

DUPLICITY, PHASE LAGS, AND DESTRUCTIVE
INTERFERENCE IN MESOPIC AND SCOTOPIC FLICKER PERCEPTION

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Recently there has been a lot of interesting work on how the dynamics signals change with changing light levels and with the transition from cones to rods. These changes are reflected in our capacity to produce and analyze both flicker and motion. In this paper we concentrate on flicker because it is simpler to produce and analyze and (presumably as a result) has been studied in more detail.

The traditional way to characterize visual temporal resolution is to determine the highest frequency of flicker that can be seen. This frequency, above which a flickering light appears steady, is referred to as the critical flicker fusion frequency or CFF. CFF varies with intensity in a characteristic way, which has been produced in thousands of experiments, notably those of Hecht and Shlaer (1936). Generally, the more intense the light the higher the frequency that can be resolved. This improvement, however, occurs in two well-defined phases. First, the rods mediate flicker detection. They typically reach a limit at about 15 Hz, so that further increases of intensity produce no improvement in the CFF. Then, the cones take over detection and allow a further increase up to above 50 Hz where they reach their limit. Unfortunately, such data indicate little about the dynamics of the visual system, that is, about the time course of the visual signals. For instance, the rise in CFF with increasing intensity might occur because the visual signals persist for a longer time in dim light. But, alternatively, it could be explained--and this was essentially how the model of Hecht and Shlaer (1936) explained it--by an improvement in differential sensitivity in bright light that allows detection of a smaller modulation or a smaller functional change in excitation. In the 1950s, however, DeLange (1952) established a method of characterizing the dynamics of the visual system much more completely--through its frequency response. To measure the visual frequency response, the time-averaged intensity is kept constant. For the data shown in

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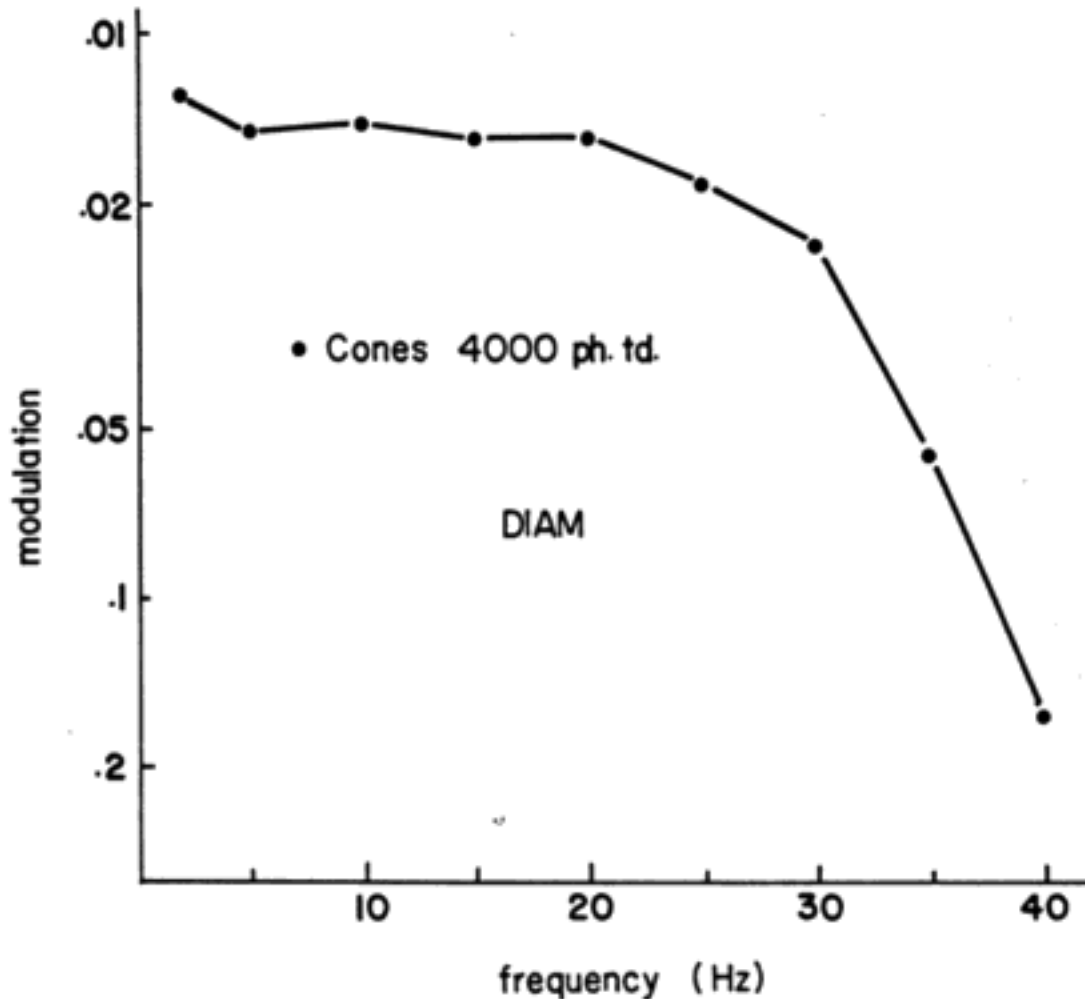


FIGURE 1 Cone modulation sensitivity measured as a function of temporal frequency at an adaptation level of 4,000 photopic trolands (ph td). Test field, 668 nm; 6.2-degree diameter; adapting field, deep red (Wratten no. 70 gelatin filter), 11.5-degree diameter; fixation, 13 degrees temporal; observer, DIAM.

Figure 1, it was set at a high photopic level (4,000 photopic trolands). Then, for each flicker frequency, the observer's sensitivity is determined by finding the smallest modulation at that frequency that can be distinguished from a steady light. The smaller the threshold modulation, the greater the sensitivity (in Figure 1 sensitivity is plotted increasing upward). Sensitivity holds up well at frequencies up to 30 Hz and then falls off with increasing rapidity.

With rod vision at a low scotopic light level, however, the frequency response looks very different, dropping sharply with increasing frequency until it reaches its limit at about 15 Hz. So rods, unlike cones, are extremely sluggish at low light levels.

