Spatial relations of flicker signals in the two rod pathways in man

Lindsay T. Sharpe, Jörg Hofmeister, Clemens C. Fach and Andrew Stockman*

Neurologische Universitätsklinik, Hansastraße 9, D-79104 Freiburg im Breisgau, FRG
*and *Department of Psychology, University of California at San Diego,*
CA 92093–0109, USA

1. Flicker signals originating from the human rod photoreceptors seem to have access to two retinal pathways: one slow and sensitive, the other fast and insensitive. The phase lag between signals in the two pathways grows monotonically with frequency, reaching 180 deg near 15 Hz.
2. At 15 Hz, destructive interference between the slow and the fast signals can cause two related phenomena: (i) a suprathreshold intensity region – the perceptual null – within which the perception of flicker vanishes, and (ii) a double branching of the 15 Hz rod-detected flicker threshold *versus* intensity (TVI) curve.
3. Here we investigate the effect of changing target size on these phenomena in normal human observers. We find that the double-branched flicker TVI curve and the perceptual null are found for all targets larger than 2 deg in diameter. For smaller diameter targets, however, neither the lower branch of the double-branched flicker TVI curve nor the null are found.
4. While this might suggest that the slow rod signals are selectively disadvantaged by the use of small targets, phase measurements relative to a cone standard reveal that the slow signals are always present. For targets $\leqslant 2$ deg in diameter, however, they remain below detection threshold because of destructive interference with the fast rod signals. Thus, for small targets, the perceptual null is not absent, but has merged with (and therefore obliterated) the lower branch of the double-branched flicker TVI function.
5. This situation could arise if decreasing the target size causes a parallel reduction in the sensitivities of both pathways, rather than a selective reduction in the sensitivity of either one. Our findings are therefore consistent with a model in which the large-scale spatial organization of the two rod pathways is roughly similar.

Psychophysical (Hecht, Shlaer, Smith, Haig & Peskin, 1938, 1948; Conner & MacLeod, 1977; Conner, 1982; Hess & Nordby, 1986; Sharpe, Stockman, & MacLeod, 1989) and electrophysiological (Stockman, Sharpe, Zrenner & Nordby, 1991) findings in the normal and achromat human are consistent with a model in which rod flicker signals have access to either a slow or a fast retinal pathway (for a review, see Sharpe & Stockman, 1991). The slower pathway (for convenience labelled π_0 after the notation of Stiles, 1978) is more sensitive and dominates from absolute threshold up to low mesopic levels; the faster pathway (labelled π_0') is less sensitive and takes over flicker detection at moderate and high mesopic levels. The transition between the two pathways is evidenced by a prominent break in rod-mediated flicker threshold *versus* intensity (TVI) curves at a background intensity near 0 $\log_{10}$ scotopic troland (td), for all target frequencies greater than 6 and less than 18 Hz (Conner, 1982; Sharpe *et al.* 1989).

Evidence from both human psychophysics and electroretinogram (ERG) Ganzfeld recordings suggests a difference in transmission speed between the two pathways such that for frequencies near 15 Hz the signals emerging from the slow pathway are delayed by half a cycle relative to those from the fast (Sharpe *et al.* 1989; Stockman *et al.* 1991). Since they are 180 deg out of phase, the slow and the fast 15 Hz rod signals destructively interfere to diminish or cancel the perception of flicker. Accordingly, an intensity region can be found well above the rod flicker threshold and well below the cone flicker threshold, within which the sensation of flicker vanishes. This perceptual null is easily demonstrated, not only psychophysically (Sharpe *et al.* 1989), but also in the rod b-wave of the Ganzfeld ERG, which falls to a minimum at retinal illuminances corresponding to the perceptual null and reverses in phase as the null is traversed (Stockman *et al.* 1991).

The rod b-wave is thought to be determined predominantly by the influence of the depolarizing (on) rod bipolar cells on the Müller cells (see, for example, Dick & Miller, 1970; Stockton & Slaughter, 1989; Gurevich, Stockton & Slaughter, 1990). To the extent that this is true, the ERG results and the correspondence between the ERG null and the perceptual null suggest that the two rod pathways separate and recombine at or before the rod bipolars, for otherwise the two signals and the null should not be apparent in the b-wave. Yet plausible models of the retinal substrate of the two rod pathways suggest that the null occurs at a later stage. In the most widely accepted model of a duality within the rod system (see Daw, Jensen & Brunken, 1990, for a review), the slow rod pathway would correspond to the scotopic rod pathway from rods to rod bipolars to AII amacrines to cone bipolars and ganglion cells, whereas the faster pathway would correspond to the mesopic rod pathway from rods to cones (via rod–cone gap junctions) to cone bipolars to ganglion cells (Sharpe *et al.* 1989; see also Sterling *et al.* 1986). If this model is correct, the neural null presumably occurs after the rod bipolars, suggesting that the null in the ERG reflects the electrical averaging of activity produced by many retinal elements (rod bipolars, cone bipolars and perhaps amacrine cells).

An important clue as to the retinal origins of π_0 and π_0' might lie in any differences in their spatial properties, since these are likely to reflect underlying differences in the lateral and/or reciprocal retinal connections of the two pathways. Indeed, a reasonable expectation is that π_0, the more sensitive rod pathway, integrates signals over a larger retinal area than π_0'. A previous investigation of the two pathways, however, did not reveal any differences in their spatial organization. Using counter-phase modulated flickering gratings of different spatial frequency, Sharpe *et al.* (1989) found that the intensity at which the null occurred did not depend upon the spatial frequency of the gratings. This finding suggests that at the null intensity the areas over which π_0 and π_0' integrate signals are approximately the same. Yet, a duality in spatial organization within rod vision is suggested by the scotopic spatial acuity measurements of Hallett (1962), who found that the acuity curve for detecting black disks against a large (46 deg) briefly flashed (2·6 ms) surround, as a function of luminance, was double branched, even though detection on both branches was by the rods. The transition from the plateau of the low acuity branch to the high acuity branch occurred at around $-2{\cdot}5$ to $-2{\cdot}0$ $\log_{10}$ scotopic troland seconds (td s) (for a 10 ms flash this corresponds to a retinal illuminance of $-1{\cdot}5$ to $-1{\cdot}0$ $\log_{10}$ scotopic td, assuming an effective integration time of 100 ms). Hallett (1962) argued that the double branching could be due to a transition between two rod mechanisms with different receptive field sizes. Though it is tempting to suggest that this represents a spatial analogue of the rod temporal duality, the relationship between the spatial and temporal dualities is at best problematic. First, the spatial duality occurs at a lower intensity than the change in rod temporal sensitivity. Second, when steadily presented or flickering stimuli (such as those employed here) are used instead of briefly flashed stimuli, the spatial duality is not found (Hofmann, Barnes & Hallett, 1990).

