurred during the background cycle. Thus the rod system sensitivity, unlike that of the cone system, can only change slowly, and is set by a space-integrated signal rather than independently for different rods. © 2000 Elsevier Science Ltd. All rights reserved.

1. Introduction

The rod system differs from the cone system in many aspects, including its resolution in space and in time, which are both relatively poor. Here we consider the spatial and temporal resolution not of rod vision itself, but of the system that regulates the sensitivity of rod vision in changing light levels. The resolution of the sensitivity-regulating system need not be in any way linked to perceptual resolution. In the cone system, for example, sensitivity regulation is mainly strictly local: the sensitivity-regulating mechanism responds to the finest stimuli that can be encoded by the photoreceptor mosaic, allowing it to surpass the perceptual resolution limit by a factor of two or more (MacLeod, Williams, & Makous, 1992; MacLeod & He, 1993). This spatially

local adaptive mechanism is also relatively fast, with only about 15–20 ms delay and 6 ms persistence (He & MacLeod, 1998a,b). In the rod system, despite detailed studies showing an important role of sensitivity control of rods themselves in the lower vertebrates (Koutalos & Yau, 1996), there is good evidence that receptor adaptation is *not* important in humans, and that light-adapted rods retain their full dark-adapted sensitivity either under steady exposure to scotopic light levels, or after brief exposure to more intense light (Rushton & Westheimer, 1962; Rushton, 1965; MacLeod, Chen, & Crognale, 1989; Cicerone & Hayhoe, 1990; MacLeod et al., 1992). Electrophysiological studies of mammalian rods support these claims in showing that rod sensitivity does not contribute materially to the large changes of visual sensitivity associated with changing light intensity in the scotopic range.

At higher intensities, above 1 troland (td) or so, human vision is dominated by the cone system, (which at these levels provides a level of performance exceeding that of rods), though complete overloading or 'satura-

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tion' of the rod system is thought to require a light level of several hundred trolands (Aguilar & Stiles, 1954). Within this higher intensity range, electrophysiological investigations have indicated modifications of sensitivity in isolated primate rods, but with some disagreement as to the intensity required. In one study of Cercopithecus, sensitivity was halved at a background illumination level of around 5 td, well below the onset of rod saturation (Tamura, Nakatani, & Yau, 1991); in a study of human rods the halving of sensitivity occurred at about 15 td (Kraft, Schneeweis, & Schnapf, 1993). Since the rods in these investigations are functioning under far from natural conditions, studies in vivo with the electroretinogram (ERG) are also an important source of evidence. The ERG evidence has ambiguities of its own, since many different cell types contribute to it. One analysis of ERG responses to double flashes (Pepperberg, Birch, & Hood, 1997) indicates a halving of rod sensitivity at around 30 td; other studies (limited to considering rising phase of the response to test flashes, where the contribution of the receptors predominates) suggest little or no sensitivity loss except at near-saturating levels (Hood & Birch, 1993; Thomas & Lamb, 1999).

It is important to recognize that modifications of rod photoreceptor sensitivity at such high light levels have no demonstrated relevance at all to human visual function. Any functionally relevant account of light adaptation in rod vision must address the roughly 100-fold loss of visual sensitivity found within the scotopic and low mesopic intensity ranges, where the sensitivity of rod vision varies over several orders of magnitude, roughly in conformity with Weber's Law. As noted, there is no evidence that any of that loss is traceable to the rods themselves: no investigation, whether based on microelectrodes, psychophysics or electroretinography, has shown a role for the rod photoreceptors in scotopic adaptation. But since the proposal that light-adapted rods retain their full dark-adapted sensitivity remains difficult to accept, we here report psychophysical experiments to check this point using more refined methods than those used up to now — in particular, using interference fringe patterns as test targets. With such targets, local sensitivity regulation can be revealed in the cone system by the generation of nonlinear distortion products at spatial frequencies greater than 100 cyc/deg (MacLeod et al., 1992; MacLeod & He, 1993). Even a slight adaptive modification of sensitivity in individual rods should have similar perceptual consequences. Our first experiment tests for this, concentrating on the high intensity range where the cited physiological data suggest that local adaptation would be observable. Whether functionally important or not, these sensitivity changes found physiologically at high intensity require explanation, and their basis is not entirely clear. It seems fairly clear that rod saturation is