ROD VISION IN THE MESOPIC RANGE

The first important point to be made here concerns the performance of rod vision in the mesopic range. This is difficult to investigate because in this range the rods are upstaged at high frequencies by the more agile cones. Conner and MacLeod (1977), however, were able to characterize the behavior of rod vision at these intensities by adopting special procedures to keep the cones out of the way. The results were surprising. What we did was superimpose a flickering test light of a middle wavelength (actually green), to which rods are highly sensitive, on a red steady background to which cones are much more sensitive than the rods. For cones the steady red completely swamps the flickering green; for rods the red is almost negligible. In addition, the test light was presented obliquely incident to the retina. This was done because the cones are significantly less sensitive to obliquely incident light than to light that strikes them axially, whereas rod sensitivity is nearly independent of the angle of incidence.

Under these conditions, Conner and MacLeod were startled to find that the rod CFF, after appearing to reach an asymptote at 15 Hz in the scotopic range, suddenly begins to improve again at levels above 1 troland (td), so that the CFF-log I intensity curve is still double-branched, with a second conelike rod branch that is normally hidden behind the real cone branch (Figure 2). It is known that this second rod branch is not a cone branch on four grounds. First, CFFs measured during the cone plateau of dark adaptation (filled triangles, Figure 2) require a greater intensity by about a factor of 10 for attaining a given frequency than is needed after rod recovery. Second, if the experiment is repeated with axially incident test lights, this considerably improves sensitivity for cones as shown by the cone plateau, but has little effect on either branch of the rod curve (see Figure 1B in Conner and MacLeod, 1977). Third, when the wavelength of the test light is varied, a rod spectral sensitivity is found on both these branches (open symbols, Figure 2). Finally, a fourth indicator of the rod origin of the responses is that vision fails, with a precipitous decline in CFF, at intensities greater than 100 td, at which it is known that rods saturate. This rod saturation-related decline in CFF, from a peak close to 30 Hz, is illustrated in Figure 6 of Conner (1982). So there is clear evidence for a duplicity within the rod mechanism itself that allows rods to pick up frequencies at mesopic light levels nearly twice as high as the scotopic limit of 15 Hz found by Hecht and Shlaer (1936).

It has been known for some time that rod monochromats also show a double-branched CFF-log I curve. As one example among many, recent data from a current investigation by Hess and Nordby (in preparation) agree very well with Conner and MacLeod's (1977) data, the only difference being that the low-intensity branch on the rod monochromat starts at a higher detection threshold, as it might if some ambient light were present during testing. The prevailing view on this has been that this second branch in rod monochromats, which does show a rhodopsin spectral sensitivity, is due to rhodopsin-filled cones; this is an unlikely hypothesis, especially because the rod saturation above 100 td shows up

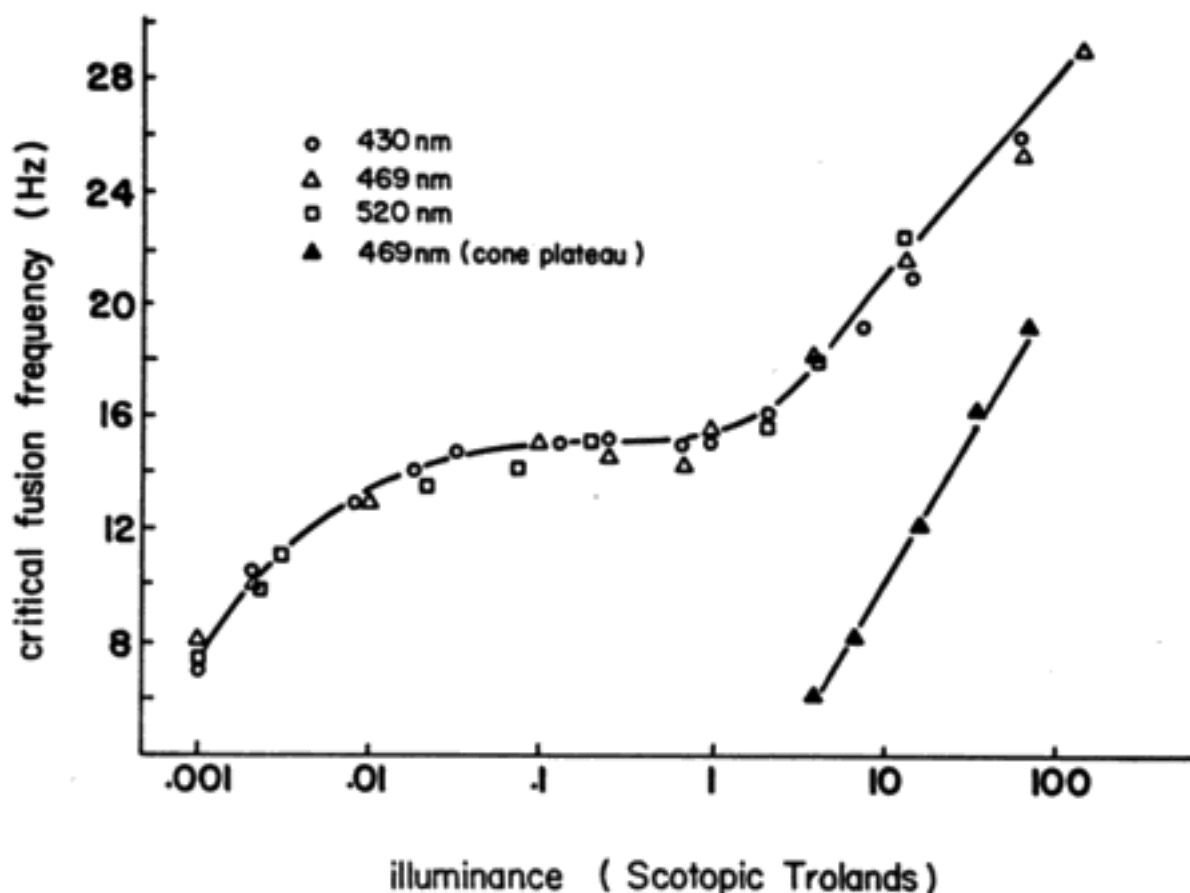


FIGURE 2 Critical flicker frequency measured as a function of stimulus intensity. Settings were obtained either after complete dark adaptation and with a test stimulus of 430 nm (open circles), 469 nm (open triangles), or 520 nm (open squares) or during the cone plateau phase of dark adaptation and with a test stimulus of 469 nm (filled triangles). Test field, 9 degrees; adapting field, 670 nm, 13 degrees; fixation, 16 degrees temporal. In this experiment only the test lights (but not the adapting field) were obliquely incident on the retina. The coincidence of the double-branched CFFs (open symbols) supports a scotopic spectral sensitivity for both branches. Data from Conner and MacLeod (1977).