Nevertheless, Hallett's finding encouraged us to adopt another approach to investigating the spatial extent of the excitation pools of the two pathways. In this paper, we measured the influence of target size upon the shape of the rod flicker TVI profile and the position of the perceptual null at 15 Hz. Although we know that the two branches and perceptual null are found when large (6 deg) peripheral targets (Sharpe *et al.* 1989) or Ganzfeld stimulation (Stockman *et al.* 1991) are used, we do not know how these attributes are spatially constrained (i.e. if they are also found with smaller targets).

METHODS

Subjects

Three observers, T.A., C.F. and J.H., served in this study. They gave their consent, after being informed about the nature of the experiment and that no risk to their health was involved. All have normal colour vision as indicated by conventional colour vision tests. C.F. and J.H. are both emmetropic; T.A. is myopic, requiring a $-3{\cdot}0$ dioptre correction.

Apparatus and stimuli

A three-channel Maxwellian-view stimulator, described in more detail in Nordby & Sharpe (1989), produced the flickering rod and cone test stimuli as well as the steady background field and the bleaching light. All three channels originated from a 100 W tungsten–iodine lamp run at constant current. One channel provided the flickering rod test light, which was 1, 2, 3, 6 or 10 deg in diameter. Its wavelength was shaped by a grating monochromator (V-10, Jobin-Yvon Instruments, Longjumeau, France) into a triangular profile, peaking at 500 nm and having a half-bandwidth of 4 nm. The entry point was offset in the pupil by 3 mm from the pupillary centre to favour its detection by rods.

A second channel provided a second 15 Hz flickering light, which served as the cone reference light in the phase experiments (see below). It was 6 deg in diameter and rendered monochromatic by an interference filter (Schott), having a peak transmittance at 679 nm and a half-bandwidth of 5·5 nm. Its entry point was central.

A third channel provided a 18 deg in diameter background. It was rendered monochromatic by an interference filter (Schott), having a peak transmittance at 640 nm and a half-bandwidth of 5·5 nm. This channel also provided the white (3100 K) bleaching light required for measuring the cone plateau thresholds.

The two targets and the background field were centred 12 deg from the fovea in the nasal field of view. Fixation was aided by an illuminated red cross.

Electromagnetic shutters were positioned in each channel near focal points of the filament lamp. The shutters in the rod and cone test channels were run by shutter drivers connected to a frequency generator (Philips PM 5127). With this arrangement we could obtain reliable square-waves at all frequencies employed, as monitored periodically using a Pin-10 photodiode (United Detector Technology Instruments, Orlando, FL, USA) and oscilloscope. The higher sinusoidal harmonics of a 15 Hz square-wave (at 45, 75, 105 Hz and so on) are unlikely to be detectable in scotopic vision.

In the phase experiments, the frequency and phase relation of the rod and cone test lights were controlled by a variable phase function generator (Hewlett Packard, model 203a).

Fine control over the luminance of the stimuli was achieved by variable, circular neutral density wedges (Barr & Stroud), positioned close to image points of the filament lamp, and by the insertion of fixed neutral density filters in parallel portions of the beams.

The radiant fluxes of the test and adapting field stimuli were measured at the plane of the observer's entrance pupil with a calibrated radiometer/photometer (United Detector Technology, model 80X optometer).

Procedure

Flicker TVI profiles. Before beginning each experimental session, the observer had his right pupil dilated with 0·5% tropicamide (Mydriaticum Roche®). Following 40 min of dark adaptation, he positioned himself in the optical system by biting into a silicone-base, dental-wax impression of his teeth mounted in a machine tool rest, and fixated the illuminated cross. Using a computer-controlled procedure, the intensity of the square-wave flickering rod stimulus was adjusted until the flicker was just detectable. Threshold was defined as the mean of twelve wedge settings. Thresholds were then measured on a series of adapting fields of increasing intensity. At each new intensity level, the observer adapted for at least 3 min.

After completing flicker threshold settings at several background intensities, the observer determined, in a separate experiment, the limits of the null region. He found the intensity of the suprathreshold rod stimulus at which the sensation of flicker vanished (this was possible only for frequencies near 15 Hz). This setting repeated 12 times defined the lower limit of the null region. The upper limit of the null region (i.e. the intensity level of the suprathreshold rod stimulus at which the sensation of flicker is once again seen) was similarly defined.

Cone thresholds were also obtained by making measurements during the plateau that terminates the cone phase of recovery from a white (3100 K) bleaching light of 7·7 $\log_{10}$ photopic td s (i.e. between 4 and 9 min following the end of the bleach).

RESULTS

Effect of target size on rod-detected 15 Hz flicker TVI curves

If π_0 and π_0' integrate signals over different areas, then changing the target size may selectively favour one process over the other, and so alter the position of the null and the upper and lower branches of the 15 Hz TVI curve (see Figs 1*D*, 2*D* and 3*D* for typical double-branched 15 Hz TVI profiles). A decrease in target size could cause either: (1) a selective reduction in the sensitivity of π_0, in which case the lower branch of the 15 Hz flicker TVI should be displaced upwards (since a higher flicker luminance would be required for threshold), and the null downwards; or (2) a selective reduction in the sensitivity of π_0', in which case both the π_0' branch and the null should be displaced upwards.

A third alternative is that the decrease in target size could produce a parallel reduction in the sensitivities of both π_0 and π_0' together, thus keeping their relative sensitivity unchanged. This should have the effect of raising the lower branch of the 15 Hz flicker TVI curve, and broadening the null. If the loss of sensitivity is large enough, the null should extend all the way to the lower branch of the TVI curve, whereupon the flicker will be visible only when the luminance of the flickering target exceeds the upper limit of the null. A parallel reduction in sensitivity could result from a loss in sensitivity applied separately but equally to the two pathways, or applied to a common pathway after the two signals have recombined.

Yet a fourth alternative is that the decrease in target size could cause a sensitivity loss before the non-linearity at which π_0 and π_0' first diverge. Within limits, this should raise the double-branched flicker TVI curve and the null region (i.e. the whole flicker detection profile) together.

The results of varying target size on the 15 Hz flicker TVI profile and perceptual null are shown in Figs 1–3 for normal observers C.F., J.H. and T.A., respectively. Five sorts of thresholds are shown: (1) the lowest intensity at which the target itself can be detected, i.e. the visual or contrast threshold (■); (2) the lowest intensity at which the flicker can be detected, i.e. the flicker threshold (●); (3) the lower (▲) and (4) the upper (▼) limits of the null, defining the region within which suprathreshold flicker vanishes; and (5) the lowest intensity at which flicker can be detected during the cone plateau following a full bleach of 7·7 $\log_{10}$ photopic td s, i.e. the cone flicker threshold (○).

