THE TEMPORAL PROPERTIES OF ROD VISION

BY J. D. CONNER*

From the Psychology Department, University of California at San Diego, U.S.A.

SUMMARY

1. Profiles which represent rod thresholds for flickering fields seen against backgrounds of various intensity have shapes which depend on flicker frequency. Low frequency profiles rise smoothly as background intensity is increased. High frequency profiles are only affected by bright backgrounds, which cause them to rise steeply. Intermediate frequency profiles contain two distinct branches which resemble separate increment threshold functions.

2. The high intensity branches of two-branched threshold profiles cannot be attributed to cone intrusion. Instead, both branches of such profiles are mediated by visual mechanisms which have the spectral properties, the dark adaptation properties and the directional insensitivity of rod vision. Thus, the stimuli are detected by rods.

3. Plots of critical flicker frequency (c.f.f.) as a function of intensity contain two rising branches which are separated by a plateau (when modulation depth is large), or they form two enclosed lobes so that only intermediate frequencies, but neither high nor low ones, are seen (when modulation depth is small). C.f.f. is profoundly depressed by very bright light (above 100 scotopic trolands) which saturates rod vision.

4. In dim light rod modulation sensitivity functions resemble those of low-pass filters, but in bright light they resemble those of band-pass filters.

5. Several forms of rod mediated interference occur at moderate intensities, where rod vision's temporal properties ordinarily improve abruptly. With certain stimuli, rod signals conveying temporal information disrupt one another so completely that suprathreshold flicker cannot be seen within a ten-fold intensity range.

6. Many of these observations can be explained by the hypothesis that rod vision comprises two temporal channels which have different properties.

INTRODUCTION

The temporal properties of light-adapted rods are difficult to measure, because their thresholds are frequently obscured by cone activity at mesopic intensities (Le Grand, 1972). Therefore, rod temporal resolution has usually been measured in dim light, where rods function alone (Brown, 1965). Such studies have shown that the temporal resolution of rods is so poor that they never discriminate frequencies above 10 or

* Present address: Physiology and Biophysics Department, University of Washington Medical School, Seattle, WA 98195, U.S.A.

15 Hz. So, it is widely believed that fine temporal discrimination must always be mediated by cones. This is not true. Conner & MacLeod (1977) used special conditions to isolate and measure the temporal resolution of light-adapted rods, and they found that rod resolution improves abruptly in moderate illumination so that 30 Hz flicker can be seen. Thus, the temporal properties of human rod vision are complex and incompletely understood. Now additional studies of rod vision's temporal properties suggest that moderate illumination activates a supplemental rod channel whose signals usually improve, but sometimes impair, rod temporal resolution.

<div style="text-align:center">

METHODS

</div>

General procedure. Since cone activity frequently obscures rod activity in bright light, special rod isolation procedures were used in these experiments, so that light adapted rods could be studied. The rationale of these rod isolation techniques has been discussed elsewhere (Aguilar & Stiles, 1954; Conner & MacLeod, 1977).

After dark adapting for 40 min, observers adjusted the intensity of a sinusoidally flickering field until the sensation of flicker was at threshold in the presence of a background light of fixed intensity. Observers began alternate trials at an intensity which was either above or below threshold. Every threshold reported here is the mean of at least six independent settings, which rarely spanned a range exceeding 0·1 log units of intensity. The standard errors of the means of these settings generally fall within the boundaries of the symbols which have been used here to represent the means. Two observers participated in all of the experiments reported here, and two supplemental observers participated in a portion of the experiments. Thus, every experiment was conducted on at least three experienced observers. Further, these experiments were repeated several times on each of the two primary observers during a span of 18 months. The variability between subjects, and the variability between the settings for different experimental sessions for a particular subject, were somewhat greater than those for a single subject during a single session, but the qualitative features of the results did not change. To minimize the effects of variability on the data reported here, thresholds for a particular flicker frequency were obtained during a single four to five hour experimental session.

In most experiments the test stimulus was a uniform disk, but in some experiments the field was vertically bisected into adjacent hemifields which flickered out of phase. Settings were made for flicker frequencies of 1–21 Hz and for background intensities of 0·00001–10,000 scotopic trolands (sc td; Le Grand, 1968). These data were tabulated, and the logarithm of flicker threshold was plotted against the logarithm of background intensity. The resulting curves are analogous to increment sensitivity functions measured with brief flashes (Aguilar & Stiles, 1954), but the stimuli used to obtain them differ in two ways. First, sinusoidal stimuli contain a single temporal element, but flashes contain many superimposed frequencies. Secondly, sinusoidal stimuli can contribute a significant fraction of a display's average illuminance, but brief flashes rarely do. To underscore these differences, thresholds measured with sinusoidal stimuli will be called threshold profiles, and thresholds measured with flashes will be called increment threshold functions.

Apparatus. A three channel maxwellian view stimulator, whose features have been described elsewhere (Conner & MacLeod, 1977), produced the flickering and background fields. One channel formed the flickering field, whose intensity varied sinusoidally with time as a linear polarizer was uniformly rotated so that its axis repeatedly crossed the axis of a fixed-position polarizer. The remaining channels formed background fields. Field diameters were controlled by suitably positioned apertures. When a bipartite field was needed, the maxwellian stimulator was modified by inserting a beam splitting cube in the test-field channel, so that two subsidiary channels were formed. These beams passed through different spinning and fixed linear polarizers, so that their intensities varied sinusoidally as identical functions of time. However, the orientation of the fixed linear polarizers could be adjusted separately, so that the phase of the two flickering channels could be altered. These beams then passed through suitable apertures and a beam combining cube, which juxtaposed them to form adjacent hemifields. Beam intensities were controlled by calibrated discrete neutral filters and graded neutral wedges. Wave-length was fixed either by a red Kodak

no. 92 Wratten filter (the main background) or by narrow-band interference filters (the flickering field and the supplemental background).

Stimuli. The flickering field was a short-wave-length (usually 519 nm), 9° disk which was centred on the red, 13° background that was located 16° temporally of the observer's fovea.