very clearly in rod monochromats as well as in normal trichomats. The evidence for rhodopsin-filled cones comes from an experiment by Alpern et al. (1960) which showed a loss of sensitivity for marginal pupil entry of the stimuli in their observer. However, using the same rod monochromat who was the subject in the Hess and Nordby study, recent experiments by Sharpe and Nordby (1984) have now shown that the sensitivity to eccentric stimuli is that of rods not cones. No cone function whatsoever has been found in this subject, so if rhodopsin-filled cones do exist in humans, which now seems doubtful, they are clearly not the basis for the improved mesopic flicker detection in this true rod monochromat, or indeed under our conditions in the normal eye. Instead, the evidence shows that light-adapted rods can detect rapid

flicker, at least at frequencies up to 30 Hz. Moreover, the transition between low and high mesopic behavior is extremely abrupt, as if two separate mechanisms are involved.

So why is there this abrupt improvement in the temporal resolution of rods in this intensity range? Is it a change in frequency response, or just an abrupt improvement in differential sensitivity? As Conner (1982, Figure 7 therein) has shown, the answer is that the frequency response is dramatically altered. At the lowest scotopic luminance, sensitivity drops off monotonically with increasing frequency. At higher scotopic luminances, still below cone threshold and below the breakpoint found in the rod CFF, the curve begins to take on a bandpass characteristic. This becomes much more pronounced at still higher scotopic luminances, until at a level just below rod saturation there is a sharp peak in sensitivity at about 10 Hz. The curve, in fact, becomes quite conelike. However, if Conner's rod frequency response at the highest scotopic luminance that he used is compared with the results for cones at a high photopic luminance, (e.g., Figure 1), cones still come out ahead, with a response much more extended to high frequencies. In this comparison, however, the cones are working at a much higher intensity or quantum flux level than the rods. What would happen if the intensity were set to the same level, in terms of quanta absorbed per second per degree², for both rods and cones? That comparison is made in Figure 3. The result is that the cones still retain an advantage, but it is relatively slight: if rod and cone sensitivities are equated at low flicker frequencies, it is not until 20 Hz that rod sensitivity drops by a factor 2, or 0.3 log units, below that of the cones.

Therefore, it is found that the bandpass type of temporal response, peaking close to 10 Hz, is a pronounced and general characteristic of visual function under moderate or high illumination. It has not yet, as far as we know, been exploited for practical purposes, but Figure 4 suggests a way in which it might be exploited to improve the detectability of large, low-contrast and indistinct targets, notably when natural vision is degraded by fog or haze. Natural vision relies on haphazard, more or less involuntary eye movements to convert spatial contrast into temporal transients. The optical chopper of Figure 4 does this more efficiently and at a rate close to what is optimal for visual sensitivity by presenting the target alternately with a uniform field of equally spaced average luminance, so that any deviations from that luminance across the target region are converted into a highly detectable flicker. The chopper could be used independently or incorporated into viewing instruments. In electronic image intensifiers it could be implemented more efficiently by making provision for a contrast reversal of the image (rather than simply intermittent presentation) at a visually effective rate.

PHASE LAG

A relatively neglected but interesting aspect of the frequency response of rods and cones is the phase lag. A phase lag or delay is inevitably found in any sluggish system that has a reduced sensitivity

