*Vision Res.* Vol. 22, pp. 827 to 833, 1982
Printed in Great Britain

0042-6989/82/070827-07$03.00/0
Pergamon Press Ltd

# STABILIZED VISION THROUGH A BLEACHING WINDOW

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(*Received* 28 *September* 1981)

**Abstract**—The visibility of stimuli flickering at low temporal frequencies was studied with images viewed normally and when stabilized by a new technique (bleached-window stabilization) that produces perfectly stabilized images without attachment to the eye. Contrary to expectation, sensitivity to low-frequency flicker was *higher* in the stabilized than in the unstabilized case. Several controls exclude the possibility that the paradoxical increase in sensitivity is an artefact of the new technique, and suggest that, in normal viewing, transient activity created by fixational eye-movements can mask the signals arising from the low-frequency flicker.

## INTRODUCTION

The fading of steadily illuminated, retinally stable images (see Ditchburn, 1974) has implications for sensitivity to low frequency sinusoidal flicker: in stabilized viewing, sensitivity must approach zero as frequency decreases towards zero, whereas in normal viewing fixational eye-movements maintain intensity discrimination no matter how gradually the illumination is varied. Little is known about the fading process. The experiments reported here were begun with the aim of investigating the dynamics of fading by examining the effects of image stabilization on sensitivity to flicker at various frequencies lower than those used by Keesey (1970) in a previous study of this question. However, the experiments yielded an unexpected result, incompatible with our preconceptions: sensitivity to slow intensity modulation proved *greater* in the stabilized case. We conclude that the transient stimulation created by fixational eye-movements is capable of masking externally imposed intensity modulation.

An important aspect of these experiments is that true stabilization of the retinal image was not generally attempted. The procedure used instead was one that may be generally useful as a substitute for true stabilization. We simply limited the extent of the stimulated area not by a field-stop in the incident light beam, but by bleaching all of the retina surrounding the test patch so as to make it incapable of registering the applied stimuli. The physical test stimuli were spatially uniform and covered a retinal area substantially larger than the intended test patch, so that eye-movements never altered the illumination of the test patch. Some surrounding retina is always being illuminated by the test beam, but this stimulation is rendered ineffective by the bleaching. With a suitable bleaching and testing procedure, the following conditions necessary for the technique to work are easily satisfied: no afterimage of the bleached area persists to prevent fading of the outline of the test area under steady illumination; the sensitivity of the unbleached patch is uniform almost to its edge and remains constant over time; and the bleached area remains practically blind to the applied stimuli over a period long enough for leisurely measurement. The applied stimuli are seen through a retinally stable window provided by the bleach.

This new technique of bleached-window stabilization (BWS) has two great advantages: it is very easy to use, requiring no expensive equipment or attachments to the eye and it eliminates any possibility of unintended residual image motion. Its drawback is that since it differs from pure stabilization in that receptors surrounding the test patch have been bleached, its validity as a substitute for true stabilization could be questioned. Some consequent ambiguities in the interpretation of our results are discussed below.

## METHODS

Most of our observations were made with rod vision because a number of factors make the BWS technique more successful with rods than with cones. Cone participation was prevented by using a test stimulus of 483 nm at a scotopic luminance level. The test patch was normally a large (5.3 deg) disc centred 6 deg in the temporal retina. The two main conditions were (1) normal (unstabilized) viewing of the test field, and (2) bleached-window stabilization (BWS). In the normal condition, a field stop in the apparatus limited the test field size in the usual way (Fig. 1a). For the BWS condition (Fig. 1b) this field stop was removed so that the incident light illuminated a large patch of retina 9.1 deg across, and at the same time the size of the effectively stabilized region was kept down to 5.3 deg by bleaching, with an annular field (inner dia 5.3 deg, outer dia 11.8 deg), all of the surrounding rods that received light from the enlarged test beam.

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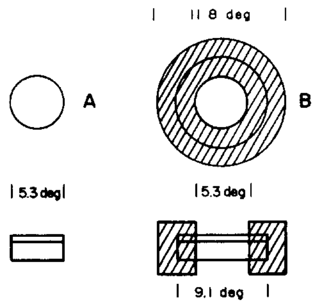


Fig. 1. Stimulus configuration. (A) Normal (unstablized) viewing. Co-extensive test and background fields 5.3 deg in diameter. In some experiments the background only was enlarged to 9.1 deg. (B) Bleached-window stabilized fields. Co-extensive test and background fields (dia 9.1 deg) were limited to a visible field of dia 5.3 deg by an annular bleach (shown hatched) of inner diameter 5.3 deg, outer diameter 11.8 deg.

