Mutual rod–cone suppression within the central visual field

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Under mesopic conditions the contrast sensitivity of the central visual field is reduced as the result of a non-linear interaction between rod- and cone-mediated signals, each of which is capable of higher sensitivity in isolation. The interaction is produced only when the rod-mediated system is driven at flicker rates above 6 Hz. This finding bears upon how rod and cone signals are combined and therefore affects our interpretation of the significance of the relationship between retinal illuminance and both contrast sensitivity and temporal resolution.

One of the most impressive features of primate vision is the ability to maintain high contrast sensitivity over a large operating range of illumination. This is achieved by the combined effects of a duplicity of receptoral function and a gain control of neuronal sensitivity at the retinal level. This latter factor is reflected in our psychophysical performance since sensitivity varies with mean retinal illuminance for almost all spatiotemporal stimuli according to two rules: the Weber rule and the deVries–Rose rule[1,2]. Within the photopic region, contrast sensitivity is invariant with retinal illuminance[3], reflecting a Weber relationship whose physiological basis is thought to be a variable gain control within the retina[4]. Within the scotopic region contrast sensitivity varies with the square root of the retinal illuminance, termed a deVries–Rose relationship, which is thought to arise from quantal noise or quantal-related neural noise. The spatial and temporal conditions under which sensitivity is measured determines the illuminance at which one type of behaviour gives way to the other, termed the transition illuminance[3]. This is thought to represent the illuminance at which the gain control of retinal cells begins to operate.

Surprisingly, very little is known about the relative contributions of rods and cones to psychophysical performance at different light levels. Early attempts[5] were flawed by the use of spatio-temporally broadband stimuli, since discontinuities in performance were more likely to be due to a change in the postreceptoral filtering of the most sensitive mechanism than to a change in receptoral function[6].

In the present investigation we examine the rod–cone contribution to the detection of visual stimuli whose spatial and temporal frequency properties are confined to the low spatial and medium-high temporal part of our visible range. These stimuli have a restricted spatial and temporal frequency content, and for a number of reasons are ideal for exploring the relative rod–cone contributions to performance and developing an understanding of how signals from rods and cones are combined. The low spatial frequency properties of these stimuli ensure that they are detected by both receptor systems. We assessed the relative rod–cone contributions for different temporal frequencies of stimulation. Our results suggest that the combination of rod and cone signals depends on a number of factors; the temporal frequency of stimulation, the region of the retina and the level of illumination. At low rates of stimulation the combination of rod and cone signals is 'passive' in that the most sensitive mechanism determines threshold. At medium to high rates of stimulation rod-mediated flicker signals inhibit more sensitive cone-mediated flicker signals resulting in an overall sensitivity which is considerably worse than the capabilities of either receptoral system alone. In peripheral vision, no such temporal frequency specific interaction is seen and the more sensitive mechanism determines threshold regardless of the temporal frequency of stimulation.

Methods

Stimuli

Stimulus patterns consisted of vertically oriented sinusoidal gratings which were sinusoidally modulated in time. The luminance distribution of each stimulus is specified by

$$L(x, t) = L_0(1 + \sin(2\pi f_x)\cos(2\pi f_t))$$

where

L_0 is the mean luminance
f_x is the spatial frequency
and
f_t is the temporal frequency.

The stimuli were generated by a PDP11/34a computer and displayed on a Joyce Electronics (Cambridge, UK) DM1 raster monitor. The mean luminance was 200 cd m^{-2} and the frame rate was 100 Hz. Field size was varied between a diameter of 5 and 20 degrees by changing viewing distance. A large 40 × 50 degree outer surround

matched to the mean luminance of the display screen was provided. Mean luminance was altered with calibrated neutral density filters fitted to light-tight goggles worn by the subject. In some experiments the photoreceptor pigments were bleached using a white 6.7 log scotopic troland s bleach from a 30 degree field, viewed for 10 s with a fixed dilated pupil. Subsequent recovery was measured by making rapid threshold settings. The pupil was fixed and dilated with two drops of mydriatic (2% homatropine) and the pupil size measured before and after each experimental session using a photographic method.

General procedures

Monocular contrast detection thresholds were measured using a method of adjustment in which the contrast of the sinusoidal grating pattern was varied with a logarithmic attenuator in 0.5 dB steps. Ten threshold settings were averaged to produce a mean and standard error.