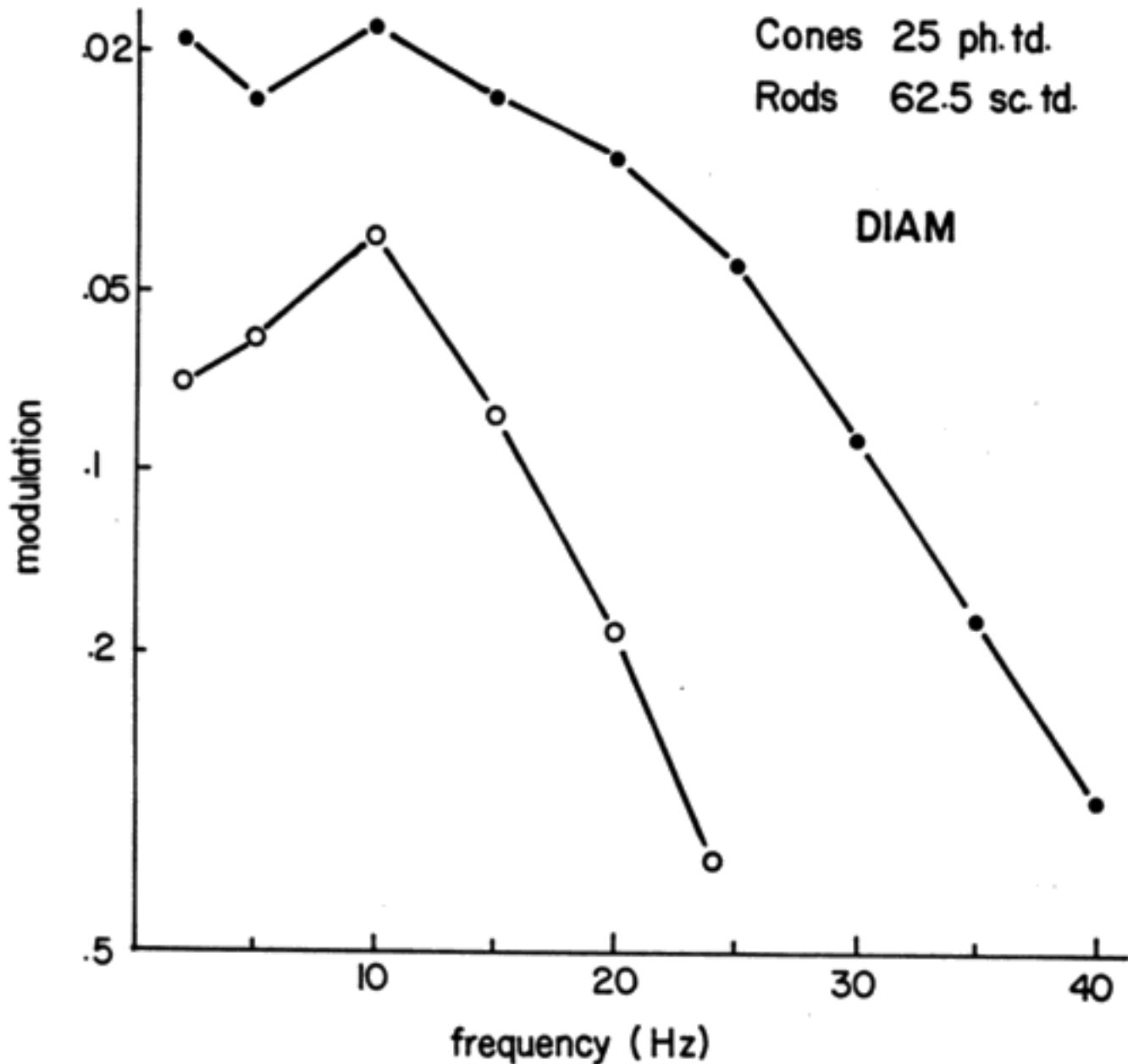


FIGURE 3 Modulation sensitivities of the rods (open circles) and cones (filled circles) measured as a function of temporal frequency at adaptation levels of 62.5 scotopic trolands (sc td) and 25 photopic trolands (ph td), respectively. The levels were chosen so that the quantal absorptions in the rods and cones are approximately equal in the two cases (see text for details). Test fields, 510 nm (rods) or 668 nm (cones), 6.2-degree diameter; adapting field, deep red (Wratten no. 70), 11.5-degree diameter; fixation, 13 degrees temporal; observer, DIAM.

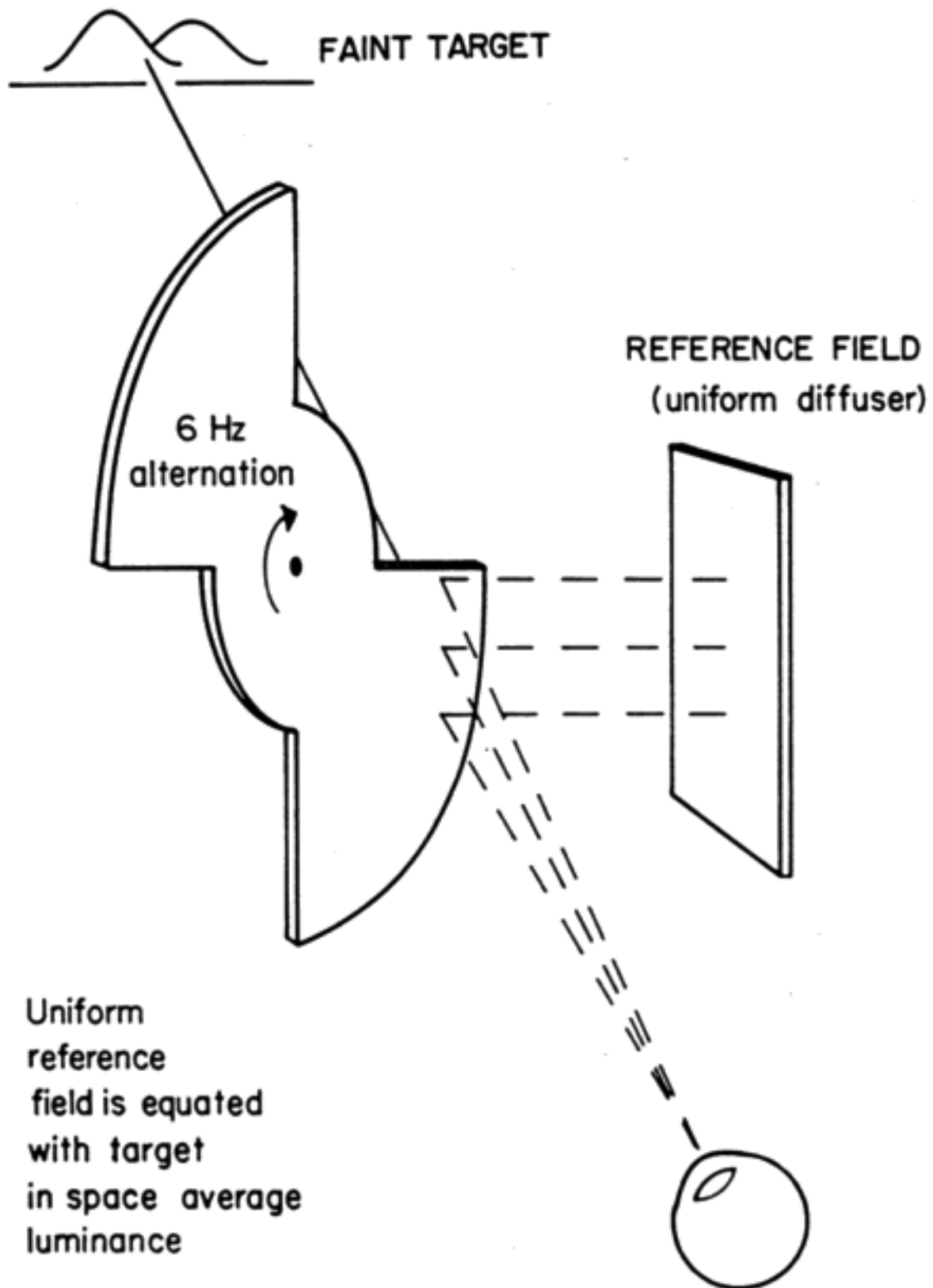


FIGURE 4 An optical chopper to aid low-contrast vision (see text for details).

to high-frequency stimuli. The phase lag of rods relative to cones can be measured by stimulating them in alternation, for instance with green and red lights, respectively. Any phase difference in the resulting signals prevents the rod and cone signals from canceling completely when the two signals are added together. (For now the ganglion cell is thought to add together the signals from rods and cones.) If the greater delay of the rod signal is compensated for by advancing the rod stimulus by an equal amount, the two signals will be brought into opposite phase and will cancel to yield a constant sum, that is, a steady or minimally flickering light. The amount by which the rod stimulus must be advanced from the opposite phase to minimize flicker is an index of the rod signal's phase lag relative to that of the cones.