For all three observers, the same pattern of results is found for target diameters $\geqslant 3$ deg (panels *C* and *D* of Figs 1–3, and panel *E* of Fig. 1). The absolute threshold for rod flicker is low (between $-1·5$ and $-3·0$ $\log_{10}$ scotopic td). The flicker curve (●) is conspicuously double branched, with the second branch emerging on backgrounds between $-1·0$ and 0·0 $\log_{10}$ scotopic td. There is also a clearly definable suprathreshold region (▲ and ▼), below cone flicker threshold (○), lying between target amplitudes of $-1·0$ and 0·5 $\log_{10}$ scotopic td, where flicker vanishes (the perceptual null). As the target diameter approaches 3 deg, the threshold for seeing the target, the rod flicker threshold (●) and the cone flicker threshold (○) move slightly upwards along the ordinate. But the loss of sensitivity for all three types of threshold is relatively small, despite a change in target area of 11 (C.F.) or 4 (T.A. and J.H.) times.

For target diameters $\leqslant 2$ deg (panels *A* and *B* of Figs 1–3) the pattern changes dramatically in all three observers. Compared with the results obtained for the larger targets, the absolute threshold for rod flicker is considerably higher, lying between $-0·5$ and 0·5 $\log_{10}$ scotopic td for C.F. and J.H. and above 0·5 $\log_{10}$ scotopic td for T.A. Moreover, the flicker curves are characterized by a single, monotonic aspect below the cone plateau flicker threshold (○). The region between the rod and cone plateau threshold is very narrow. Neither a break in the 15 Hz curve nor a distinct perceptual null can be found. Moreover, the flicker threshold corresponds more or less to the upper limit of the null region obtained with larger diameter targets.

For observer T.A., with targets $\leqslant 2$ deg in diameter, the flicker threshold measured in the unbleached state is the same or higher than the flicker threshold measured during the cone plateau following a full bleach, suggesting that in the unbleached state the flicker threshold is determined, at least in part, by cones. The elevation of the flicker threshold in the unbleached state above the cone plateau threshold

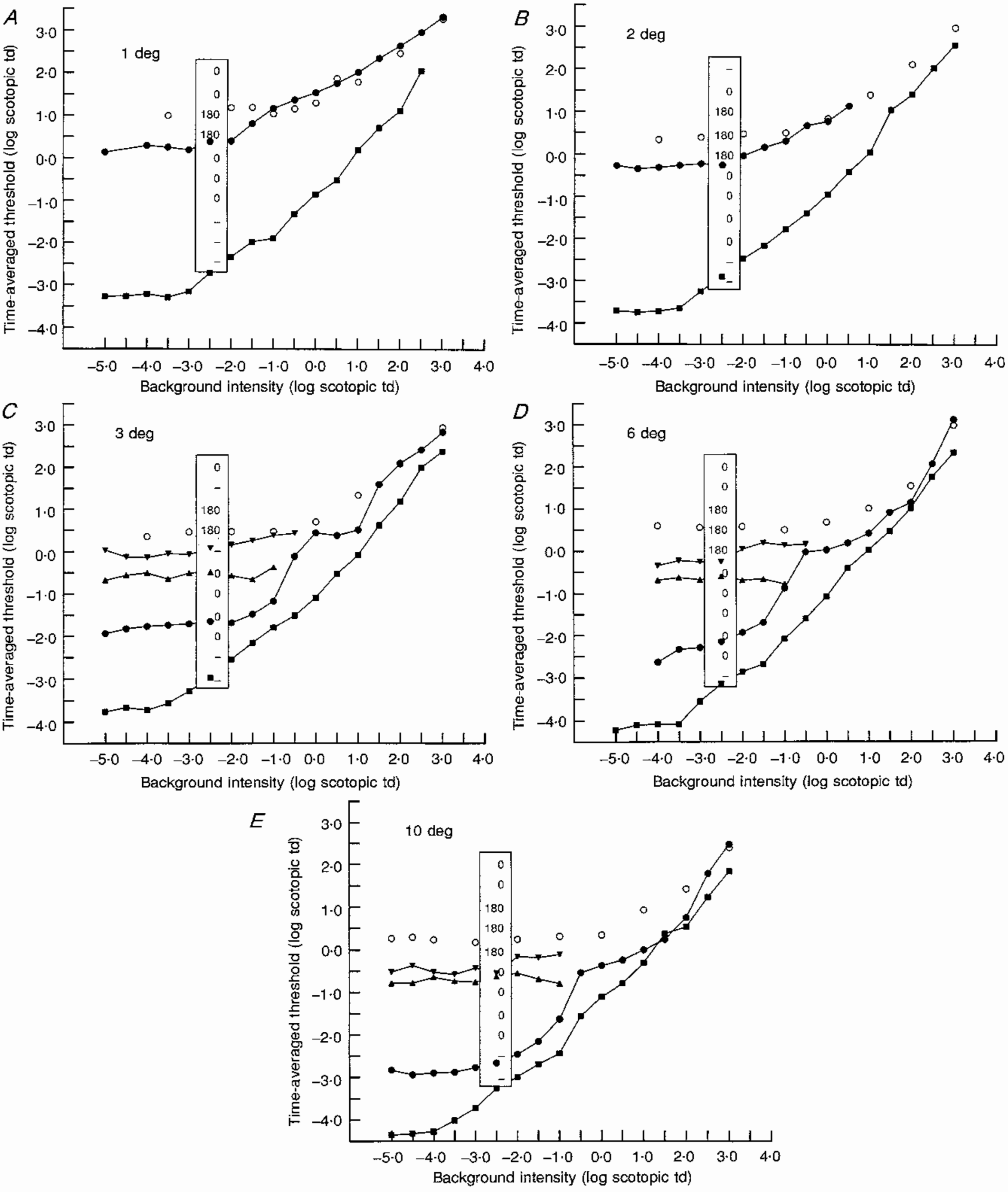

Figure 1. The effect of target size on detection of a 500 nm, 15 Hz flickering light as a function of background intensity (observer C. F.)

The target and the 18 deg diameter, 640 nm background were centred at 12 deg in the temporal retina. Thresholds are shown for 5 target sizes: 1, 2, 3, 6 and 10 deg. The symbols indicate the threshold for seeing the target (■), the flicker threshold (●), the lower (▲) and upper (▼) limits of the null, and the cone plateau flicker threshold (○). The values in the columns indicate the relative phase in degrees between the 500 nm target, as a function of its intensity, and a superimposed 679 nm reference target at which the subjective flicker appears maximal (see the text and Fig. 4 for details). The position of the column along the ordinate indicates the background intensity at which the phase relations were measured.