traceable to the photoreceptors themselves, and may arise through closure of light-sensitive channels in their outer segments (Penn & Hagins, 1972). In accordance with this proposal, psychophysical observations (Hayhoe, MacLeod, & Bruch, 1976) on the one hand and microelectrode or ERG recordings on the other (Kraft et al., 1993; Pepperberg et al., 1997; Thomas & Lamb, 1999), both suggest a half-saturating intensity in the neighborhood of 100 td. Yet one experiment on cat ganglion cells (Lennie, Hertz, & Enroth-Cugell, 1976) found that individual regions within the receptive field center could not be saturated independently. We therefore included in our first experiment the highest testable background intensity levels, with the aim of testing whether human rods undergo saturation independently.

We here use the phenomenon of 'contrast-modulation flicker' to test for local modifications of sensitivity, just as we did in the cone system (MacLeod & He, 1993; He & MacLeod, 1998a,b). In the cone system, when the contrast of a perceptually unresolvable grating was modulated while its spatial average luminance was kept constant, flicker was seen. This is not expected if the visual system is spatially integrating linear signals, but it is expected if a nonlinear mechanism can resolve the grating, for then the space average output of the nonlinear mechanism will fluctuate as the contrast of the stimulus is modulated. When a uniform field changes to a grating without change in mean luminance, the light added to the bright bar is equal to the light taken from the dim bar. But in a compressively nonlinear representation of local luminance the incremental signal will be less than the decremental one, and a reduction in the space-average signal will result. Conversely, when the grating is succeeded by a uniform field, the removal of light from the strips of light-adapted retina (where the light bars had been) will count for less than the addition of the same amount of light to the intervening strips of dark-adapted retina. An increment in the space-average signal will result. If later spatial integration transmits the space-average of these nonlinear signals, the grating pattern will not be seen, but the invisible pattern will generate uniform-field flicker. In cone vision — including short-wavelength cones as well as long-wavelength cones (He & MacLeod, 1998a,b) — such contrast-modulation flicker can be generated at spatial frequencies far above the perceptual resolution limit. The resolution limit is the one imposed by the apertures of the cone photoreceptors themselves, as expected if the nonlinear signal is associated with individual cones. Here we test for contrast-modulation flicker in the rod system.

Contrast-modulation flicker also allows us to investigate the dynamics of the nonlinear process, and in the case of the cone system has allowed us to identify it as a fast sensitivity-regulating mechanism rather than an instantaneous nonlinear compression. That the cone

system can adapt very quickly is also suggested by measurements of increment threshold for a brief 'probe' on a modulated background. The increment threshold varies when the probe flash is presented at different phases of a very fast background modulation (Boynton, Sturr, & Ikeda, 1961; Sperling, 1963; Powers & Robson, 1987; Bone, McTavish, et al., 1991). As yet, however, little is known about how rapidly the rod system can adjust its sensitivity. Although there is evidence that rod system adaptation consists of a fast multiplicative and a slow subtractive mechanism (Geisler, 1979; Adelson, 1982), these studies are concerned with time scales on the order of seconds or minutes. The rod system can detect flicker up to around 28 Hz (Conner & MacLeod, 1977; Conner, 1982). We wanted to assess its ability to rapidly adjust its sensitivity during rapid modulation of the background light level. That is the aim of our second experiment.

2. Experiment 1. Searching for local adaptation in rods

Decades ago Rushton and Westheimer (Rushton & Westheimer, 1962; Rushton, 1965) proposed that illuminated or pre-adapted rods retain their full dark-adapted sensitivity, and that the entire job of sensitivity regulation for the rod system is done further downstream in postreceptoral neural 'pools', that collect input from the rods over a neighborhood roughly comparable in size with the area of spatial integration in rod visual perception. Early psychophysical experiments on rod adaptation consistently supported this proposition (for reviews see MacLeod, 1978; Shapley & Enroth-Cugell, 1984; Green, 1986; Hood, 1998). Later, MacLeod et al. (1989) searched for difference-frequency gratings, a sensitive perceptual indicator of nonlinearity in the response to local luminance that is observable in cone vision when a pair of unresolvable gratings are superimposed (Burton, 1973) or viewed successively (MacLeod et al., 1992). Difference-frequency gratings were never seen in rod vision with gratings above the rod perceptual resolution limit, a negative result suggesting that the sensitivity of individual rods remains uniform (to within error of measurement) after pre-exposure to a patterned illumination that reduces the sensitivity of the rod system as a whole.