Rod-equated lights. Several experiments required different spectral lights which affected rods equally. Although these rod matches were guided by photocell measurements of the lights' radiance, no match was accepted until the following psychophysical criteria were met. First, the lights looked alike when they were viewed near absolute threshold. Secondly, when the lights were presented as flickering fields their thresholds were identically affected by identical, dim background light. Thirdly, the threshold for seeing a slowly flickering field near its absolute threshold was identically affected by the lights when they acted as backgrounds. Fourthly, when the lights were crisply exchanged, they failed to revive the afterimage of a bleaching stimulus during the rod phase of recovery from the bleach (MacLeod & Hayhoe, 1974; Hayhoe, MacLeod & Bruch, 1976).

The Stiles-Crawford effect. Ordinarily the maxwellian images of the flickering and background fields were centred in the observer's pupil. In some experiments, though, it was necessary to measure the Stiles-Crawford effect (Crawford, 1972), or the directional selectivity, of the mechanism which mediated visual threshold. Mydriacyl was used to dilate the observer's pupil, and the image of the flickering field, but not the background, was shifted to the pupil's margin. Thus, the flickering field's beam struck the retina more obliquely than the background's beam.

Data analysis. Data were plotted on log–log co-ordinates as flicker threshold against background intensity, and a smooth curve was fitted by eye to the points for each flicker frequency. Thus, threshold profiles were constructed.

Critical flicker frequency. Points of fixed modulation were located on the threshold profiles graphically by constructing straight lines with a slope of 1 which intersected the profiles. Such lines connected points which had identical modulation depth, calculated from the relationship

$$\text{Modulation} = \frac{I_f}{I_f + I_b} \tag{1}$$

where I_f is the amplitude of the flickering field in scotopic trolands and I_b is the retinal illuminance of the background. The intersection of a threshold profile and a modulation line corresponded to stimulating conditions for which the stimulus was at threshold. Thresholds for various flicker frequencies were calculated at each of several fixed illuminances from the relationship

$$\text{Illuminance} = \frac{I_f}{2} + I_b \tag{2}$$

and in each case the fastest flicker which could be seen at each intensity was plotted to form a critical flicker frequency (c.f.f.) function. Thus, c.f.f. functions were constructed for stimuli whose modulation ranged from 0·2 to 1·0.

Modulation sensitivity. A template was constructed so that lines drawn with it connected points on the threshold profiles which had identical time-average retinal illuminances. The intersection of a particular threshold profile and one of these lines corresponded to a flicker threshold for the particular time-average illuminance which the line represented. Each point's modulation was calculated by equation (1), so that modulation sensitivity could be plotted as a function of flicker frequency for each of many intensities.

<div style="text-align:center">RESULTS</div>

Threshold profiles

When flicker threshold was plotted against background intensity, it was seen that every threshold profile could be assigned to one of three classes based on its shape. An example of each class is shown in Fig. 1, where profiles for 1, 15 and 21 Hz are plotted. The 1 Hz profile, like the profiles for frequencies up to 9 Hz, resembles a conventional increment threshold function. The threshold for this stimulus is low when the background is dim, and it is raised steadily as the background intensity is
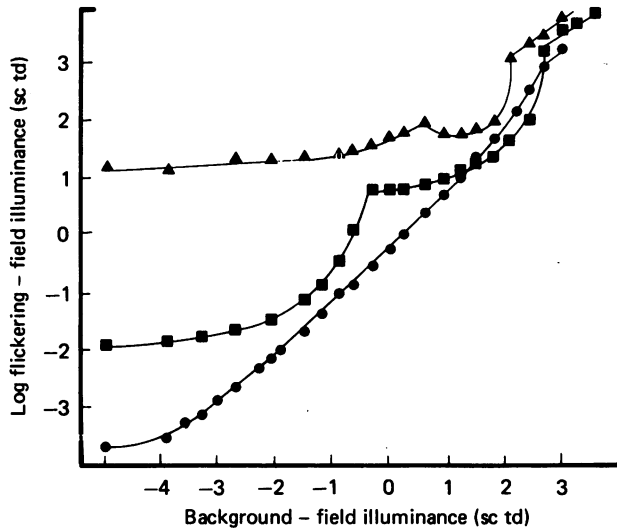
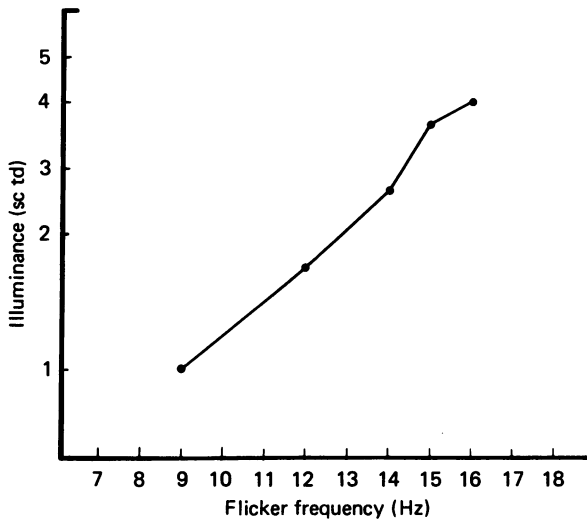Fig. 1. Flicker frequency sensitivity profiles for 1 (●), 15 (■) and 21 (▲) Hz stimuli.

Fig. 2. The intensity of the visual display (background plus the time-average of the flickering field) at the intersection of the first and second branches of two-branched profiles.

increased. At high intensities, where rods saturate (Aguilar & Stiles, 1954), the profile rises steeply. By contrast, the 21 Hz profile, like the profiles for other frequencies above 16 Hz, is only affected by bright background lights, which cause it to rise steeply. This is not surprising, since the threshold for this stimulus is always so high that the stimulus contributes a large component to the display's average intensity.