Results

In *Figure 1a* contrast sensitivity for central retinal stimulation is plotted against mean retinal illuminance for a 0.25 c/deg sinewave grating, contrast reversing at either 1 or 8 Hz. These results in themselves are neither new nor surprising. For the 1 Hz stimulus one can see the characteristic Weber behaviour at photopic levels and the deVries–Rose behaviour at scotopic levels. For the 8 Hz stimulus, rather than the square-root dependence at lower light levels there is in fact a linear dependence. Hence for this stimulus, incremental sensitivity is independent of retinal illuminance. This particular type of behaviour has attracted considerable interest in the past for two reasons. First, it remains the only exception[7] to the deVries–Rose description of the dependence of contrast sensitivity on retinal illuminance at mesopic and scotopic levels. Second, there is considerable evidence to demonstrate that this breakdown of light adaptation occurs in the most peripheral parts of the visual pathway, for example it is seen in the response of horizontal cell in the turtle[8], in the local electroretinogram in the monkey[9] and in man[10]. Lamb has argued that the sensitivity to these stimuli of low spatial and high temporal frequency is limited by the performance of cone photoreceptors[11].

These results take on added complexity when the experiment is repeated in peripheral vision. The results in *Figure 1b* are for the same stimulus conditions as shown in *Figure 1a* except that the stimulus field is imaged 10 degrees into the temporal field. Notice that contrast sensitivity for the 8 Hz stimulus now falls off with the more usual square-root dependence in the scotopic region, and this allows contrast sensitivity to be maintained down to a further 2.5 log units of illumination compared with central stimulation. This difference could be explained by supposing that the linear dependence of contrast sensitivity on illumination seen for central vision was due solely to cones whereas the square-root dependence seen in peripheral vision is due to rods. However when the stimulus includes both central and peripheral regions (*Figure 1c*) one does not find a response that represents the upper envelope of sensitivity to both the central and peripheral parts of the field. Instead a linear dependence is found followed by a 'notch' or discontinuity in
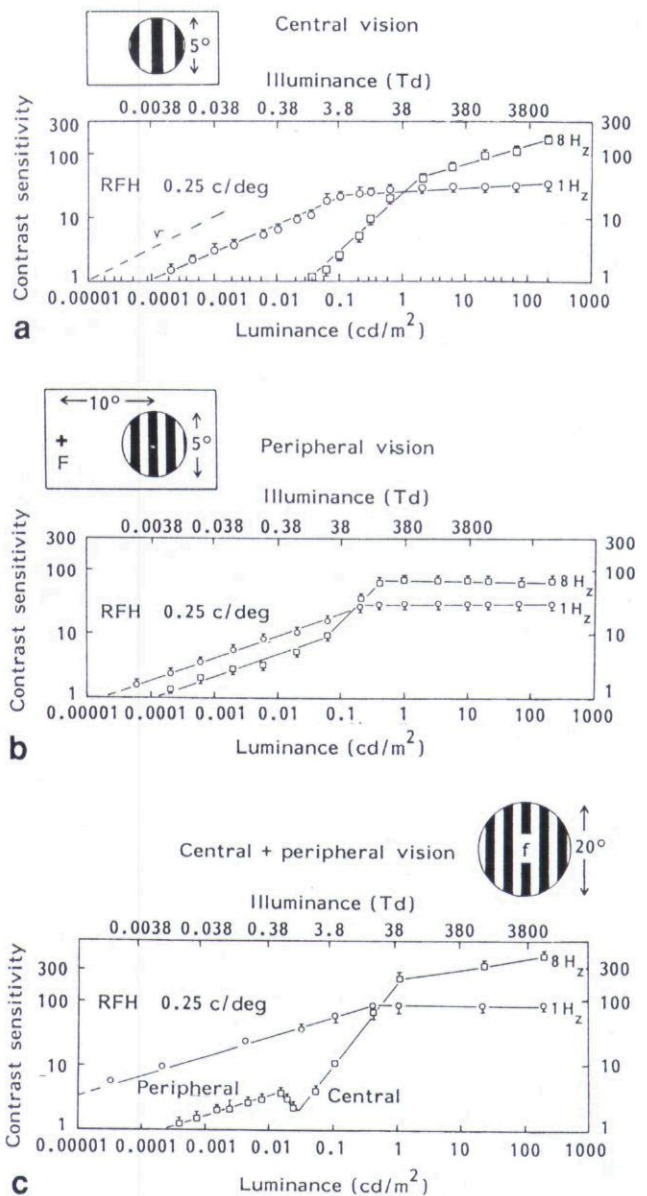