Here we use contrast-modulation flicker to test for local adaptation in the rod system. Contrast-modulation flicker (MacLeod & He, 1993; He & MacLeod, 1998a,b) is an expression of nonlinear processing of intensity, somewhat analogous to difference-frequency gratings, but with temporal rather than spatial modulation of the grating contrast. Compared with the difference-frequency gratings, it has four advantages. (a) It requires only a single interference fringe, rather than two; (b) it allows the amplitude of the perceptual

distortion product to be measured easily with a nulling procedure; (c) it makes no demands on the spatial resolving power of the perceptual system; and (d) it makes possible investigation of the dynamics of the nonlinearity. As with difference-frequency gratings, contrast-modulation flicker should appear when a grating is resolved by the sensitivity control mechanism, whether the grating can be resolved perceptually or not, and investigation of the phenomenon's dependence on spatial frequency should allow us to assess the size of the adaptation pool. In particular, if rods adapt independently, contrast-modulation flicker should remain visible up to 100 cpd or more, as was the case for cones. In the other extreme case, if rods have no role in adaptation, and if the adaptation 'pool' can resolve no better than the perceiving subject, contrast-modulation flicker will not be visible above the low resolution limit of rod vision.

2.1. Subjects

Three observers with normal vision (including the authors) and one rod monochromat participated in this experiment. The rod monochromat, a female college student in her forties, exhibited an apparently typical congenital achromatopsia, a condition that appeared within her family with an autosomal recessive pattern of inheritance. She required dark glasses for effective vision outdoors or in bright indoor environments. She generally exhibited fixational nystagmus. Her Snellen acuity was about 20/120, and in the interferometer her resolution limit was about 5 cyc/deg; we were unable to discover any evidence of cone function.

2.2. Procedure

2.2.1. Rod isolation

Procedures very similar to those described in He and MacLeod (1998a,b) were used, but under rod isolation conditions (Aguilar & Stiles, 1954) designed to allow us to monitor rod function at high light levels with minimal cone intrusion. Stimuli were generated with the laser interferometer using an Argon laser. The wavelength of 514 nm was selected with a narrow band interference filter. The test field was a disc 3.4° in diameter in the center of a 15° background. The background was produced from a Xenon lamp with a broadband filter centered at 654 nm, and served to desensitize the cones while sparing rod sensitivity as much as possible. The fields were placed in the temporal retina, centered 15° from the fovea. Since we wished to investigate the intensity range where rods are close to their saturation level with minimum cone intrusion, we measured individual observers' t.v.i. curves before we tried to measure rod contrast-modulation flicker. The test field was arranged to enter the subject's eye at the

edge of their pupil, and the background at the center of their pupil. This arrangement exploits the reduced sensitivity of cones for obliquely incident light (Stiles & Crawford, 1933; Chen & Makous, 1989) to minimize cone intrusion. It was used for both the t.v.i. measurement and the subsequent contrast-modulation flicker experiment. Fig. 1 shows the results of t.v.i. measurement. The test field was presented for 200 ms every second at the center of the background, and the observer adjusted its intensity to render it just visible. The open circles are rod thresholds. They show a threshold elevation roughly proportional to background intensity, in conformity with Weber's Law (the dashed line of unity slope), with the onset of rod saturation at about 100 td the decrease of sensitivity with increasing background level becomes more precipitous until cones take over (Aguilar & Stiles, 1954). The squares represent cases where detection was by cones. The open squares, like the open circles, were obtained during steady state adaptation to the background, but these threshold situations differed from the putatively rod-determined ones in that the test flash appeared vividly bluish at or slightly above threshold. To trace cone threshold at the lower background levels where rods undercut the cone threshold in steady state adaptation, we measured thresholds during the cone plateau of dark adaptation

(when rods are still less sensitive than cones), and obtained the values shown by the two filled squares.