Thus, the threshold for rapid flicker is only altered by backgrounds which are bright enough to significantly increase the display's average intensity. The third type of profile, which is represented by the 15 Hz thresholds in Fig. 1, is quite unconventional, since it contains two distinct branches that intersect at a moderate intensity. Other intermediate flicker frequency profiles (9–16 Hz) also contain two branches, but the intensity at which their branches intersect depends on flicker frequency (Fig. 2). Such profiles resemble intersecting increment threshold curves for different visual mechanisms (Enoch, 1972).
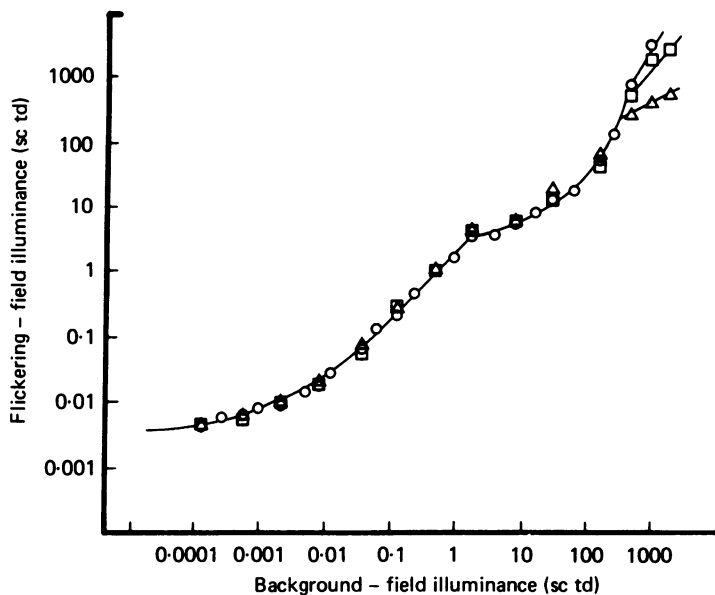

Fig. 3. Flicker frequency sensitivity profiles for a 12 Hz stimulus. Sensitivity was measured with a 469 ($\triangle$), 500 ($\square$) or 519 ($\bigcirc$) nm stimulus.

Control experiments. It is surprising that the threshold profiles for intermediate flicker frequencies contain two distinct branches, since two-branched increment threshold functions have not been previously reported for rod vision or for any visual process which is mediated by a single mechanism. One may doubt, therefore, that rods actually mediate both branches of these curves. This suspicion is unwarranted, however, as several control experiments demonstrate. Although the control experiments reported here were confined to the use of a 12 Hz stimulus, similar control experiments were performed for the other flicker frequencies which were studied. The results of those other control experiments confirm the conclusions reached here, but they have been omitted for brevity.

1. Since the action spectra of rod and cone photoreceptors are different, lights of different wave-length affect rods and cones differently (Le Grand, 1968). So, thresholds measured with spectral lights equated for rods will be identical only if they are detected by rods; thresholds will differ if the lights are detected by cones. Fig. 3 shows

12 Hz threshold profiles which were measured with three spectrally different rod-equated lights. These profiles are indistinguishable, and their thresholds overlap along both branches of the threshold profile. They diverge only near 1000 sc td, where cones detect them. Thus, the mechanism mediating these two-branched curves has the action spectrum of rod vision.

2. Apparently only rods can see the flickering stimulus, but both rods and cones can see the background, which is well above their threshold. So, if cone signals
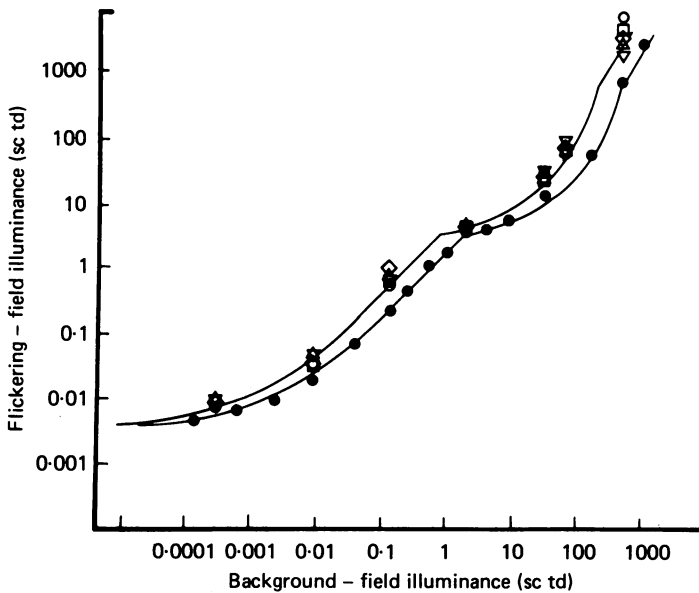

Fig. 4. Flicker frequency sensitivity profiles for a 12 Hz stimulus measured in the presence of the standard red background (●) and in the presence of a 469 (▽), 500 (◇), 546 (○), 600 (△) or 681 (□) nm supplemental background. The curve which fit thresholds measured against the main background has been shifted laterally about 0·3 log units to fit each set of thresholds obtained after the addition of the supplemental background.

contribute to an adaptation pool which regulates rod sensitivity, they might affect the threshold profile's shape even though they could not see the flickering stimulus. This hypothesis was tested by adding supplemental backgrounds of different rod-equated wave-lengths to the main red one. If rod sensitivity is regulated solely by the rod response to the background, then flicker thresholds will be identically affected by every supplemental background regardless of its wave-length. If the cone response to the background affects rod sensitivity, though, thresholds will be differently affected by the rod-equated backgrounds, since they affect cones differently. In fact, the curves are alike, as Fig. 4 shows. The supplemental backgrounds' effects are indistinguishable, as they all shifted the profile about 0·3 log units. Therefore, these background lights affected rod flicker thresholds solely through their effect on the rods (by contrast, see Makous & Boothe, 1974; Ingling, Lewis, Loose & Meyers, 1977).