Figure 5 shows some data on the rod phase lag (relative to that of the cones). The first thing to note here is that the phase data support the idea that rod vision has an internal duplicity, with a fast process operating at moderate mesopic intensities and a sluggish one at low scotopic intensities. The lower curve shows the phase lags recorded at mesopic intensities. At scotopic intensities (the upper curve) the phase lags are considerably larger. At 15 Hz, for example, the scotopic lag is nearly a whole cycle, whereas the mesopic lag is a half cycle. The lags in both cases are substantial, except at very low frequencies. They appear to be greater than would be theoretically expected to result from rod visual persistence alone, and they suggest what amounts to an additional latency of close to 50 ms for the sensitive, slow rod mechanism and about half that for the insensitive, fast one. So both the mechanisms are quite slow by this criterion.

It is almost certainly on account of these phase lags that the technique of flicker photometry has never been successfully applied in mesopic vision. Fortunately, a more recent but related technique may solve the problem. In minimum motion photometry (Anstis and Cavanagh, 1983; Anstis et al., in press), measurements equivalent to flicker photometric ones can be made using drifting gratings. Unlike flicker photometry this can work well at extremely low drift rates, where the phase difference between rod and cone signals appears from Figure 5 to be small.

An interesting special situation occurs when the rod phase lag is 180 degrees. Then, a single mesopic flickering stimulus will give rise to rod and cone signals that are in opposite phase, and if these are of the same size they will cancel (Figure 6). This does happen, and the condition has been called the mesopic null (MacLeod, 1972, 1974). In the mesopic null, light of a certain frequency looks steady, even though it can be seen to flicker at either higher, cone-dominated or lower, rod-dominated intensities. This is illustrated in Figure 7 for 7.5-Hz flicker, under conditions where a rod-cone phase difference of 180 degrees was actually measured at that frequency. The vertical axis is the intensity of a yellow test stimulus. The filled circles define flicker threshold contours for 7.5 Hz. On an increase in the test intensity, a range of intensities is found where flicker is more or less abolished. As would be expected, the addition of a steady background to knock out rods destroys the mesopic null phase and reveals flicker where none was seen before. Nothing like that happens at 4.5 Hz