For the contrast-modulation flicker measurement, the intensity of the background and flickering test were then chosen as shown by the crossed ellipsoid so that the rods were very close to their saturation level and yet there was only negligible cone intrusion. The 514 nm field was sinusoidally modulated in intensity, with a peak intensity 40 times the rod flash incremental threshold. The modulation depth seen by the rods under the conditions selected, and denoted by the hatched ellipse, was approximately 65%, at a time-average luminance of 150 scotopic td, 50 td of which was due to the steady background. Note that even though the stimulus was close to cone threshold, the cone contrast was very low ($< 5\%$). With full contrast modulation under optimal conditions, the cone system generates 40% contrast modulation flicker. Under the current conditions, the contrast-modulation flicker generated by the cone system would be negligible ($< 0.1\%$) since the magnitude of contrast-modulation flicker depends approximately on the square of the modulation contrast (see Fig. 5 and Appendix in He and MacLeod, 1998a).

2.2.2. Pedestal-aided contrast-modulation flicker detection

The pedestal-aided procedure described in He and MacLeod (1998a) was used. In two temporal intervals, a base amplitude of flicker (generally 20%) was present in the test field; the contrast of the test grating was modulated at the same temporal frequency, but in the opposite temporal phase relative to the luminance modulation in the two intervals. Any difference in perceived flicker between these two intervals is evidence of contrast-modulation flicker. Subjects would attempt to cancel any perceived flicker difference with a luminance flicker of suitably chosen amplitude; this nulling modulation was always in phase with the contrast modulation, since this phase relationship was found in our previous work to be appropriate for nulling contrast-modulation flicker.

For the rod monochromatic subject, we adopted a simpler procedure. We first measured her flicker threshold with a uniform field, and then the same threshold was measured with a contrast-modulated grating. The contrast was modulated in phase with the luminance modulation in one case and out of phase in another. If the contrast modulation does not affect the space-average signal, as would be expected for a linear system, the flicker threshold would be the same in these two situations. If contrast modulation generates flicker in the rod system, then the flicker threshold measured would be different for the in-phase and out of phase condition.
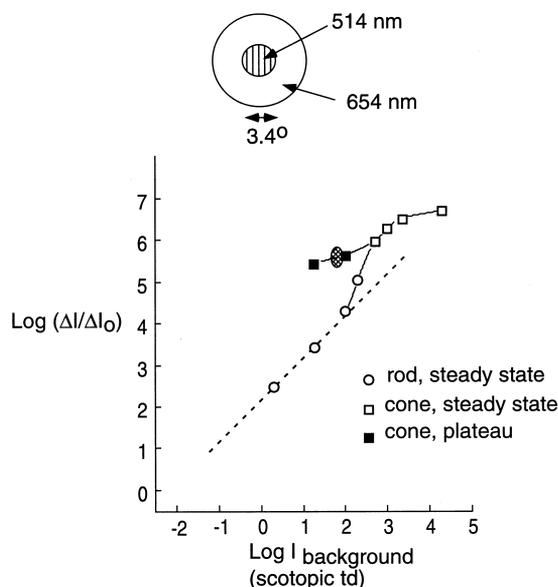

Fig. 1. Intensity selection for the rod contrast-modulation flicker experiment. Individual subjects' t.v.i. functions were measured under steady state adaptation (open symbols) and also at the cone plateau during dark adaptation after bleach (filled squares). Open squares are steady state thresholds where the perceived color of the test flash suggested detection by short-wavelength cones rather than by rods. The dashed line shows a proportional relationship between threshold and background intensity (Weber's Law). ΔI_0 is the absolute threshold. Cross-hatched ellipse indicates the test and background luminance used for the subsequent contrast-modulation flicker experiments.
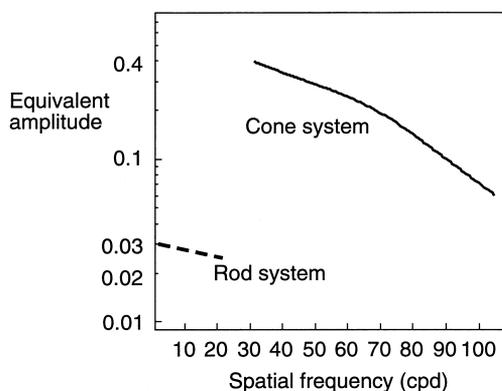
Fig. 2. Comparison of contrast-modulation flicker nulling amplitudes in rod and cone vision, at a range of spatial frequencies. The curve for cone system is based on data from He and MacLeod (1998a). For rod vision, there was no perceived flicker from modulating the contrast of the test grating when the spatial frequency was above the rod perceptual resolution. At lower spatial frequencies, the perceived flicker was minimal and never required more than 3% luminance modulation to null. The curve represents the upper boundary of the nulling amplitude based on data from two subjects.
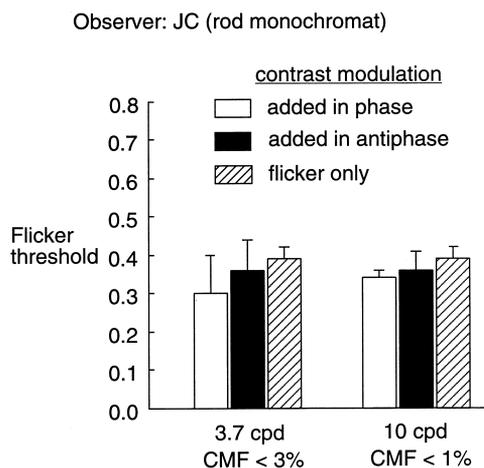