a

b

c

Figure 1 Contrast sensitivity is plotted against mean retinal illuminance for a 0.25 c/deg sinewave grating, sinusoidally contrast reversing at either: ○, 1 Hz; □, 8 Hz. In (*a*) results are for a centrally fixated 5 degree diameter field. In (*b*) results are for a peripherally fixated (10 degree eccentric, 5 degree diameter) field. In (*c*) the field size is 20 degrees with central fixation. The error bars represent 1 SD for the measurement

sensitivity occurring at around 1 troland which suggests an underlying interaction of some kind.

It is of obvious importance to understand the nature of the receptoral contribution to the 8 Hz results, and in particular at the illuminance corresponding to the 'notch' in sensitivity evident in *Figure 1c*. To assess the receptoral contribution at the low luminance limb of the 8 Hz results of *Figure 1a*, we bleached the photopigments and measured the recovery of contrast sensitivity for this retinal illuminance. These results for peripheral (*a*) and central (*b*) viewing (corresponding to the conditions of *Figures 1b* and *a* respectively) are displayed in *Figure 2a*. The results for the peripherally imaged stimulus show the classical duplex dark-adaptation recovery with the initial cone phase and the later rod phase. Increasing temporal frequency differentially reduces the sensitivity
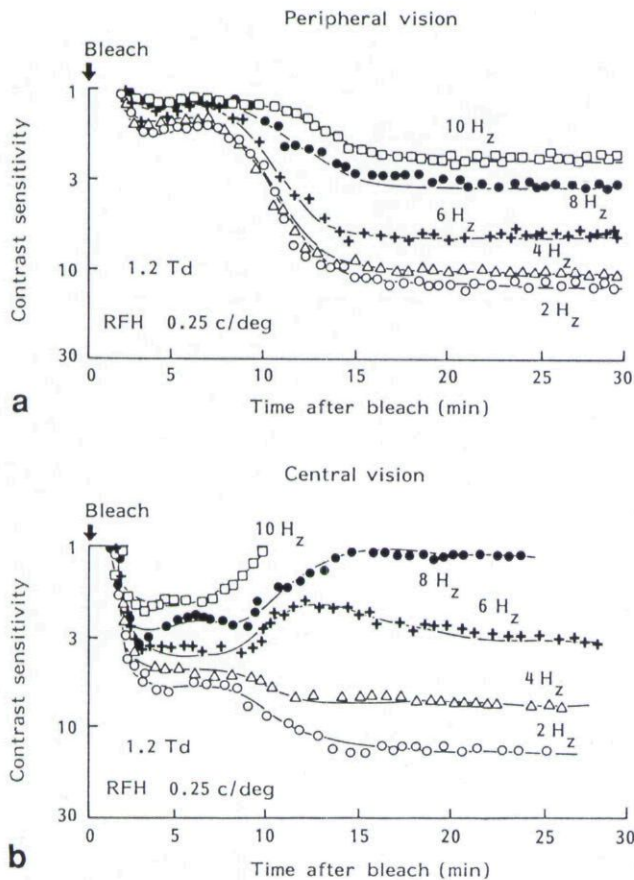
Figure 2 Contrast sensitivity is plotted against the time in min following a 6.7 log troland s bleach for a range of different temporal frequencies of stimulation. The spatial frequency is 0.25 c/deg and the mean illuminance corresponds to the sensitivity notch in *Figure 1c*. The field size is 5 degrees and it is either centrally (*b*) or peripherally (*a*) fixated