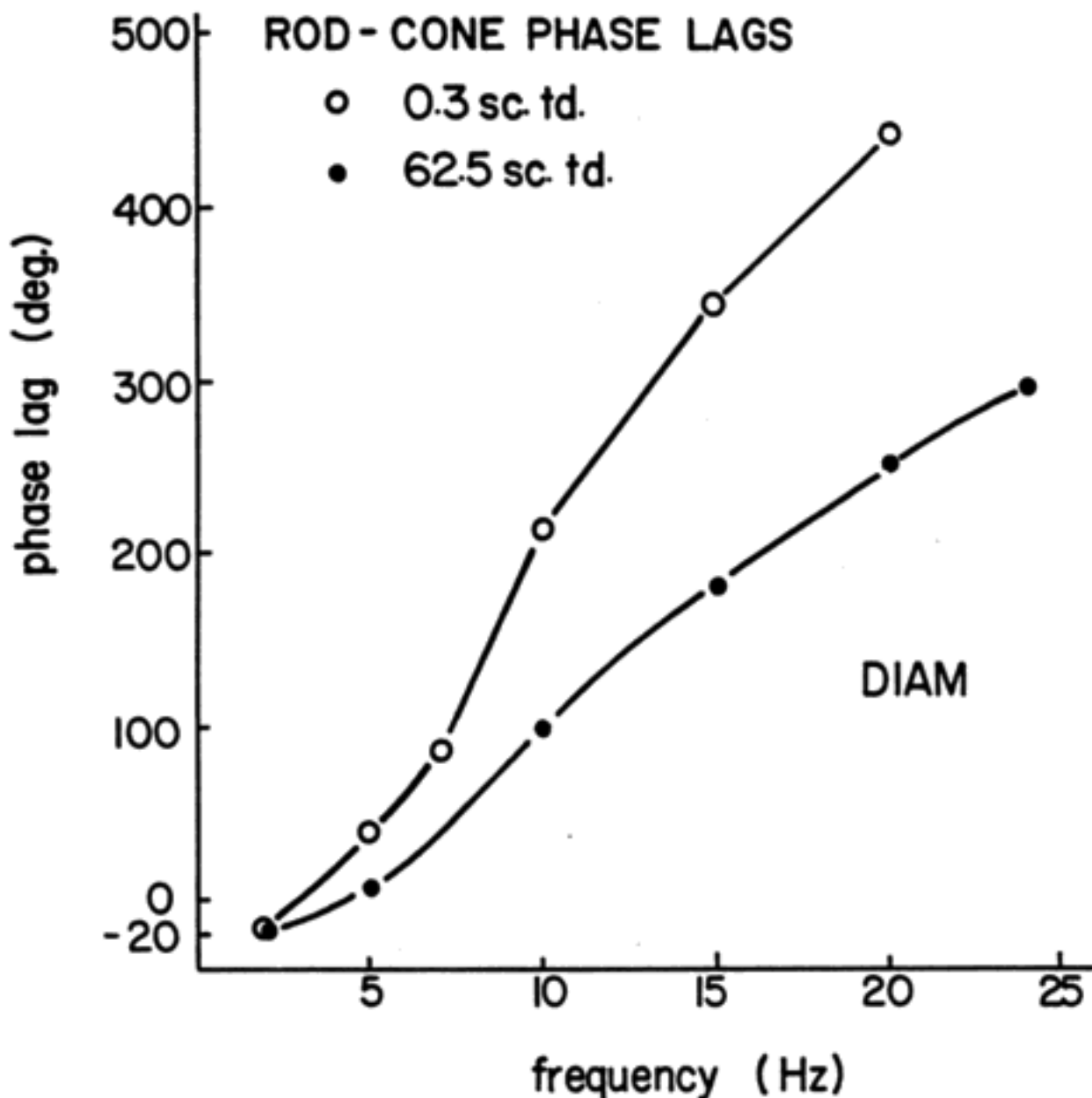


FIGURE 5 Phase lags measured at two adaptation levels: 0.3 sc td (open circles) and 62.5 sc td (filled circles). Phase lags were estimated by varying the phase difference between a 510-nm flickering light seen by the rods and a 668-nm light seen by the cones. By adjustment the subject found the phase difference at which the resultant flicker appeared to be null, or of least amplitude. Necessarily, the rod phase lags are relative to those of the cones; they are given by the amount that the rod stimulus must be advanced from opposite phase to yield a null. Test fields, 6.2-degree diameter. At the low adaptation level no adapting field was present. The adapting field at the high adaptation level was deep red (Wratten no. 70), 11.5-degree diameter, and 3,000 ph td. Fixation, 13 degree temporal; observer, DIAM.

MESOPIC NULL

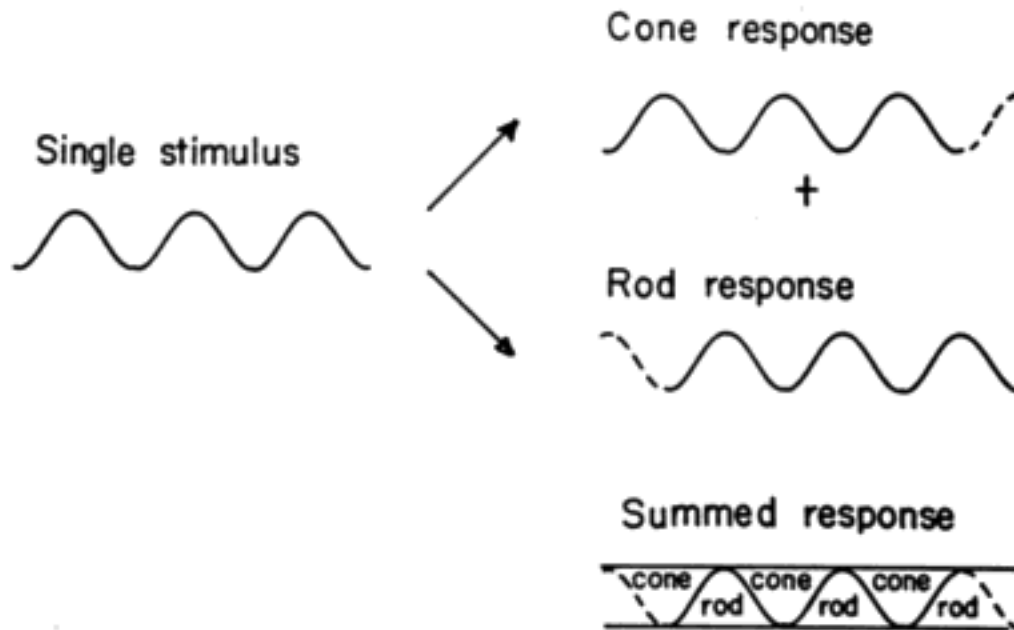


FIGURE 6 An illustration of the origin of the mesopic null. This type of null can occur under conditions where the rods lag behind the cones by 180 degrees (e.g., at 0.3 sc td and about 7.5 Hz--see Figure 5). Under such conditions a single mesopic flickering stimulus gives rise to rod and cone responses that are in opposite phases. If the amplitude of the rod and cone responses are equal, the summed response will be a steady signal. Thus, destructive interference between rod and cone signals can cause a single stimulus, flickering above rod and cone threshold, to appear steady.

(open triangles) where the measured phase lag under these conditions was only about 90 degrees. The curves fitted to the data are generated by the simplest possible theoretical model (MacLeod, 1974), in which rod and cone signals each satisfying Weber's law are added together either in opposite phase (for 7.5 Hz) or in quadrature phase (for 4.5 Hz), and flicker visibility depends on the amplitude of the resultant or vector sum.

If the rods have an internal duplicity, a scotopic null where cones are not involved, but where the fast and slow rod signals come out in opposite phase may be expected. This prediction was tested by Conner (1982), and he did indeed discover a scotopic null attributable to rod-rod interference at a frequency of about 15 Hz. To demonstrate this null, Conner found it necessary to present the stimulus as a bipartite field with opposite phase modulation of the two sides, but more recently we have found it easy to observe the scotopic null without this complication (L.T. Sharpe, D.I.A. MacLeod, and A. Stockman, in preparation).