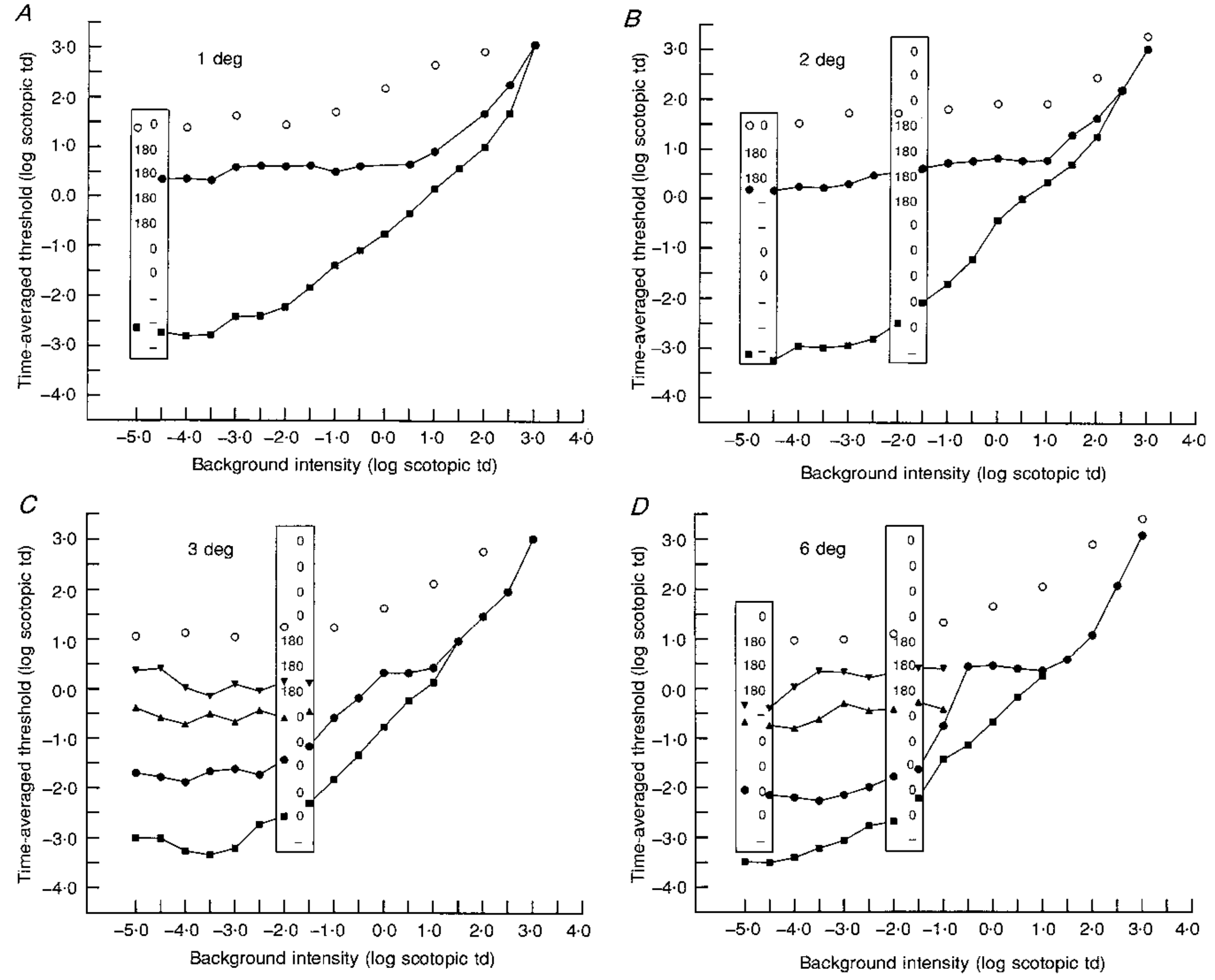

Figure 2. The effect of target size on detection of a 500 nm, 15 Hz flickering light as a function of background intensity (observer J. H.)

Same conditions as in Fig. 1, except no thresholds were measured for the 10 deg target.

could be due to destructive interference between the signals generated by π_0' and the cones, which, like π_0 and π_0', are close to out of phase at 15 Hz (Sharpe *et al.* 1989). Such interference cannot be occurring during the cone plateau, since the π_0' signals are bleached away.

Subthreshold rod–cone phase measurements

The disappearance of the lower 15 Hz branch and the perceptual null with target diameters of $\leqslant$ 2 deg might be taken to mean that π_0 summates over a larger retinal area than π_0', and is so severely handicapped by the use of small targets that it becomes ineffective. But if that were the case, we should also expect the threshold for π_0' to go down, since it is no longer elevated by destructive interference with π_0 signals. Instead it remains at a level roughly consistent with the upper limit of the nulled regions found with the 3 deg and 6 deg targets. This supports the third alternative explanation given above; namely, that decreasing the target size produces a parallel reduction in the sensitivity of both π_0 and π_0' together, causing the null region to extend downwards to merge with and therefore obliterate the π_0 'threshold'. If this explanation is correct, π_0 and π_0' flicker signals should be present below the measured threshold, but because of destructive interference they remain below detection threshold.

Additional support for this hypothesis comes from the fact that, in contrast to the rod threshold for seeing the target, which hardly changes at all, the rod flicker threshold rises by 30 to 100 times (1·5–2·0 $\log_{10}$ units) in going from a 3 to a 2 deg diameter target (see Figs 1–3). This precipitous change is unlikely to be due to a reduction in the summation area of π_0, since we know that the total change in spatial summation in the rod visual system over its entire dynamic range is only a factor of 3–4 (Sharpe, Stockman, Fach & Markstahler, 1993*a*; Sharpe, Whittle & Nordby, 1993*b*).