Fig. 3. Flicker modulation thresholds for subject J.C. (rod monochromat) at two spatial frequencies under three different conditions: uniform field luminance flicker only, and with contrast-modulation combined with luminance flicker in either the reinforcing or the cancelling phase. Contrast-modulation flicker should create a difference between the latter two thresholds, equal to twice the effective amplitude of the contrast-modulation flicker, but no such difference was reliably found. Error bars are ± 1 SE.

The experiment was performed with temporal frequencies at 6 Hz, with checks at 3, 8 and 15 Hz. The spatial frequency of the grating could be 3, 4, 5, 6, 7, 8, 12, 16 or 20 cpd.

2.3. Results and discussion

In the pedestal-aided contrast-modulation flicker detection experiment, contrast-modulation flicker was never clearly evident under these rod-isolating conditions. Even in the complete absence of nulling lumi-

nance modulation, subjects did not notice any obvious difference between the temporal interval where contrast-modulation flicker would reinforce the pedestal flicker and the other interval where it would diminish it. The nulling flicker amplitudes were accordingly close to zero. At the unresolvable spatial frequencies, they were no greater than about 1% in peak-to-peak modulation, and were not outside the range of experimental error. At the spatial frequencies below the low resolution limit of rod vision (about 7 cpd in normal subjects), a positive nulling amplitude was reliably preferred, but the mean nulling amplitudes chosen, while clearly greater than those found above the resolution limit, were only 2–3% peak to peak even at the lowest spatial frequencies. This small value may represent contrast-modulation flicker in the rod system, but its validity is somewhat questionable since nulls made during visible modulation of spatial contrast are subjectively less well defined than nulls set with invisible patterns. Fig. 2 compares the rod results with those for cone-supported contrast-modulation flicker.

With observer J.C. (the rod monochromat), flicker detection thresholds were basically the same whether the flicker was presented alone (uniform field, no contrast modulation), with contrast modulation in-phase or contrast modulation in anti-phase (Fig. 3).

These results show that no contrast modulation flicker, or very little, was seen in rod vision even at near-saturating levels. Since rod vision does exhibit adaptation and saturation, these nonlinearities will be operative if the range of frequencies is extended sufficiently below the rod resolution limit. However, it is problematic to demonstrate a time variation in the space-average excitation when locally registered brightness fluctuates violently in antiphase in different parts of the field. One way to improve on our essentially negative result is by a better selection of test and background intensities. But the levels chosen for our measurements were the highest testable without fear of cone intrusion; and checks using lower background intensities than the 50 td background of Fig. 1 yielded similar results, in that contrast-modulation flicker was never obvious and could not be measured at spatial frequencies above the rod resolution limit.

We checked our stimulus using cone vision by simply blocking the background and using central fixation: the same stimulus yielded contrast-modulation flicker that required a nulling luminance modulation of about 15–20% at 30cpd, even though the stimulus was not optimized for cone stimulation (large field, shorter wavelength, relatively lower intensity for cones). This confirms that the failure to see contrast-modulation flicker was not due to stimulus low contrast.