Figure 3 Comparable results for a rod monochromat to those displayed in *Figures 1* and *2*. In (*a*) contrast sensitivity is plotted against mean retinal illuminance for the 8 Hz condition (+) and compared to those of the normal trichromat (○, □). In (*b*) the recovery of contrast sensitivity after a bleach is shown for monochromat (+) and normal trichromat (●). Notice that the rod monochromat does not exhibit this interaction

of the rod branch, which is to be expected since cone-mediated steady state dynamics are better than rod-mediated steady state dynamics. The corresponding results for central vision (*Figure 2b*) no longer display this classical form. At flicker rates >4 Hz, as the rods recover, sensitivity is reduced in a temporal frequency dependent manner. In this temporal range, sensitivity improves at first with the dynamics of the cone photopigment but then deteriorates with the dynamics of the rod photopigment; the opposite of the classical dark adaptation result. This suggests that the terminal or recovered sensitivities (those plotted in *Figure 1a*) are the result of a destructive interaction between rod and cone-mediated vision. We must reject our initial hypothesis that the steeper decline in contrast sensitivity with illumination for 8 Hz central stimulation can be explained by normal cone function.

To understand the nature of this interaction one needs to know the rod mediated response in isolation for these particular stimuli. We obtained this by comparing similar results for a rod monochromat whose visual characteristics are those of normally functioning rods in isolation[12–15]. These results are displayed in *Figure 3* as crosses and show that when rods alone determine threshold in this lower mesopic region, contrast sensitivity is greater than for the normal trichromat (*Figure 3*) and a square-root dependence is obtained for central 8 Hz stimulation (*Figure 3a*). Notice also that recovery is that expected of normal rods (*Figure 3b*).
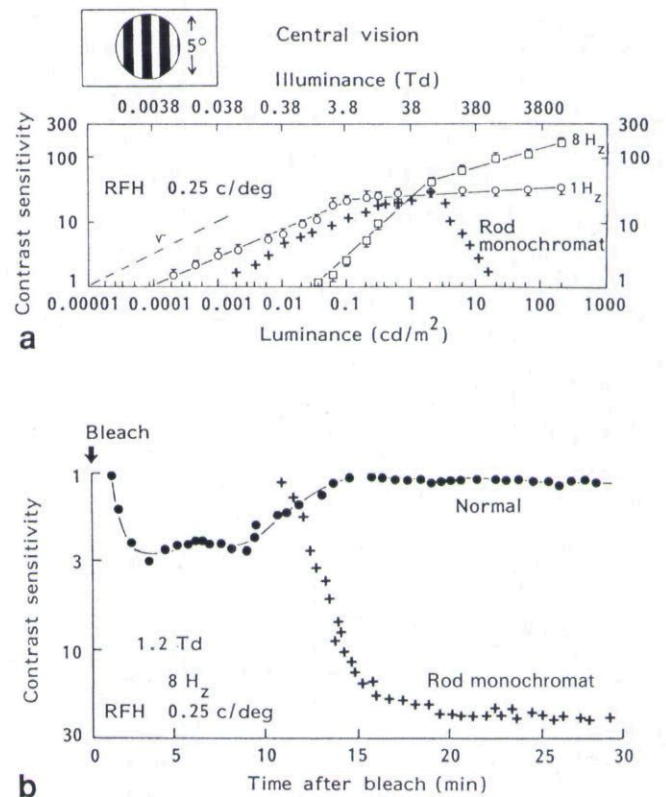
To reveal the critical characteristics of this receptor-mediated interaction we carried out a number of additional experiments, the results of which are displayed in *Figure 4*. In *Figure 4a* we compare the recovery of sensitivity for a 0.25 c/deg sinewave grating and a uniform field, each temporally modulated at 2 and 8 Hz. The results show that the strength of the interaction does not depend on the spatial distribution of light since a similar interaction is evident in 8 Hz results for both pattern and uniform fields of the same space-averaged illuminance.

This interaction is unaffected by the relative temporal phase of two flickering stimuli, one whose spectral properties were detected by rods at threshold and another whose spectral properties favoured detection by cones (*Figure 4b*). This suggests that this interaction is not the result of a linear rod–cone cancellation resulting from a delay in one pathway before their combination.

Furthermore, the receptors that underlie the raised terminal thresholds in *Figure 2b* (and hence the scotopic 8 Hz limb of *Figure 1a*) are rods, not cones, because as the results depicted in *Figure 4c* show, two spectrally different stimuli whose contrasts are scotopically equated (but whose cone contrasts are therefore very different) have the same terminal thresholds for the 8 Hz condition.