How can we determine whether the sudden elevation of the 15 Hz flicker threshold and the loss of the double branch are due to destructive interference between the π_0 and π_0'

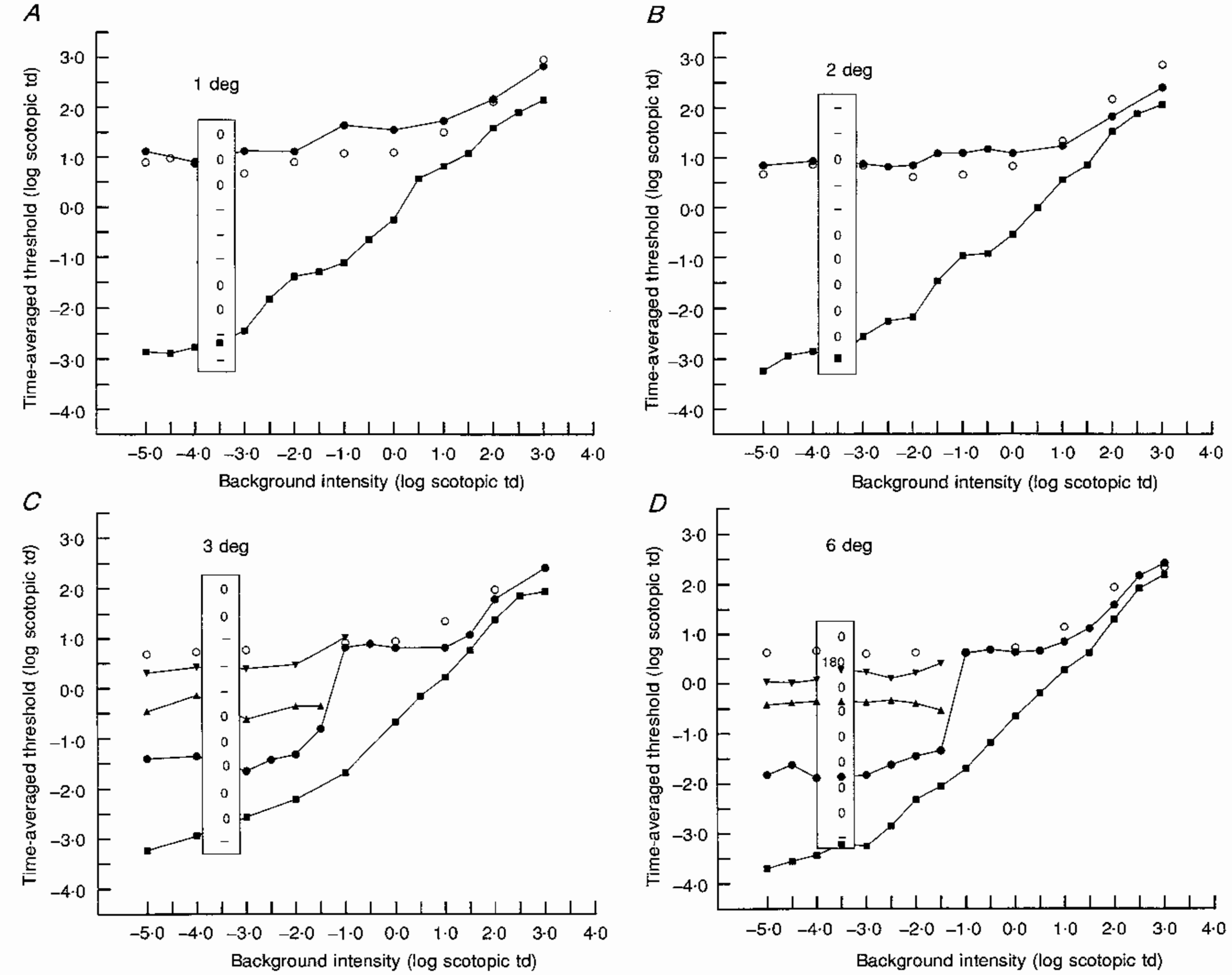

Figure 3. The effect of target size on detection of a 500 nm, 15 Hz flickering light as a function of background intensity (observer T. A.)

Same conditions as in Fig. 1, except no thresholds were measured for the 10 deg target.

signals? One way is to make phase measurements relative to a cone standard above and below the 15 Hz rod flicker threshold since, as we have reported before, such measurements can often be made even when the rod flicker is below detection threshold (Sharpe *et al.* 1989). The technique is shown in Fig. 4 (for more details, see Sharpe *et al.* 1989).

The observer is presented with two superimposed, 15 Hz flickering test lights (see Stimuli, panels *A* and *B*): a green (500 nm) target for the rods; and a red (679 nm) target for the cones. The cone-detected target is set to just above the flicker threshold. The rod-detected target is varied in intensity from below rod flicker threshold to above cone threshold. At each intensity of the rod target, the relative phase between the two lights is set at 0 deg (panel *A*) or 180 deg (panel *B*) and the observer must decide in which case the subjective flicker appears greater. Determining the rod–cone phase delay in this way can indicate which of the two rod pathways is primarily responsible for detecting the flicker, since at 15 Hz cone signals precede the rod signals in the slow pathway by a full cycle (360 deg), whereas they precede the rod signals in the fast pathway by only a half-cycle (180 deg) (Sharpe *et al.* 1989; Stockman *et al.* 1991). Hence, if the rod flicker is detected primarily by π_0 (see middle column under Flicker sensation), the subjective flicker will appear maximal when the rod and cone stimuli flicker in phase (panel *A*), whereas, if the rod flicker is detected primarily by π_0' (see right column, under Flicker sensation), the flicker will appear maximal when the rod and cone stimuli flicker out of phase (panel *B*).

If both the π_0 and the π_0' signals are present for the small diameter targets, we should still find the characteristic phase change from π_0 (360 = 0 deg) at low target intensities (below the observed flicker threshold) to π_0' (180 deg) at higher intensities that are also found with larger targets. Alternatively, if π_0 is so severely handicapped by the use of small targets that it becomes ineffective, then we should expect any phase relation that can be measured below threshold to be that of π_0' (180 deg).

The cone reference phase measurements were made for the three observers using the 1, 2, 3 and 6 deg (and 10 deg