3. Experiment 2. Slow sensitivity adjustment of rod system

Although Experiment 1 adds to the existing evidence against individual and independent sensitivity control in the rods themselves, the rod system as a whole can of course adjust its sensitivity to light over many orders of magnitude with the changes in ambient light level. As was mentioned earlier, the cone system can adjust its sensitivity very quickly, and can track background modulation faster than 30 Hz (Boynton et al., 1961; Sperling, 1963; Powers & Robson, 1987; Bone et al., 1991). However, there is very little information about rod system sensitivity control on a fine time scale. Will the system still be able to change its sensitivity when background is rapidly modulated? This question can be addressed, as has been done in the cone system, by measuring the increment threshold for detecting a small, brief test flash on a modulated background. Naturally, when the background is modulated sufficiently slowly, a test flash presented at different phases of the background modulation will have a different detection threshold. It is expected that as the background modulation becomes fast, the threshold change will become smaller, until eventually, as the modulation frequency becomes too high to be resolved by the sensitivity controlling mechanism, the detection threshold will remain the same (determined by the time-average background level) regardless of when the test flash occurs during the background cycle.

3.1. Procedure

Fig. 4 shows a schematic diagram of the stimulus. The test field was a $2 \times 2°$ 488 nm light, which was flashed for 6 ms once per second at the center of a 632 nm modulated background. The use of a relatively large test field favored the Weber law behavior of detection threshold over the square root law (Daitch & Green, 1969), and thus one can be confident that the
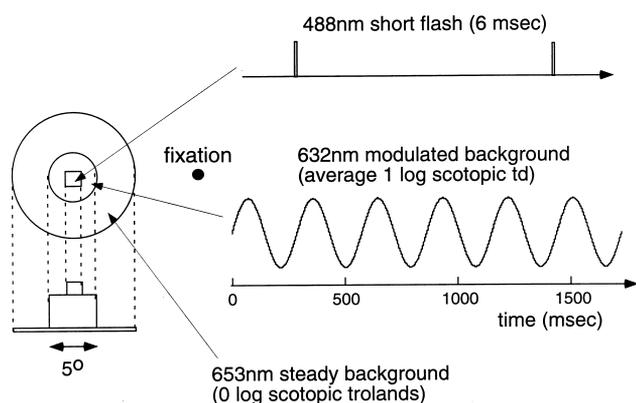
results reflect the adaptation behavior of the rod system rather than simple modulation of signal to noise ratio. This 632 nm background was 5° across in size and had an average luminance of 10 scotopic td. At this intensity level both rods and cones respond to the background, but the use of a shorter wavelength for the test stimulus made the rods more sensitive to it. A steady long wavelength background centered at 653 nm was added to the field in order to further suppress the cone sensitivity. A red LED fixation point was provided at 10° to the right side of the center of the stimulus, so the stimulus was at 10° to the temporal side of the right eye's retina. The 632 nm background was modulated sinusoidally at a certain temporal frequency, and the 488 nm test flash was presented at different points in the cycle. Subjects adjusted the test flash intensity with a mouse trackball to set the threshold level for seeing the test flash. This was repeated with the test flash temporally centered at 0, 45, 90, 135, 180, 225, 270 and 315° of the background modulation.

3.2. Results and discussion

Fig. 5 shows incremental threshold intensity versus phase. Solid lines are best fits (least square) to the data points with a cosine waveform, with amplitude and relative phase as free parameters. It is obvious that when the background was slowly modulated at 2 Hz, the increment threshold for the brief flash was high when the background intensity was high, and low when the background was low, just as you would expect from Weber's law. As the modulation became faster, the change of increment threshold became smaller and smaller, almost disappearing at 6 Hz. Meanwhile, the modulation of the increment threshold underwent a phase shift relative to the background modulation, actually advancing relative to it. The dotted line connects the lowest point of each solid fitted curve to illustrate the phase advance of the threshold modulation.

The results are further summarized in Fig. 6. In this figure we plotted the threshold modulation as a function of modulation frequency. The threshold modulation dropped rather quickly as the background modulation became faster. For comparison, the flicker sensitivity for rod vision at the same light level (Conner, 1982) is schematically plotted in the same graph: the modulation in threshold ratio drops much faster than flicker detection sensitivity. Although the rod system can detect a 6 Hz flicker at this light level with fairly high sensitivity, the increment threshold on a background modulated at this frequency is almost constant. As mentioned above, the threshold modulation did not just become flatter as the background modulation became faster, it was also phase shifted. Fig. 6B summarizes this relationship. A possible explanation of this phase shift is discussed later.