3. Although rods and cones lose their sensitivity when a large fraction of their photopigment is bleached, cones regain their sensitivity quicker than rods do (Barlow, 1972). Therefore, there is an interval, the cone plateau, when cones have regained their full sensitivity but rods have not. During this interval, cone thresholds can be measured for stimuli which would otherwise be detected by rods. If the thesholds measured during the cone plateau match those measured after complete recovery, then cones mediate threshold in both cases. However, if thresholds measured during
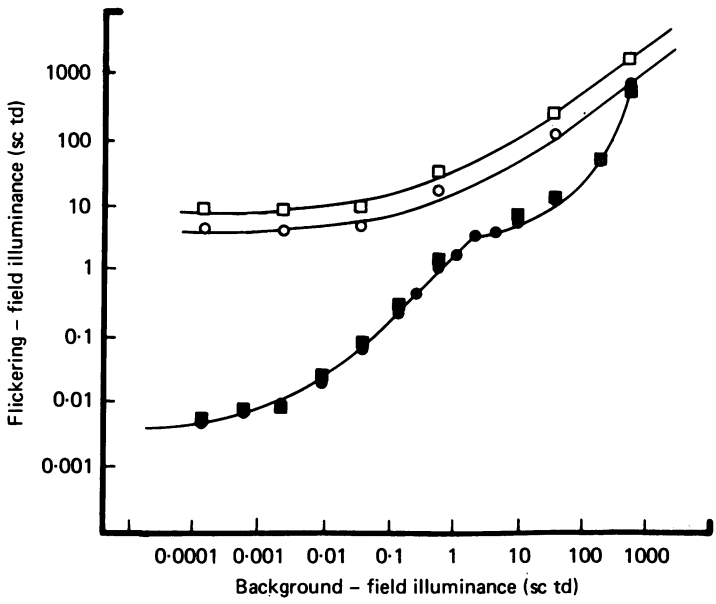

Fig. 5. Flicker frequency sensitivity profiles for a 12 Hz stimulus measured during the cone plateau (open symbols) which followed a bleaching light of about 7·6 log troland-seconds or after complete recovery (filled symbols). The maxwellian image of the flickering beam was either centred in the observer's pupil (circles) or displaced to its margin after it had been dilated by a mydriatic (squares).

the cone plateau lie above those measured after complete recovery, then rods detect the stimulus after complete recovery. Fig. 5 shows that the profiles measured during the cone plateau (open circles) lie above those measured after complete recovery (filled circles). Thus, the two-branched thresholds are mediated by rods.

4. Cone photoreceptors are much less sensitive to lights which strike them obliquely than to lights which strike them axially (Crawford, 1972), but rods are not much affected by this difference unless it is very large (Van Loo & Enoch, 1975). Therefore, threshold profiles measured with axially and obliquely incident lights will be alike if these stimuli are seen by rods, but they will be different if they are seen by cones. Fig. 5 shows thresholds which were measured with axially (circles) and obliquely (squares) incident stimuli either during the cone plateau (open symbols) or after full recovery (closed symbols) from a bleaching light. As expected, thresholds measured during the cone plateau were higher for obliquely incident lights than for

axially incident ones, but thresholds measured after complete recovery were not affected by this difference. Thus, the visual mechanism mediating the two-branched profile is directionally insensitive, as rods are.

These control experiments demonstrate that the visual mechanism which mediates the two-branched threshold profile for 12 Hz has the action spectrum, the directional sensitivity, and the dark adaptation properties of rod vision. They also show that the background acts through rods alone. These observations lead to the conclusion that rods mediate thresholds along both branches of the two-branched threshold profile. Thus, rod vision's flicker sensitivity changes abruptly in moderate light so that the profiles of intermediate flicker frequencies develop distinct high-intensity branches. Similar control experiments were conducted for the other flicker frequencies used here, and they, too, support this conclusion with one qualification. Rods and cones are nearly equally sensitive to 21 Hz flicker, the highest frequency studied here, when the background is dim. As background intensity is increased, though, cones are more strongly desensitized than rods, so that rods, not cones, mediate thresholds against brighter backgrounds. At the point where the cone thresholds begin to rise above the rod ones (Fig. 1 when the background is about 3 sc td), a slight bump appears in the 21 Hz profile. This bump is probably due to the interference of rod and cone signals with one another (MacLeod, 1972; Van den Berg & Spekreisje, 1977). Only those thresholds mediated solely by rod vision, as determined by control experiments of the sort reported here, have been included in the following analyses of critical flicker frequency and modulation sensitivity.

Critical flicker frequency. Fig. 6 plots critical flicker frequency (c.f.f.) for stimuli of different modulation depth. When the flickering field's modulation depth is large (above 0·6) it yields a c.f.f. function that contains two rising branches which are separated by a plateau (see Conner & MacLeod, 1977). Thus, rod temporal resolution improves as intensity is increased if the intensity is either dim or bright, but not if the intensity is moderate (around 0·1 sc td). When the stimulus has a modulation depth of 0·8, for example, c.f.f. rises to 15 Hz as intensity rises to 0·1 sc td, but additional increases in intensity do not increase c.f.f. until intensity exceeds 3 sc td. For smaller modulation depths (below 0·6), the c.f.f. function forms a closed space within which flicker is visible. Thus, a stimulus of low modulation depth can not be seen to flicker either slowly or rapidly. When modulation depth is 0·2, for example, flicker can only be seen when the display's intensity lies between 0·2 and 200 sc td: within this range frequencies of 2–16 Hz can be seen, but higher and lower frequencies are never visible. Thus, stimuli with intermediate modulation depths yield enclosed c.f.f. contours which contain two separate lobes: a low intensity lobe where slow flicker frequencies are visible and a high intensity lobe where fast flicker can be seen. Finally, c.f.f. is generally depressed slightly when the display is moderately bright (about 1 sc td), and it drops precipitously at very high intensities where rod saturation begins.