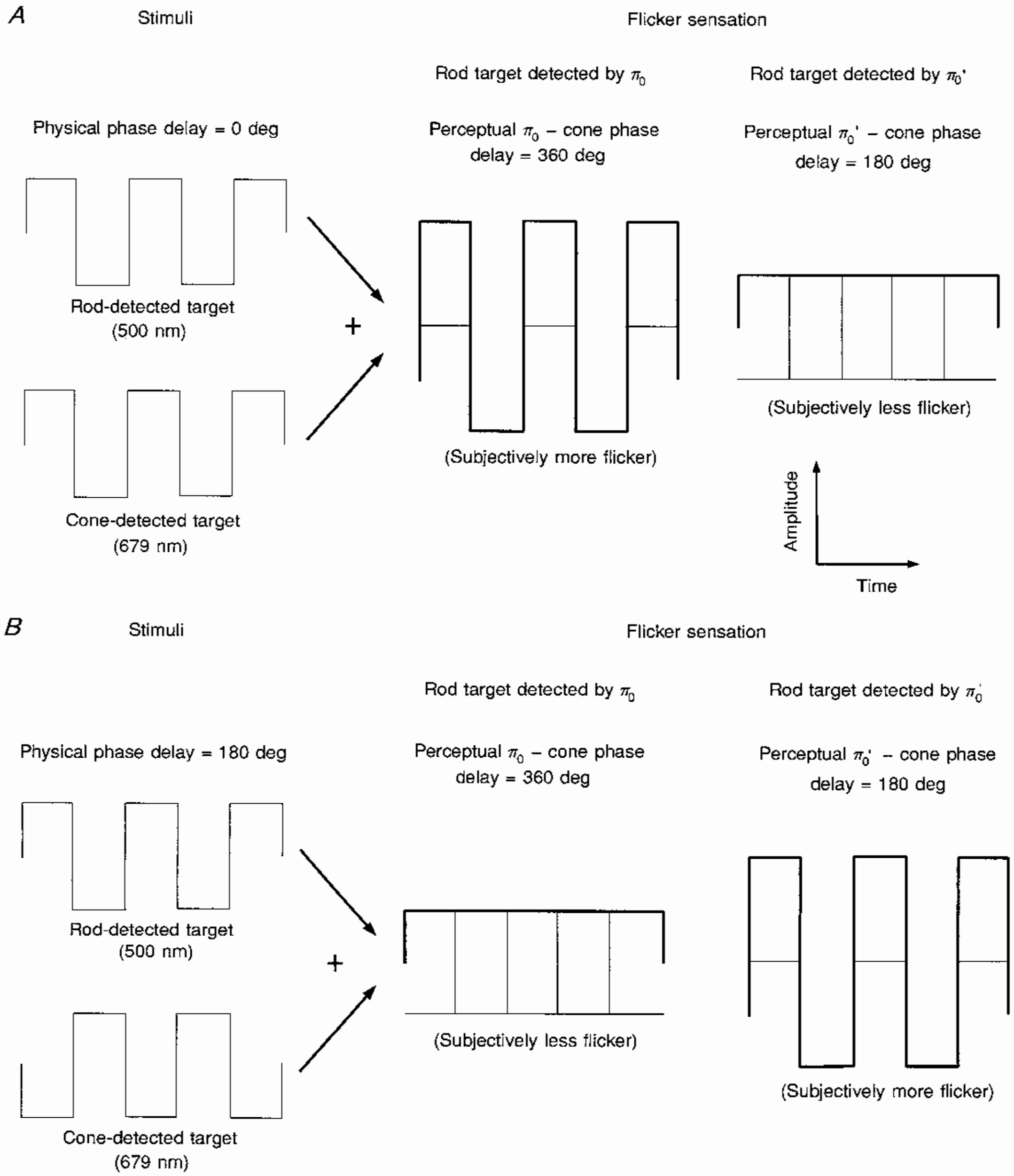

Figure 4. The conditions and expected results for the relative phase adjustment experiment
As indicated by 'stimuli', the subject sees two superimposed, 15 Hz flickering test lights. The 500 nm target is rod detected, except at the highest intensities; the 679 nm target is primarily cone detected. The phase relation of the cone-detected target relative to the rod-detected target is either 0 (*A*) or 180 (*B*) deg. The subject must choose which condition produces the strongest flicker sensation. The modulation depth of the cone-detected target is adjusted through the course of the experiment to prevent it from swamping the rod detected target. Under 'flicker sensation' are shown the expected results, when the rod-target is detected by π_0 (middle column) and when it is detected by π_0' (right column).

for C.F.) diameter targets either in the dark (i.e. on a $-5{\cdot}0 \log_{10}$ scotopic td background, J.H.) or against a dim long-wave (640 nm) adapting field of $-3{\cdot}5$ (T.A.) $-2{\cdot}5$ (C.F.) or $-2{\cdot}0$ (J.H.) $\log_{10}$ scotopic td.

The results are listed in Tables 1–4, which indicate, as a function of the intensity of the 500 nm rod-detected target (R), whether flicker was visible (V) or invisible (I) and whether adding the cone-detected target (+C) in phase (0 deg) or out of phase (180 deg) enhanced (+) or nulled (–) the flicker sensation. ('?' indicates that there was no perceptible influence of adding the cone-detected target either in or out of phase.) The results are ordered according to the target diameter used. To help orient the reader, the relative phase in degrees (0 or 180 deg) at which the subjective flicker appeared

Table 1. Subthreshold and suprathreshold rod–cone phase measurements for observer C. F. at a background intensity of −2·5 log scotopic td

Target intensity	1 deg target			2 deg target			3 deg target			6 deg target			10 deg target		
R (log scot. td)	R	+C 0	+C 180	R	+C 0	+C 180	R	+C 0	+C 180	R	+C 0	+C 180	R	+C 0	+C 180
−3·0	I	?	?	I	?	?	I	?	?	I	?	?	I	?	?
−2·5	I	?	?	I	?	?	I	?	?	I	+	−	V	?	?
−2·0	I	?	?	I	+	−	I	+	−	V	+	−	V	+	−
−1·5	I	?	?	I	+	−	V	+	−	V	+	−	V	+	−
−1·0	I	+	−	I	+	−	V	+	−	V	+	−	V	+	−
−0·5	I	+	−	I	+	−	I	+	−	I	+	−	I	+	−
0·0	I	+	−	V	−	+	I	?	?	V	−	+	V	−	+
0·5	V	−	+	V	−	+	V	−	+	V	−	+	V	−	+
1·0	V	−	+	V	−	+	V	−	+	V	−	+	V	−	+
1·5	V	+	−	V	+	−	V	?	?	V	+	−	V	+	−
2·0	V	+	−	V	?	?	V	+	−	V	+	−	V	+	−

Details as for Table 2.

Table 2. Subthreshold and suprathreshold rod–cone phase measurements for observer J. H. at a background intensity of −5·0 log scotopic td

Target intensity	1 deg target			2 deg target			6 deg target		
R (log scot. td)	R	+C 0	+C 180	R	+C 0	+C 180	R	+C 0	+C 180
−3·0	I	?	?	I	?	?	I	?	?
−2·5	I	?	?	I	?	?	I	+	−
−2·0	I	?	?	I	?	?	I	+	−
−1·5	I	+	−	I	+	−	V	+	−
−1·0	I	+	−	I	+	−	V	+	−
−0·5	I	−	+	I	?	?	I	?	?
0·0	I	−	+	I	?	?	V	−	+
0·5	V	−	+	V	−	+	V	−	+
1·0	V	−	+	V	−	+	V	−	+
1·5	V	+	−	V	+	−	V	+	−

I, flicker invisible; V, flicker visible; ?, no difference in flicker perception; +, flicker perception enhanced; −, flicker perception diminished or nulled. For each size of the 500 nm rod-detected target (R; 1, 2, 3, 6 or 10 deg diameter) the 679 nm cone-detected target (+C) of the same size was added in phase (0 deg; 0) or out of phase (180 deg; 180).

maximum, as a function of the intensity of the rod-detected target, is also shown in Figs 1–3, within the circumscribed columns.