Fig. 4. Stimulus arrangement for measuring rod increment threshold for a brief (6 ms) flash on a modulated background.
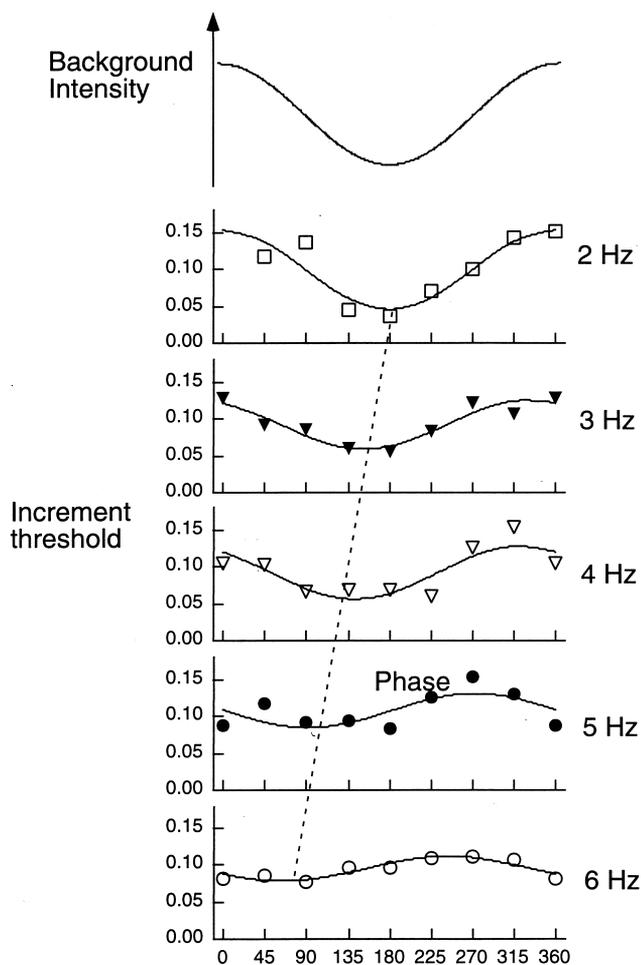
Fig. 5. Threshold measurements for subject S.H. with different background temporal frequencies. The depth of the threshold modulation decreases and its phase advance relative to background modulation increases, with increasing background frequency. The background was modulated at 100% modulation depth at the mean luminance of 1 log scotopic td.

4. General discussion

4.1. Failure to see rod 'contrast-modulation flicker'

Despite considerable effort, we failed to see 'contrast-modulation flicker' from rods. Our results are consistent with previous ones (Rushton & Westheimer, 1962; Rushton, 1965; MacLeod et al., 1989, 1992) in indicating that adaptation occurring independently in individual rods makes little or no contribution to light adaptation in human vision. Under rod-isolating conditions, the reduction of net contrast by the uniform adapting background reduces the expected contrast-modulation flicker amplitudes, but on the assumption that each rod's sensitivity is inversely proportional to the background level, the calculated nulling amplitudes are about 10% peak to peak at all spatial frequencies considered here — much higher than we observe, and much higher than our experimental uncertainty.

A potential factor that could affect our search for rod contrast-modulation flicker is the temporal modulation frequency. We used mostly 6 Hz in the first experiment, but the second experiment revealed that the rod system sensitivity-regulating mechanism operative in the Weber intensity range has already lost most of its temporal resolution at 6 Hz. Although the intensity levels used in the two experiment were quite different, it is possible that we failed to find contrast-modulation flicker in rods simply because 6 Hz is too fast for the rod local sensitivity control or saturation mechanisms. To test this, we ran checks for contrast-modulation flicker at 3 Hz. The results here were also negative, but we place less confidence in these results because nulls at 3 Hz are subjectively rather unsatisfactory, perhaps due to the influence of uncontrolled eye movements. The conclusion from the results of the first experiment should therefore be amended: the results are evidence against the existence of any powerful sensitivity regulating mechanism or saturation process, operative under our conditions, that is both strictly local and fast enough to track 6 Hz modulation well.