Modulation sensitivity

Fig. 7 shows modulation sensitivity profiles for stimuli which spanned a 5 log unit range of intensity. Modulation sensitivity generally improves, so that higher frequencies become visible, when intensity is increased. The sensitivity functions also
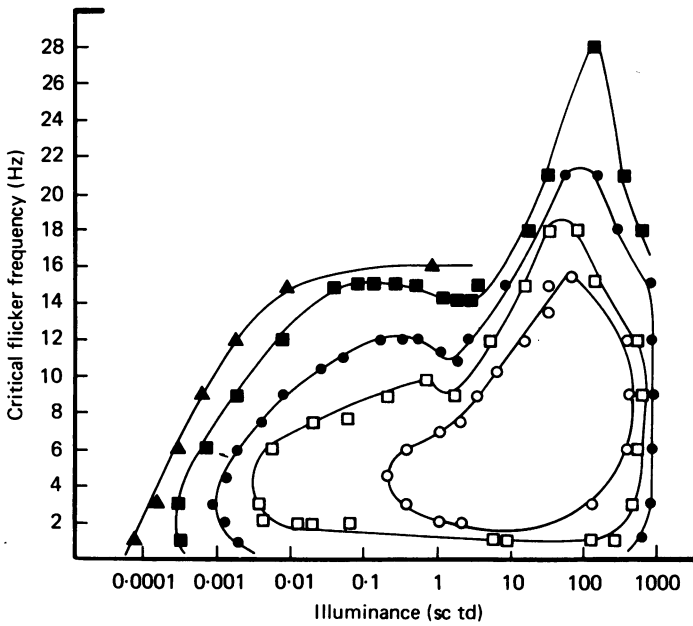
Fig. 6. Critical flicker frequency as a function of intensity for stimuli whose modulation was 0·2 (○), 0·4 (□), 0·6 (●), 0·8 (■) or 1·0 (▲).
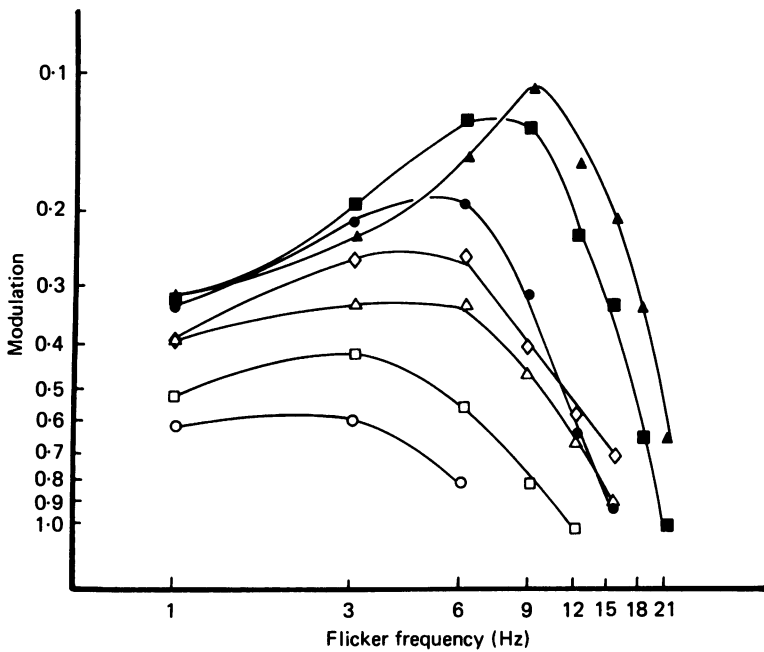

Fig. 7. Modulation sensitivity functions measured when the intensity was 0·00025 (○), 0·002 (□), 0·022 (△), 0·219 (◇), 2·14 (●), 21·4 (■), or 45·7 (▲) sc td.

change shape, however, as intensity is increased. Thus, in dim light they manifest the properties of a sluggish low-pass temporal filter, but in bright light they develop sharp peaks such as are characteristic of band-pass filters. At very high intensities (45·7 sc td, for example), the low frequency portion of the modulation profiles cross below the profiles measured at slightly lower intensity. Thus, rod vision loses relative sensitivity to low frequencies at these intensities, while it gains relative sensitivity to high frequencies.

Rod-mediated visual interference

In the course of these experiments several forms of rod-mediated visual interference were observed. First, as Fig. 8 shows, the slope of the 15 Hz profile's lower branch
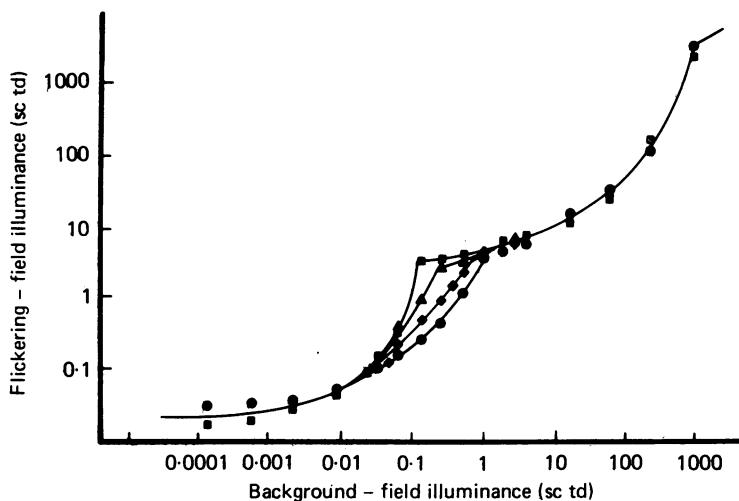

Fig. 8. Sensitivity profiles for a 15 Hz stimulus which was located 13° (●), 19° (◆), 22° (▲) or 25° (■) from the observer's fovea.

becomes steeper as the field's retinal eccentricity is increased. For large displacements of the field, the curve's abrupt rise manifests a profound loss of sensitivity which resembles the effect of rod saturation (Aguilar & Stiles, 1954). Yet it occurs at intensities which are much too dim to saturate rods.