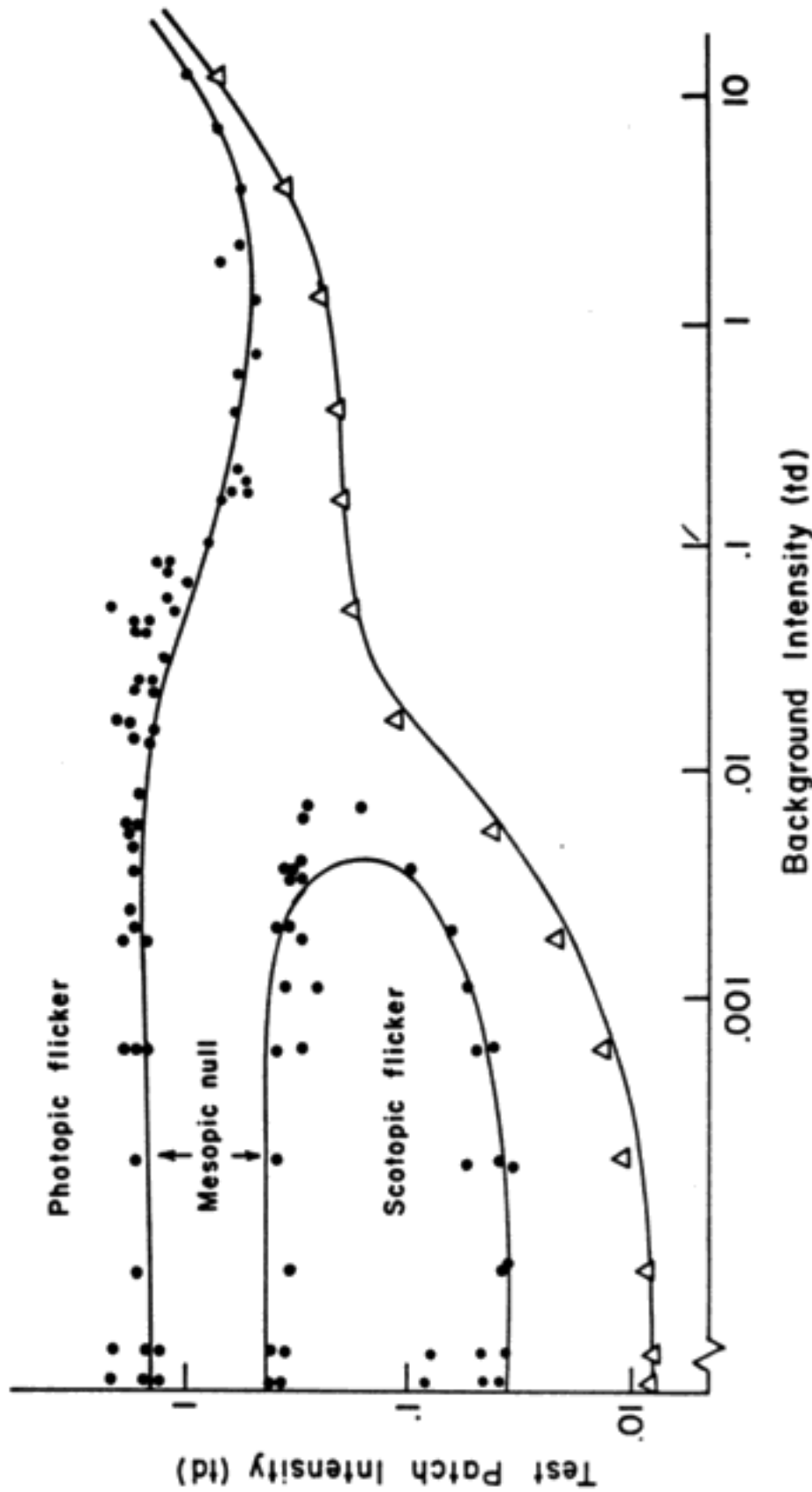


FIGURE 7 Flicker threshold contours, for a 100 percent sinusoidally modulated 3-degree-diameter yellow test field superimposed on a larger (8-degree diameter), blue-green steady background and centered 5 degrees from the line of sight. Open triangles, 4.5 Hz; filled circles, 7.5 Hz (showing mesopic null). Observer, DIAM. The curves represent theoretical predictions from a model (MacLeod, 1974), in which rod and cone signals simply add with a phase difference of 90 degrees (4.5 Hz) or 180 degrees (7.5 Hz). Each signal is assumed to be proportional to the ratio of the intensity excursion, ΔI , to the time-averaged excitation, that is, to $\Delta I/W(I + i + \Delta)$, where for each receptor system (and for each frequency) W is the Weber fraction and i is a constant chosen to predict correctly the absolute threshold.

All the standard controls were done--directional sensitivity, spectral sensitivity, comparison with cone plateau--with results indicating that cones are not a factor. The occurrence of a scotopic null at 15 Hz or so is consistent with the measured phase lags shown in Figure 5 for the fast and slow rod mechanisms. However, those lags were measured at very different levels of adaptation, whereas the scotopic null requires the two mechanisms to generate opposite phase signals at one and the same adaptation level. In fact, this requirement is satisfied, because the transition from slow to fast behaviors is abrupt (Sharpe, MacLeod, and Stockman, in preparation). For Conner's interpretation of the scotopic null to be sustained, the net rod signal just on the high intensity side of that null must be in opposite phase with the rod signal from a stimulus just on the low side of the null. Sharpe, MacLeod, and Stockman have measured the rod phase lag, relative to that of cones, at stimulus intensities just 0.4 log units apart, straddling the scotopic null. They were found to differ by nearly 180 degrees--strong evidence that the null results from two separate rod signals that destructively interfere with each other. The hypothesis that cones are involved is contradicted by the observation, in agreement with Figure 5, that on the high-intensity side of the scotopic null the supposed rod signal has a phase lag of nearly 180 degrees relative to that of the cones. Thus, it cannot be a cone signal. So, in addition to the four types of evidence already mentioned for the view that the fast and slow processes that yield this null are both rod driven, this result provides a fifth type.

THE LIMITS OF ROD SENSITIVITY: DETECTION VERSUS AMPLITUDE DISCRIMINATION

These experiments on rod-cone and rod-rod null phases have led to one other very striking observation. When a cone stimulus flickers just above the flicker threshold, a rod stimulus of suitably chosen phase can reduce that flicker even when the rod stimulus itself is set invisible (MacLeod, 1974). This at first sight seems to contradict the simple notion that rod and cone signals just add up, but actually there is no inconsistency--it only needs to be assumed that a high threshold is applied to the resultant (rod and cone) flicker signal so that no flicker at all is registered when the resultant amplitude is below the threshold amplitude. Differences in amplitude above the threshold could then be discriminated with a precision far greater than threshold sensitivity measures might suggest. This was tested by measuring interaction or beat sensitivity (using a technique first developed to study the temporal properties of the blue cone mechanism; Stockman and MacLeod, in preparation). To measure the beat sensitivity to a rod stimulus of a particular frequency, it is presented not by itself but along with a flickering cone stimulus that differs very slightly in frequency from the rod stimulus. The cone stimulus remains present at a fixed flicker amplitude (chosen to be close to the flicker threshold) throughout the experiment. The observer's task is to adjust the amplitude of the rod stimulus so that its presence can just be detected in the form of an alternate waxing and waning of the flicker amplitude, as the two