Finally, we show that no such interaction occurs for an 8 Hz rod-isoluminant stimulus (*Figure 4d*, unfilled symbols) indicating that the interaction seen in *Figure 2b* is not mediated by rods that are tonically stimulated by the time-averaged luminance. However we also show
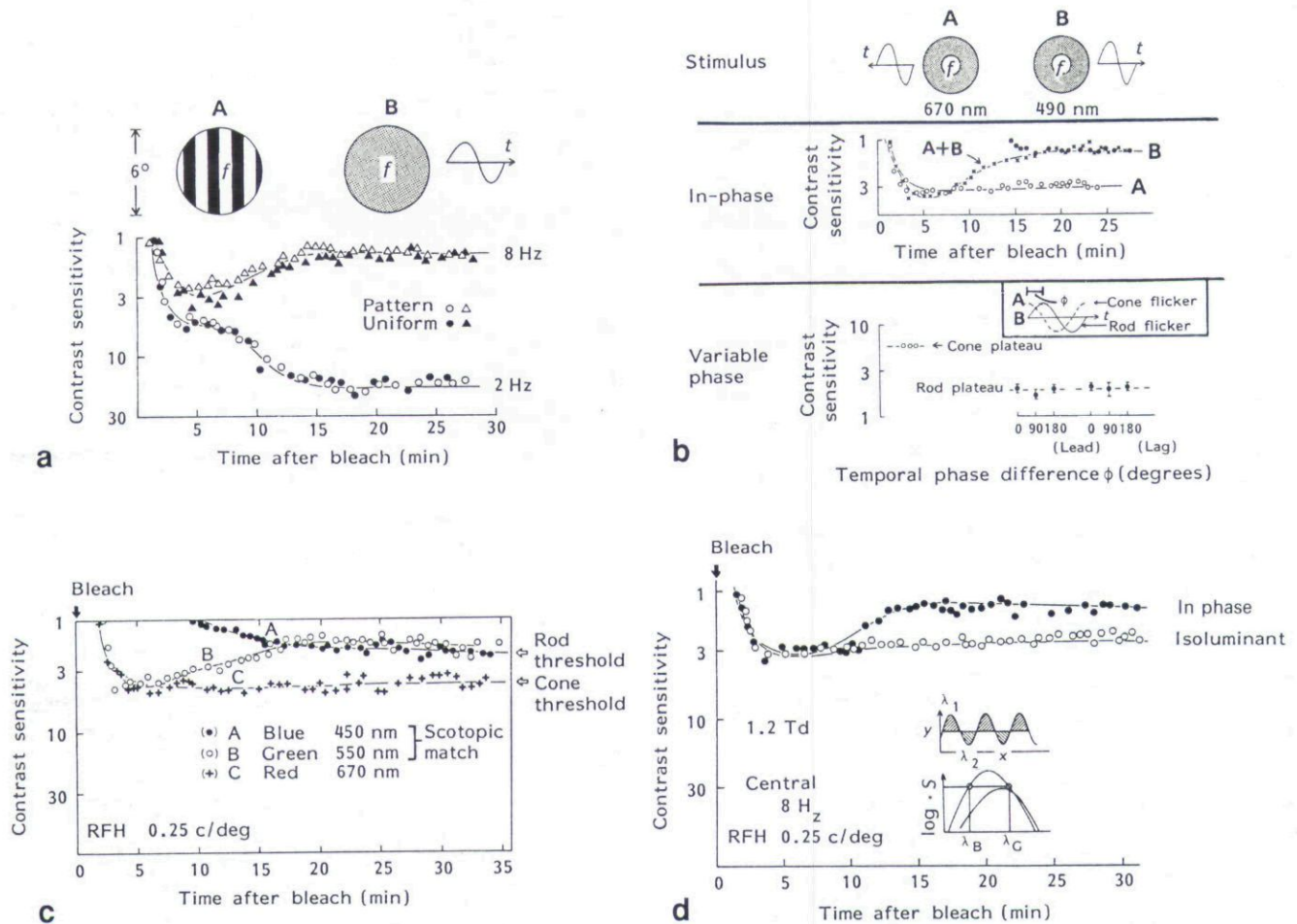
Figure 4 Recovery of contrast sensitivity after a bleach to the mean illuminance corresponding to the sensitivity notch in *Figure 1c* is shown for a number of conditions. In (*a*) the results obtained for the 0.25 c/degree condition are compared to those obtained for an unpatterned uniform-field for two rates of temporal stimulation. In (*b*) the influence of the relative temporal phase is shown for two stimuli, one of which is detected by rods and the other by cones. The interaction is not affected by the relative temporal phase between these stimuli. In (*c*) recovery is compared for three stimuli, one is detected by cones only (+) whereas the other two are scotopically matched in contrast. Notice that the results for these two latter stimuli converge on the elevated terminal thresholds. In (*d*) recovery is compared for a rod-isoluminant stimulus (○) for which there is no interaction and for the same components but put in phase (rod and cone stimulation, ●) for which there is the interaction