Secondly, the slope of two-branched profiles depends on the spatial configuration of the flickering stimulus. This is illustrated in Fig. 9, where 15 Hz sensitivity profiles obtained with uniform and bipartite fields, whose halves flickered 180° out of phase, are plotted. These profiles differ from one another in two ways: the bipartite field profile manifests an extreme loss of sensitivity near the intersection of its two branches, and threshold actually declines along the upper branch as intensity is increased beyond the intersection. This decline is real, as the following experiment shows. The flickering field's intensity was set so that flicker was just below threshold in the presence of a 0·25 sc td background. In every case, though, flicker became visible when a weak neutral filter (0·3 density) was removed so that the background
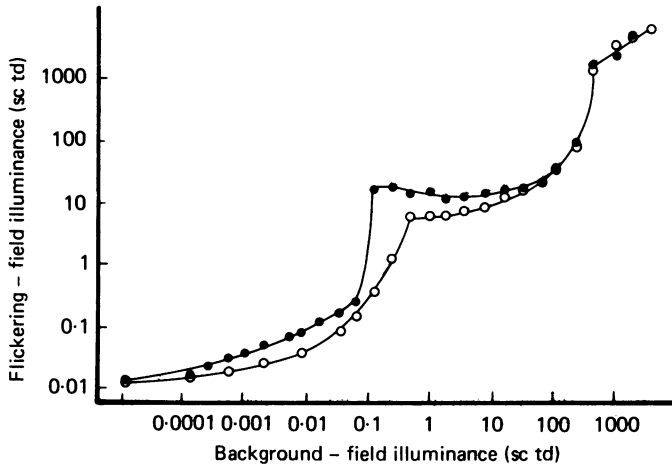
Fig. 9. Flicker frequency sensitivity profiles for 15 Hz 519 nm bipartite (●) and uniform (○) fields.
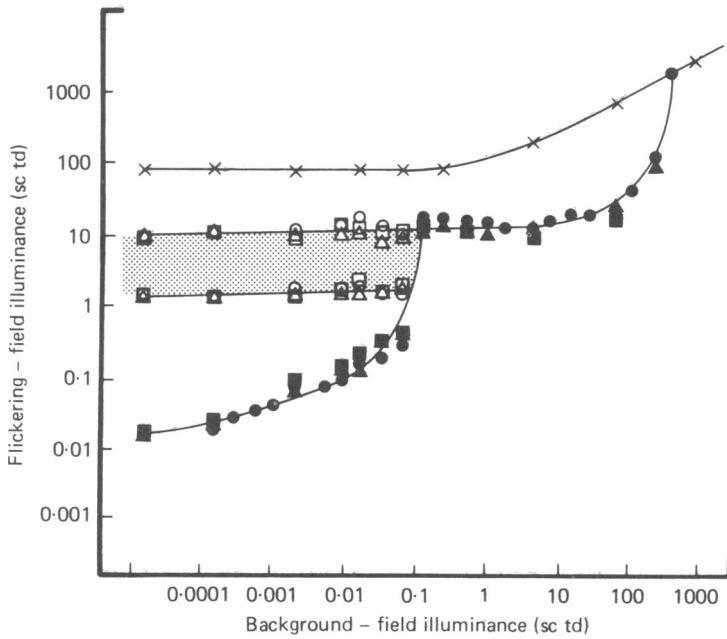
Fig. 10. Flicker thresholds measured with 469 (triangles), 500 (squares) and 519 (circles) nm rod-equated lights, whose halves flickered 180° out of phase. Open symbols mark the region (stippling) where flicker vanished. Crosses mark cone thresholds measured during the plateau which followed a bleaching light of about 7·6 log troland-seconds. These cone thresholds lie well above the null.

beam became brighter. Thus, subthreshold flicker was revealed by an increase in background intensity.

Thirdly, near the intersection in the bipartite field's profile, an intensity region was discovered where suprathreshold flicker was completely invisible (the stippled region of Fig. 10). Flicker could be seen when the stimulus was brighter or dimmer than the flicker null's boundaries, but it could not be seen within the stippled area. There, the sensation of flicker vanished uniformly and simultaneously from every part of both hemifields. If stimulus intensity was changed so that it again fell outside the null,
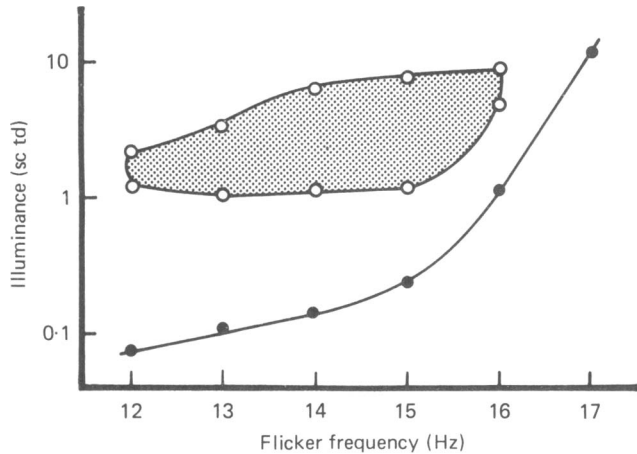

Fig. 11. The flicker null's boundaries (○) at various flicker frequencies. The stimulus was viewed against a 0·00027 sc td background. Filled symbols represent flicker thresholds measured in the background's presence. Thus, the null begins and ends above flicker threshold for each frequency. The halves of the bipartite field flickered 180° out of phase.

the sensation of flicker re-appeared, but within the null the sensation of flicker could not be revived. This null depended on the spatial interaction of the signals produced by the field's halves, as the following observations demonstrate. First, a null was never detected when the stimulus was spatially uniform. Rather, a bipartite field whose halves flickered out of phase was a prerequisite for producing this null (see also the following discussion of the null's phase dependence). Secondly, flicker could never be cancelled within the null region if either flickering hemifield was replaced by a steadily illuminated field. Thirdly, the sensation of flicker was revived within the null region whenever one flickering hemifield was occluded. Thus, rod-mediated flicker signals act across retinal distances subtending 4·5–9° and disrupt one another so that temporal information is destroyed within the null. Other aspects of the visual signal are apparently unaltered, however, since the size, shape, brightness and distinctness of the stimulus were unaffected in the null region and since the field's brightness grew uniformly as stimulus intensity was increased.

The null also depended critically on the frequency and the phase of the stimulus. Thus, if the flickering field's intensity was adjusted to fall within the null, it was visible at low frequencies and at moderately high ones, but it was not visible at

intermediate frequencies. Further, the null's width varied with flicker frequency, as Fig. 11 shows. The null's width also depended on the phase relationship of the flickering hemifields. For 15 Hz flicker, as Fig. 12 shows, the null was widest when the fields were 180° out of phase, and it grew smaller or vanished as the phase lag was reduced.