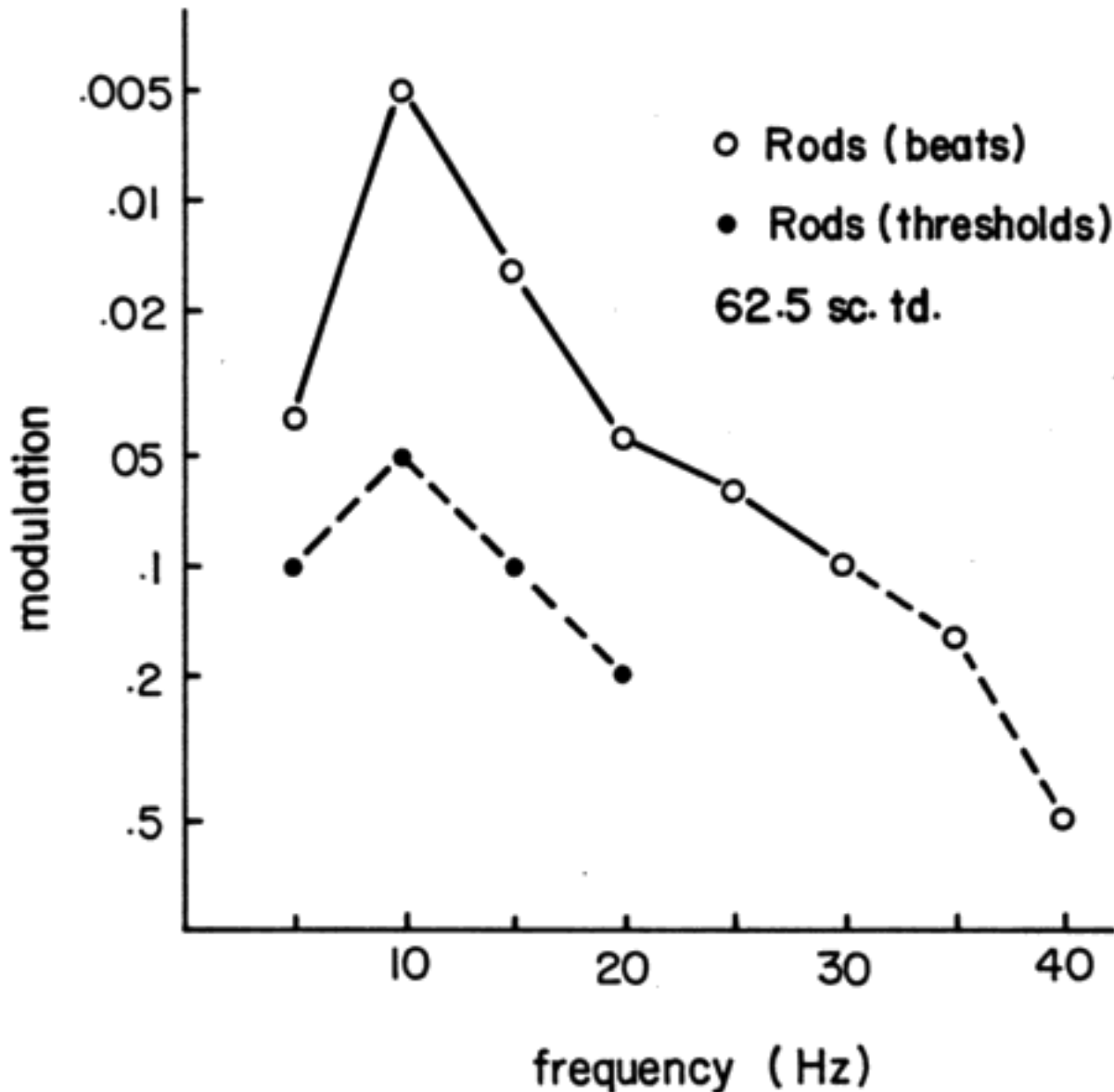


FIGURE 8 Modulation sensitivity (filled circles) and beat sensitivity (open circles) measured as a function of temporal frequency at an adaptation level of 62.5 sc td. For the modulation sensitivity estimates 510-nm test fields were used. By adjustment the observer set the modulation of the 510-nm light at which flicker was no longer seen. For the beat sensitivity estimates, an additional 668-nm test field was presented flickering at a slightly higher or lower frequency than the 510-nm light and at a near-threshold amplitude. Under suitable conditions this gives rise to an amplitude modulation of flicker at the difference or beat frequency. By adjustment the observer set the modulation of the 510-nm light at which beats were no longer seen (for details see text). Test fields, 6.2-degree diameter; adapting field, deep red (Wratten no. 70), 11.5-degree diameter; fixation, 13 degrees temporal; observer, DIAM.

components of the flicker stimulus come into or out of phase. The frequency of this beating was set to be 0.5 Hz or less, and the rod test stimulus frequency was varied from 2 to 40 Hz, keeping the difference in frequency between rod and cone stimuli constant. With this procedure, it was found (Figure 8) that rods can detect intensity modulations as small as 0.5 percent or 0.005 log units, corresponding to a Weber fraction of 1/200. That peak sensitivity, which is reached at 10 Hz, is more than 10 times greater than has been achieved in rod vision with a conventional flicker detection task, for which our results shown by the filled symbols in Figure 8 are typical.

In conclusion, work on flicker detection by rods has demonstrated three points: (1) there is an internal duplicity of organization, with a sluggish sensitive process and a fast, less sensitive process; (2) the rod signals have large phase lags and can interfere destructively with each other or with cones; and (3) rod modulation sensitivity can be improved by an order of magnitude by providing a fixed stimulus of slightly mistuned frequency for the test stimulus to beat with.

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