For targets ⩾ 3 deg in diameter, the results are straightforward and predictable from the observer's 15 Hz flicker threshold profiles. When the 500 nm target is so dim that it is near to or below the threshold for seeing the target at all (Figs 1–3, ■), changing the phase relation between the 500 and 679 nm targets from 0 to 180 deg does not affect the flicker sensation produced by the suprathreshold 679 nm (cone-detected) target alone. Any rod signals that are generated by the subthreshold 500 nm target are too weak to cancel or enhance the cone signals generated by the 679 nm target enough to produce a detectable change in the flicker saliency.

At slightly higher intensities of the 500 nm target, which are above the visual threshold for the rods and which are near or slightly below the rod flicker threshold, the flicker of the superimposed targets appears maximal (enhanced) when the phase relation is 0 deg and minimal (nulled) when it is 180 deg. This is consistent with the signals produced by the 500 nm target being transmitted by the more sensitive, slow rod pathway, π_0, since π_0 produces signals that are in phase with cone signals at 15 Hz. A phase relation of 0 deg for maximum flicker is found until the intensity of the 500 nm rod-detected stimulus approaches the intensity associated with the upper limit of the flicker null region. (In the null region itself, it was often impossible, especially for observer T. A., to find a best phase position, presumably because destructive interference severely weakens the rod signal.)

Table 3. Subthreshold and suprathreshold rod–cone phase measurements for observer J. H. at a background intensity of −2·0 log scotopic td

Target intensity	2 deg target			3 deg target			6 deg target		
R (log scot. td)	R	+C 0	+C 180	R	+C 0	+C 180	R	+C 0	+C 180
−3·0	I	?	?	I	?	?	I	?	?
−2·5	I	+	−	I	+	−	I	+	−
−2·0	I	+	−	I	+	−	I	+	−
−1·5	I	+	−	I	+	−	V	+	−
−1·0	I	+	−	V	+	−	V	+	−
−0·5	I	+	−	I	+	−	I	+	−
0·0	I	−	+	I	−	+	I	−	+
0·5	V	−	+	V	−	+	V	−	+
1·0	V	−	+	V	−	+	V	−	+
1·5	V	−	+	V	+	−	V	+	−
2·0	V	+	−	V	+	−	V	+	−
2·5	V	+	−	V	+	−	V	+	−
3·0	V	+	−	V	+	−	V	+	−

Details as for Table 2.

Table 4. Subthreshold and suprathreshold rod–cone phase measurements for observer T. A. at a background intensity of −3·5 log scotopic td

Target intensity	1 deg target			2 deg target			3 deg target			6 deg target		
R (log scot. td)	R	+C 0	+C 180	R	+C 0	+C 180	R	+C 0	+C 180	R	+C 0	+C 180
−3·0	I	?	?	I	?	?	I	?	?	I	?	?
−2·5	I	?	?	I	+	−	I	+	−	I	+	−
−2·0	I	+	−	I	+	−	I	+	−	V	+	−
−1·5	I	+	−	I	+	−	V	+	−	V	+	−
−1·0	I	?	?	I	+	−	V	+	−	V	+	−
−0·5	I	?	?	I	+	−	I	+	−	I	+	−
0·0	I	?	?	I	?	?	I	?	?	I	+	−
0·5	I	+	−	I	?	?	V	?	?	V	−	+
1·0	I	+	−	V	+	−	V	?	?	V	+	−
1·5	V	+	−	V	?	?	V	+	−			
2·0				V	?	?	V	+	−			

Details as for Table 2.

Thereafter, the flicker appears maximal when the phase relation is near 180 deg and minimal when it is near 0 deg. This is consistent with the signals produced by the 500 nm target being transmitted along the less sensitive, fast rod pathway, π_0', since π_0' produces signals that are out of phase with cone signals at 15 Hz. A phase relation of 180 deg is found until the 500 nm target becomes so bright that it is predominately or exclusively seen by the cones. Then the best phase relation for maximal flicker is 0 deg, since both targets are now being seen by the cones.

For observer T. A., with the 3 deg diameter field, no best phase position could be determined within the null region or above it (below the cone plateau threshold). Since the upper limit of his null lies very close to his cone plateau threshold, destructive interference between the cones and fast rod signals (π_0') may be weakening the signals of the fast rod pathway, making it difficult or impossible to measure their phase relation relative to the cones.

For all subjects, only a single branch of the flicker TVI curve is found for targets ≤ 2 deg in diameter, and it is greatly elevated relative to the lower branch obtained with 3 deg diameter targets. Nevertheless, at intensities between the absolute threshold and the rod flicker threshold, the best-phase relation is 0 deg, implying that signals from the slow pathway are still present at intensities below the rod flicker threshold. Moreover, near the rod flicker threshold, the phase relation for maximum (or enhanced) flicker reverses to become 180 deg for observers C. F. and J. H. (For observer

T.A., no best phase position can be determined in this region.) Thus, there is a transition from π_0 and π_0' with small targets, just as there is for larger ones.

We conclude, therefore, that the faster rod pathway mediates flicker detection for targets of $\leqslant 2$ deg, not because the signals from the slow pathway are selectively reduced by decreasing the field size, but because destructive interference between the slow and fast rod flicker signals keeps the slow signals from ever exceeding threshold. This conclusion is consistent with a model in which reducing the target size from 10 to 1 deg reduces the sensitivities of the slow and the fast rod pathways together.

DISCUSSION

In a previous study, Sharpe *et al.* (1989) were unable to find any clear differences between the spatial properties of the two rod pathways near the null intensity. They replaced a uniform flickering field with counterphase flickering gratings, in which the alternate bars flickered out of phase with each other. Supposedly, if the neural excitation pools of the two rod processes differ in size, some gratings will be better resolved by one than by the other process, and this will upset the equality between the two rod signals, making flicker apparent where (in the absence of the grating) there had been a null. Introducing gratings, however, did not upset the region of the perceptual null. In fact, with high spatial frequencies, the nulling region of the field actually extended to well above and well below the uniform-field null range, suggesting that at these spatial frequencies opposite phase flicker signals from alternate bars are cancelling each other within each rod process.

Though a cursory glance at the change in the shape of the 15 Hz flicker TVI curves with target diameter (Figs 1–3) might suggest otherwise, the results obtained in this study are consistent with those of Sharpe *et al.* (1989). The loss of the lower branch of the curve with small targets occurs not because the π_0 pathway is so disadvantaged, relative to the π_0' pathway, that it no longer mediates threshold, but because cancellation between π_0 and π_0' keeps π_0 from ever exceeding threshold. Since this could result from a parallel reduction in the sensitivity of π_0 and π_0' as the target size is decreased, there is no need to appeal to large differences in the spatial organization of π_0 and π_0' to explain the substantial differences in the shapes of the 15 Hz flicker TVI curves found with different target diameters.