Similar flicker nulls have been previously reported, but these have been attributed to the destructive interaction of rod and cone signals (MacLeod, 1972; Van den Berg & Spekreisje, 1977). Therefore, one may wonder whether the experimental conditions
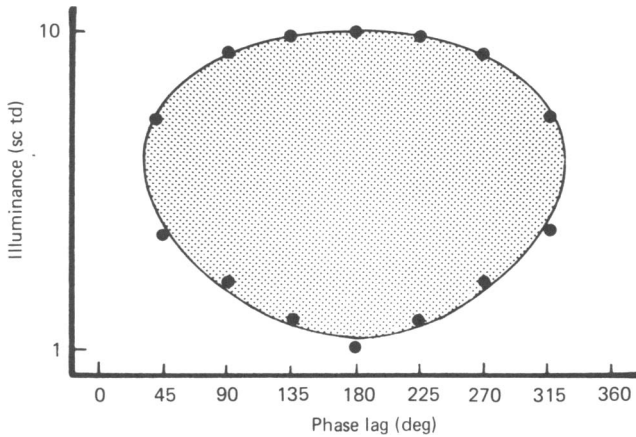

Fig. 12. The flicker null's width as a function of the phase of the halves of a 519 nm 15 Hz stimulus which was viewed against a background of 0·00027 sc td. Points above 180° are merely the reflexions of their counterparts below 180°.

used here failed to isolate rod thresholds and whether the null in Fig. 10 actually resulted from the interaction of rod and cone signals. Four facts suggest that it did not. (See MacLeod (1972) and Van den Berg & Spekreisje (1977) regarding the properties of rod-cone nulls). First, this null is about three times wider than flicker nulls produced by rod-cone interaction. Secondly, this null was not disturbed by eye-blinks, although these briefly disrupt rod-cone nulls. Thirdly, this null was absent for uniformly flickering fields, but rod-cone nulls are not. Fourthly, this null was optimal for 15 Hz (but not 7 Hz) flicker, while rod-cone nulls are clearest for 7 Hz (but not 15 Hz) flicker. These facts suggest that the null in Fig. 10 resulted from destructive interactions between rod, not rod and cone, signals. Three control experiments support this conclusion (see *Control experiments* for a discussion of the rationale of these experiments).

First, as Fig. 10 shows, thresholds obtained with three rod-equated wave-lengths overlap along the two-branched profile and along the null's boundaries. Thus, the mechanism mediating the null has the spectral sensitivity of rod vision. Secondly, as the crosses in Fig. 10 show, thresholds measured during the cone plateau lie nearly one log unit above the top of the null. Thus, the mechanism mediating the null has the

dark adaptation properties of rods. Thirdly, as Fig. 13 shows, thresholds which were measured with axially (filled symbols) and obliquely (open symbols) incident lights did not overlap during the cone plateau phase of dark adaptation, but they did overlap along the null after dark adaptation was complete. Thus, the mechanism mediating the null possesses the directional insensitivity of rods. These facts show that the null is mediated by rods.
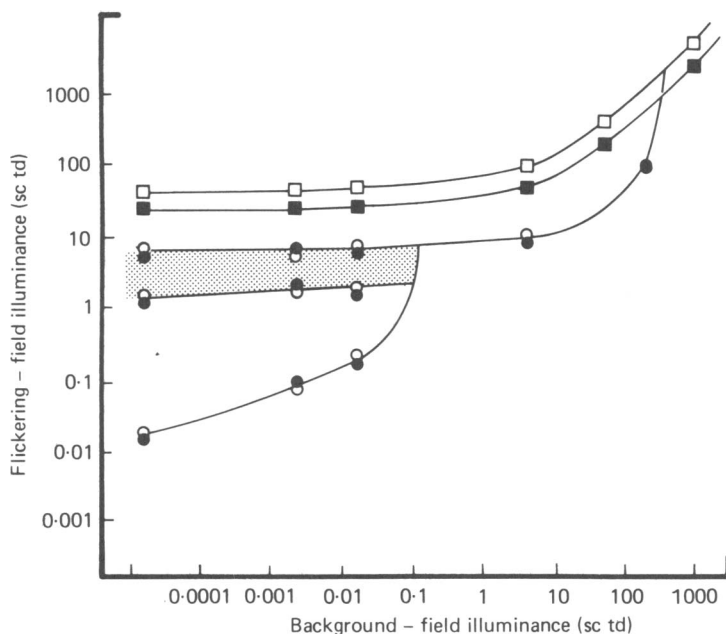

Fig. 13. Thresholds measured with a 500 nm field whose halves flickered 90° out of phase. Axially incident (filled symbols) and obliquely incident (open symbols) lights produced different thresholds during the cone plateau (squares) but comparable thresholds (circles) after dark adaptation. Notice that the null is wider for a 180° phase lag (Fig. 10) than for a 90° phase lag (Fig. 13).

DISCUSSION

Light adaptation affects the temporal properties of rod vision in several ways. First, increased illumination generally improves, but sometimes impairs, the resolution of rapid flicker (Fig. 6). Secondly, light adaptation changes the shape of the rod modulation sensitivity function. In dim light rod vision acts as a low-pass temporal filter, but in bright light it acts as a band-pass filter (Fig. 7). Thirdly, some threshold profiles manifest two distinct branches, one in dim light and the other in bright light (Fig. 1), so that increased illumination causes a transition from the first to the second branch. Fourthly, when the display's intensity is between about 1 and 10 sc td, rod-mediated signals sometimes disrupt one another (Figs. 8, 9 and 10).

These results are not fully compatible with earlier studies of rod vision (Ives, 1922; Hecht & Shlaer, 1936; Smith, 1973), but the reason for the discrepancies seems clear.

Previous studies of rod temporal resolution did not use experimental conditions which isolated rod mediated responses in bright light. Therefore, such studies could only characterize the temporal properties of relatively dark adapted rods, which, as verified here, respond sluggishly. These earlier studies have contributed to the belief that poor temporal resolution is a characteristic of rod vision, but the present results show that this view is unsatisfactory. In bright light, the rod system's temporal response quickens so that relatively rapid flicker can be seen. Indeed, the differences in temporal resolution which have been previously noted between rods and cones say more about the different illumination conditions in which those properties were measured than about intrinsic differences between these photoreceptor types. These comments do not, of course, alter the fact that under ideal conditions cones can resolve faster flicker than rods can.

Certain rod physiological processes have been described which probably contribute to the effects reported here. For example, rod photoreceptor transduction proceeds faster in bright light than in dim light (Baylor, Lamb & Yau, 1979), and this provides a basis for the improvement of rod temporal resolution in bright light. Other features of the present results cannot be explained so easily, however. For example, the physiological basis for rod-mediated visual interference (Figs. 8, 9 and 10) is unknown. Such unexplained phenomena invite hypothetical interpretations, but there is a danger that any speculative model could be counter-productive. With this in mind, the following comments are intended to achieve two limited goals: first, to emphasize basic psychophysical facts which a complete model of rod physiology must explain and second, to demonstrate that unconventional ideas may be needed to develop a complete model.