that when the two spectrally different sinusoidal components of such a rod-isoluminant stimulus are put in phase (producing an additional intermittent stimulation of rods) that such an interaction is evident (*Figure 4d*, filled symbols). This suggests that for this interaction to take place, rods must be intermittently stimulated and not just tonically stimulated.

We have also investigated the dependence of this interaction on the mean illuminance and the region of the visual field since the results of *Figure 1* highlight their importance. *Figure 5a* shows recovery curves to a range of different mean illuminances for the conditions depicted in *Figure 1a*. These results show that this interaction begins under mesopic conditions and increases in the lower mesopic region. *Figure 5b* shows recovery of sensitivity after a bleach for a small unpatterned stimulus imaged in different locations of the visual field. The region of the field where the interaction takes place is confined to the paracentral region.

One can come to a number of conclusions from the results presented above. First, since there is at least a factor of three between the cone recovery plateau and the terminal sensitivity plateau for 8 Hz stimulation (*Figure 2b*) and since the strength of the interaction increases as illuminance is decreased within the lower

mesopic region (*Figure 5a*), we conclude that the linear dependence of contrast sensitivity, observed in *Figure 1a*, is the result of a receptor-specific interaction and not the result of a single receptor, as previously assumed. Second, since the interaction is only observed during the rod recovery phase, this suggests that rod-mediated signals are destructively interfering with cone signals. The results from *Figure 4d* shows that such rod stimulation needs to be intermittent (and not just tonic) for this interaction to occur. Third, this interference is limited to the paracentral retina (*Figure 5b*). Fourth, the sensitivity 'notch' seen in the results of *Figure 1c* must, on the basis of this conclusion be the result of suppression of peripheral cone signals by more centrally located (in the retina) rod signals. Fifth, the terminal thresholds are set by rods (*Figure 4c*) but at a much reduced sensitivity compared to normal (*Figure 3*).

Discussion

These results describe a rod–cone interaction which is only revealed under a restricted set of conditions; namely for stimuli of mid- or high-temporal frequency imaged on the central retina under mesopic conditions of illumination. Its consequence is selectively to reduce the
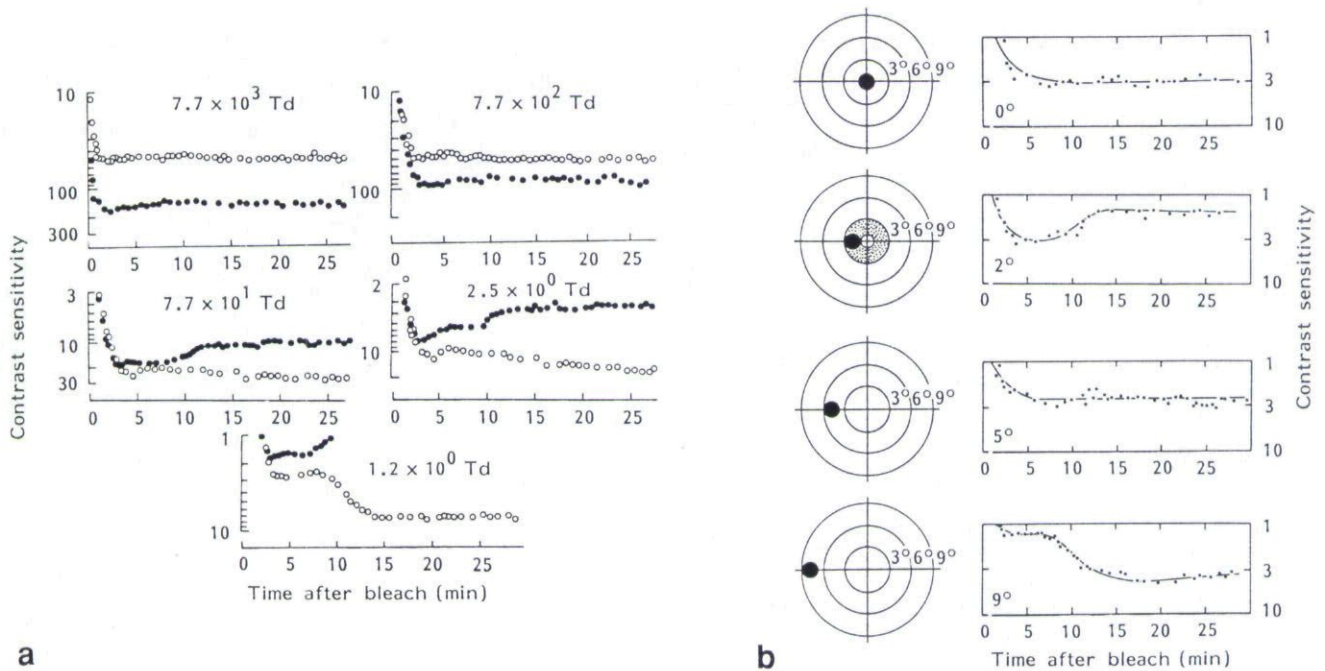
Figure 5 Recovery of contrast sensitivity after a bleach. In (*a*) the effect of the mean retinal illuminance for two rates of temporal stimulation are shown. In (*b*) the effect of retinal locus on the recovery of an unpatterned 8 Hz modulated field is shown