The failure to observe difference-frequency gratings in rod vision (MacLeod et al., 1989; MacLeod et al., 1992), as well as the physiological evidence cited in the
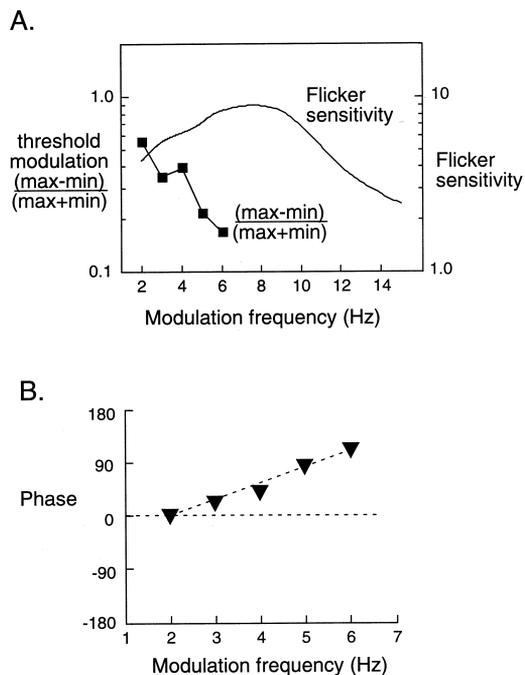

Fig. 6. Data from Fig. 5, replotted. (A) Modulation of threshold contrast ((max − min)/(max + min) based on data from curves in Fig. 5), as a function of background modulation frequency. Flicker sensitivity in rod vision at the same luminance level (10 scotopic td) is plotted for comparison (from Conner, 1982). Although the rod system still detects frequencies above 8 Hz efficiently, rod system sensitivity for incremental test flashes does not track background modulation above about 6 Hz. (B) Phase shift of the threshold modulation relative to background modulation.

introduction, supports the conclusion that local adaptation in rod system is minimal, at least in the Weber range, even when temporal constraints are not a factor. But it is surprising — indeed puzzling — that local sensitivity modulation could not be demonstrated at saturating levels. It is generally supposed that the psychophysically revealed saturation of the rod system, like the saturation observed in microelectrode or ERG recordings, originates in closure of light-sensitive channels in the outer segments. These closures presumably occur independently in different rods, since the retina provides very limited opportunities for relevant molecules to pass from one outer segment to another. But our surprising result with regard to saturation is consistent with physiological evidence obtained at the retinal ganglion cell level: Lennie et al. (1976) found that rod system saturation, as observed there, occurs in 'pools' rather than independently in different rods.

4.2. Temporal factors in rod system light adaptation

Since rods usually operate on a much weaker signal than cones, in which Poisson fluctuation in the absorbed photon count may be substantial, it makes sense that the rod system sensitivity adjustment should operates with a larger spatial integration area and also a longer integration time (Copenhagen, Donner, & Reuter, 1987). What we found in the 'test flash on a modulated background' experiment suggests that the rod system sensitivity adjustment does indeed have a long integration time. The threshold modulation data of Fig. 6A are roughly inversely proportional to frequency in the range 2–6 Hz, suggesting an integration time of at least 100 ms. for sensitivity regulation. This is notably slow by comparison with the situation in cones, where the cited work with a similar procedure, and also our work with contrast-modulation flicker, suggest an integration time several times shorter.

Our rod vision phase shift data suggest that the sensitivity regulating signal has a relative phase advance, as shown in Fig. 6B, rather than a lag as would be expected for an integrating system. One way this could happen is that at the site where the sensitivity is regulated, the signal that regulates the sensitivity actually arrives earlier than the signal to be detected. Although we ensured that it was rods that detected the probe target, cones were still modulated by the flickering background even with the steady deep red background. This makes it possible that rod system sensitivity could be modulated through cone–rod interaction. If the modulation of threshold is set at the ganglion cell level where signals from cones arrive early, the observed phase advance could result. We have no evidence for or against this possibility, although it is relevant that under steady state or slowly changing adaptation the influence of cones on rod threshold is

not generally large (Makous & Boothe, 1974; Hayhoe et al., 1976; Sharpe, Stockman & MacLeod, 1989). A roughly linear relationship between phase advance and temporal frequency as showed in Fig. 6B suggests a fixed time delay between the regulating and the regulated signals. The slope of the roughly linear phase advance data requires a constant relative time delay of rods signal about 45 msec to cones, consistent with physiological data (Gouras & Link, 1966).

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