As mentioned previously, one curious feature of some rod-mediated threshold profiles is the second, high-intensity branch which they manifest in bright light. Indeed, if control experiments had not proven otherwise, one would probably have attributed these separate branches to the separate actions of the rod and cone systems. This attribution would be unjustified, but it leads one to consider the unconventional idea that these two branches are indeed mediated by separate visual processes. Since these postulated processes share the basic properties of rod vision (including spectral sensitivity, directional insensitivity, and lengthy dark adaptation), they must be separate, rod-mediated mechanisms. That is, human rod vision may comprise two temporal channels. On this view, a sluggish, sensitive channel mediates rod vision in dim light, and a quick, less sensitive channel mediates rod vision in bright light. Although this unconventional scheme gains little support from the literature (see, however, Hecht, Schlaer, Smith, Haig & Peskin, 1948), a few assumptions make it compatible with the facts reported here. For example, the separate lobes of the rod c.f.f. function can be explained as manifestations of the different properties of the postulated channels. That is, rod signals passing through the sluggish channel mediate c.f.f. within the low-intensity lobe of the c.f.f. function, while rod signals passing through the quicker channel mediate c.f.f. within the high-intensity lobe. If one also assumes that the sluggish channel possesses low-pass properties and that the quick channel possesses band-pass properties, then one can explain the change in the shape of the rod modulation sensitivity function as intensity increases (Fig. 7). That is, increased intensity shifts rod vision from the low-pass

properties of the sensitive mechanism to the band-pass properties of the less sensitive channel which is active in bright light. Finally, this two-channel scheme provides a basis for explaining the rod-mediated interference effects reported here (Fig. 8, 9 and 10). Such interference may manifest the destructive interactions of the two channels' separate signals. Such interference might even occur through simple cancellation of the two signals, such as causes rod-cone interference (MacLeod, 1972; Van den Berg & Spekreisje, 1977).

Obviously the unconventional view that two temporal channels subserve rod vision is only one of many schemes which could be suggested. Clearly, too, its value will be determined by future studies of the physiological basis for rod temporal resolution. Unfortunately, two primary obstacles will hinder such studies. First, the physical locus of the effects reported here is not known precisely. Thus, one cannot know exactly where to look for the physiological correlates of the psychophysical effects reported here. Secondly, such studies will require the use of rod isolation techniques for the same reason that such techniques were necessary here. But such techniques are inconvenient, and their use must be carefully monitored by control experiments which can determine whether they have been applied successfully.

REFERENCES

AGUILAR, M. & STILES, W. S. (1954). Saturation of the rod mechanism of the retina at high levels of stimulation. *Optica Acta* 1, 59–64.

BARLOW, H. B. (1972). Dark and light adaptation: psychophysics. In *Handbook of Sensory Physiology: Visual Psychophysics*, VII/4, ed. JAMESON, D. & HURVICH, L. M., pp. 1–28. Berlin: Springer-Verlag.

BAYLOR, D. A., LAMB, T. D. & YAU, K.-W. (1979). The membrane current of single rod outer segments. *J. Physiol.* 288, 589–611.

BROWN, J. L. (1965). Flicker and intermittent stimulation. In *Vision and Visual Perception*, ed. GRAHAM, C. H., pp. 251–320. New York: Wiley & Sons.

CONNER, J. D. & MACLEOD, D. I. A. (1977). Rod photoreceptors detect rapid flicker. *Science, N.Y.* 195, 698–699.

CRAWFORD, B. H. (1972). The Stiles-Crawford effects and their significance in vision. In *Handbook of Sensory Physiology: Visual Psychophysics*, VII/4, ed. JAMESON, D. & HURVICH, L. M., pp. 470–483. Berlin: Springer-Verlag.

ENOCH, J. M. (1972). The two-color threshold technique of Stiles and derived component color mechanisms. In *Handbook of Sensory Physiology: Visual Psychophysics*, VII/4, ed. JAMESON, D. & HURVICH, L. M., pp. 537–567. Berlin: Springer-Verlag.

HAYHOE, M. M., MACLEOD, D. I. A. & BRUCH, T. A. (1976). Rod-cone independence in dark adaptation. *Vision Res.* 16, 591–600.

HECHT, S. & SHLAER, S. (1936) Intermittent stimulation by light. V. The relation between intensity and critical frequency for different parts of the spectrum. *J. gen. Physiol.* 19, 965–979.

HECHT, S., SHLAER, S., SMITH, E. L., HAIG, C. & PESKIN, J. C. (1948). The visual functions of the complete colorblind. *J. gen. Physiol.* 31, 459–472.

INGLING, C. R., LEWIS, A. L.., LOOSE, D. R. & MEYERS, K. J. (1977). Cones change rod sensitivity. *Vision Res.* 17, 555–564.

IVES, H. E. (1922). Critical frequency relations in scotopic vision. *J. opt. Soc. Am.*, 6, 254–268.

LE GRAND, Y. L. (1968). *Light, Colour and Vision*, 2nd edn., p. 119. London: Chapman & Hall.

LE GRAND, Y. L. (1972). Spectral luminosity. In *Handbook of Sensory Physiology: Visual Psychophysics*, VII/4, ed. JAMESON, D. & HURVICH, L. M. pp. 413–431. Berlin: Springer-Verlag.

MacLeod, D. I. A. (1972). Rods cancel cones in flicker. *Nature, Lond.* **235**, 173–174.

MacLeod, D. I. A. & Hayhoe, M. M. (1974). Rod origin of prolonged afterimages. *Science, N.Y.* **185**, 1171–1172.

Makous, W. & Boothe, R. (1974). Cones block signals from rods. *Vision Res.* **14**, 285–294.

Smith, R. A. (1973). Luminance-dependent changes in mesopic visual contrast sensitivity. *J. Physiol.* **230**, 115–135.

Van den Berg, T. J. T. P. & Spekreisje, H. (1977). Interaction between rod and cone signals studied with temporal sine wave stimulation. *J. opt. Soc. Am.* **67**, 1210–1217.

Van Loo, J. A., Jr. & Enoch, J. M. (1975). The rod Stiles-Crawford effect. *Vision Res.* **15**, 1065–1069.