Previous measurements of scotopic spatial acuity using steady stimuli also do not support an abrupt transition between two rod mechanisms of different spatial organization in the region of the perceptual flicker null. For instance, for both the normal observer and the typical, complete achromat who has no cone vision, there is a monotonic relation between sine-wave grating acuity and retinal illuminance in the region of the flicker null (Hess & Nordby, 1986). However, if briefly flashed black discs (Hallett, 1962) or gratings (Hofmann *et al.* 1990) are used, rather than steady targets, acuity measurements as a function of retinal illuminance are double branched, and this can be taken as evidence of a duality in rod spatial vision (Hallett, 1962). Nevertheless, the doubled-branched spatial acuity functions produced by transient stimulation seem to be quite distinct from the double-branched critical flicker fusion (Hecht *et al.* 1938, 1948; Conner & MacLeod, 1977; Hess & Nordby, 1986) and 15 Hz flicker TVI results shown here. For one thing, the double branching in the spatial acuity function is not found when the measurements are repeated using longer duration, flashed (1000 ms) or flickering (1, 3, 7 or 10 Hz) gratings, i.e. under conditions more similar to those used here. For another, the intensity level at which the transition in the spatial data occurs is about 1·0 $\log_{10}$ unit *below* the intensity level at which the flicker null is found.

Anatomical substrate of the two rod signals

The findings reported here impose certain constraints upon the anatomical and physiological models that can be invoked to explain the origin of the two rod signals. In particular, our findings suggest that the large-scale spatial organization of the two pathways does not markedly differ at the intensity at which flicker detection passes from one pathway to the other, thus arguing against models in which one of the rod signals depends upon far-reaching lateral, retinal connections. However, since we used targets of 1 deg diameter or greater, our results do not rule out the possibility that there are significant small-scale differences in spatial organization between the two pathways. A more precise determination of the spatial properties of the two pathways using spatially narrow-band stimuli will be required in order to reveal any small differences that might exist between π_0 and π_0'.

Small-scale differences in spatial organization between the two signals would be predicted, for example, by the dual pathway model discussed above, in which it is assumed that π_0 corresponds to the conventional rod pathway via rod bipolars and AII amacrines, while π_0' corresponds to the mesopic pathway via rod–cone gap junctions and cone bipolars. However, the predicted differences in spatial organization – based on say the differences in dendritic spreads and receptive field sizes between AII amacrine cells and cone bipolar cells – would be substantially smaller than our smallest target.

In contrast, no small-scale differences in spatial organization between π_0 and π_0' would be predicted by models in which the two rod signals derive from two distinct loci within the same rod photoreceptor or within the same pathway, or from two types of rod photoreceptor that are equally distributed but with different response properties. But such models seem to have little physiological or anatomical support in the human (see Sharpe & Stockman, 1991, for a review).

REFERENCES

Conner, J. D. (1982). The temporal properties of rod vision. *Journal of Physiology* **332**, 139–155.

Conner, J. D. & MacLeod, D. I. A. (1977). Rod photoreceptors detect rapid flicker. *Science* **195**, 689–699.

Daw, N. W., Jensen, R. J. & Brunken, W. J. (1990). Rod pathways in the mammalian retinae. *Trends in Neurosciences* **13**, 110–115.

Dick, E. & Miller, R. F. (1970). Light-evoked potassium activity in mudpuppy retina: its relationship to the b-wave of the electroretinogram. *Brain Research* **154**, 388–394.

Gurevich, L., Stockton, R. A. & Slaughter, M. M. (1990). Comparisons of the waveforms of the b-wave of the ERG and on bipolar cells. *Investigative Ophthalmology and Visual Science* **31**, suppl. 114.

Hallett, P. E. (1962). Scotopic acuity and absolute threshold in brief flashes. *Journal of Physiology* **163**, 175–189.

Hecht, S., Shlaer, S., Smith, E. L., Haig, C. & Peskin, J. C. (1938). The visual functions of a completely colorblind person. *American Journal of Physiology* **123**, 94–95.

Hecht, S., Shlaer, S., Smith, E. L., Haig, C. & Peskin, J. C. (1948). The visual functions of the complete colorblind. *Journal of General Physiology* **31**, 459–472.

Hess, R. F. & Nordby, K. (1986). Spatial and temporal limits of vision in the achromat. *Journal of Physiology* **371**, 365–385.

Hofmann, M. I., Barnes, C. S. & Hallett, P. E. (1990). Detection of briefly flashed sine-gratings in dark-adapted vision. *Vision Research* **30**, 1453–1466.

Nordby, K. & Sharpe, L. T. (1989). The directional sensitivity of the photoreceptors in the human achromat. *Journal of Physiology* **399**, 267–281.

Sharpe, L. T. & Stockman, A. (1991). Dual rod pathways. In *From Pigments to Perception: Advances in Understanding Visual Processes*, ed. Valberg, A. & Lee, B. B., pp. 53–66. Plenum Press, London.

Sharpe, L. T., Stockman, A., Fach, C. C. & Markstahler, U. (1993*a*). Temporal and spatial summation in the human rod visual system. *Journal of Physiology* **463**, 325–348.

Sharpe, L. T., Stockman, A. & MacLeod, D. I. A. (1989). Rod flicker perception: scotopic duality, phase lags and destructive interference. *Vision Research* **29**, 1539–1559.

Sharpe, L. T., Whittle, P. & Nordby, K. (1993*b*). Spatial integration and sensitivity changes in the human rod visual system. *Journal of Physiology* **461**, 235–246.

Sterling, P., Freed, M. & Smith, R. G. (1986). Microcircuitry and functional architecture of the cat retina. *Trends in Neurosciences* **9**, 186–192.

Stiles, W. S. (1978). Mechanisms of colour vision. Academic Press, London.

Stockman, A., Sharpe, L. T., Zrenner, E. & Nordby, K. (1991). Slow and fast pathways in the human rod visual system: electrophysiology and psychophysics. *Journal of the Optical Society of America* A **8**, 1657–1665.

Stockton, R. A. & Slaughter, M. M. (1989). B-wave of the electroretinogram: a reflection of ON bipolar cell activity. *Journal of General Physiology* **93**, 101–122.

Acknowledgements

This research was supported by the Deutsche Forschungsgemeinschaft, Bonn (SFB 325, B13 and Heisenberg-Programm) and by the National Science Foundation, Washington (IBN 92-10046).

Received 22 January 1993; accepted 7 July 1993.