temporal signalling capabilities of central mesopic vision below the individual capabilities of rod-mediated or cone-mediated vision. As such it represents a unique example of the vision of the rod-monochromat being better than that of the trichromat[12–14]. It is unclear whether this represents a 'design feature' in the integration of peripheral rod and central cone function across the visual field under mesopic conditions or one of its 'failure modes'.

Relationship to previous studies

There have been numerous previous reports of interactions between rods and cones which run contrary to the more accepted duplex theory of retinal function. These come in a number of different forms; linear cancellation of rod and cone signals[16,17,18], mutual cancellation of rod signals[19,20], suppressive rod–cone interactions[21,22] and peripheral habituation[23]. Since the present phenomenon involves a non-linear (see *Figure 4c*) interaction between rods and cones, only the so called 'suppressive rod–cone interactions' are sufficiently similar to warrant close comparison. However, there appear to be some important differences between these previously described phenomena and the present one. The suppressive rod–cone effects that have been reported previously are tonic in nature, affect peripheral regions of the retina and result in elevated terminal thresholds set by cones. The present phenomenon results from the *transient* signals from rods suppressing the signals from cones in only the *central* region of the retina with the resulting terminal thresholds being set by *rods*.

Relevance to visual psychophysics and electrophysiology

This interaction is relevant to two particular issues in vision research. First, the linear fall-off in contrast sensitivity with reduced illumination found in central vision for medium to high stimulus flicker rates[7–11] and,

second, the different forms of the relationship between temporal resolution and illumination found for central and peripheral vision[24,25]. In the former case, it is clear from a comparison of the bleaching recovery data of *Figure 2* that the actual slope of the sensitivity fall-off for central vision for the 8 Hz stimulus is artificially steepened by the underlying rod–cone interaction.

The second relevant aspect of these findings is to mesopic temporal resolution. Hecht and Verrijp[24,25] argued that the double branched function relating the critical flicker frequency and retinal illumination was due to the duplex nature of retinal processing, with rods determining the more scotopic branch and cones the more mesopic branch. Evidence used to support this was the finding that under peripheral viewing the scotopic branch was enhanced, whereas under central viewing critical flicker frequency was greatly reduced and only a single branched function was obtained. Contrary to Hecht's claim, recent evidence has shown that the peripheral double branched function in fact reflects two types of rod-mediated response[12,26,27] rather than a change from cone to rod-mediated response. Our results provide further evidence against Hecht's argument. Hecht assumed that the presence of a single branched function (and reduced critical flicker frequency) for central stimulation indicates normal cone function in isolation. On the contrary, our results show that Hecht's foveal data is not determined by cones but by rods under the influence of a suppressive interaction.

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