The bleaching light (6.8 log scot. td. sec), was produced by a 30 sec exposure to unfiltered light from a tungsten ribbon lamp. As a result of this exposure, the bleached area remained insensitive to scotopic stimuli until after the rod-cone transition in the dark-adaptation curve; any desensitizing effects of bleaching by scattered light falling on the spared region had dissipated within about 3 min. Throughout the bleach, and during the measurements that followed, the observer fixated a small yellow spot. During the early phase of dark-adaptation a persisting positive after-image is visible and this prevents the complete subjective merging of the test patch and surround under steady illumination, but this afterimage had disappeared under our conditions by 3 min leaving a substantial period (generally more than 10 min) during which sensitivity was practically constant, and rod thresholds in the window could be measured without the test field being detectable in the bleached annulus. Bleaches were repeated at intervals of at least 30 min.

The only available check on the validity of the BWS procedure as a stabilization technique is subjective. As expected, the test field in the BWS condition did behave very like a stabilized image, fading into uniformity with the surround over several seconds if the test field was left at a constant intensity. MacLeod (1974, Chap. 8), following Barlow and Sparrock (1964) made side by side comparisons between fields defined either by BWS or by genuine stabilization (with contact lens and stalk), and found them practically indistinguishable both during fading and after their regeneration by a change of illumination; the slight differences noted were suggestive of residual image motion in the field stabilized by the contact lens.

Sinusoidally flickering test fields were produced by a rotating polarizer in conjunction with a fixed one. Frequencies used were generally 0.17, 0.33, 0.67, 1.3, 2.7, 5.3 and 10.3 Hz. A steady background beam was always present and the 100% modulated flickering beam was superimposed on it at a mixing cube. The observer's task was to adjust the illumination of the modulated beam (by means of a neutral density wedge) so that flicker was only just detectable. Since Weber's law holds fairly well under the conditions used, results are given in terms of the modulation required for detection, modulation being the difference between the peak and time-average intensities expressed as a fraction of the time-average intensity. Actual time-average intensities varied across conditions, spanning a range of 0.3 log units around the nominal value. Thus the flicker thresholds do not define a modulation sensitivity function at constant average luminance, but the distortion introduced by deviations from Weber's Law is negligible except at the highest frequency, and in any case it does not affect the comparisons and inferences made in this paper.

The authors served as observers.

## RESULTS

### *Appearance of BWS fields and paradoxical increase in sensitivity*

Our initial experiments dealt with the flicker sensitivity of the rod system. A 483 nm flickering field was used, superimposed upon a steady background of the same colour and diameter (9.2 deg). The outside edges of the fields fell well within the external diameter of the annular bleach (11.8 deg) upon which they were presented (Fig. 1b). This annular patch rendered invisible to rods those parts of the combined field that fell upon it, so the effective stimulus was a 5.3 deg disc, bounded by the inner diameter of the bleached annulus.

The observer's task was, following a bleach (5.3 log td for 30 sec) to adjust the amplitude of the flicker so that it was just visible in the window bounded by the bleached area. Following the bleach, an annular after-image was visible for several minutes. After 3 to 5 min the after-image had faded and the flicker threshold had stabilized. Threshold then remained constant for at least another 10 min, before rods in the bleached area recovered sufficiently to detect the overlying parts of the test field. During the period of the observations, nothing was visible unless the modulation in the flickering window was above threshold. No after-image was visible and for the lowest frequencies, the windowed test field was visible only at the peaks. The completeness of the fading was exceptionally striking, as was the crispness of the edge when the field became visible. This suggests that previous reports of incomplete fading may be due to improper stabilization. The test field could be detected by looking for flicker alone or by looking for a clearly bounded field. At low temporal frequencies the field was really only detectable by being defined at its edges, as its faded image was revived once or twice on each flicker cycle—"flicker" was not perceptible as such, although, of course, it was the stimulus modulation that caused the field to be defined. At frequencies above about 1.3 Hz the field could be detected as well by looking for "flicker" as by looking for definition of its outline; for frequencies above 5 Hz the "flicker" threshold was lower by about 0.1 log unit.

Throughout this section the thresholds given for the BWS condition are obtained by whichever criterion gave the lower threshold (mostly that involving definition of the window). The judgements were very easy to make; all three observers found that thresholds were easier to set under these conditions than when flickering fields the size of the spared area were viewed normally.

By making several experimental runs using fields flickering at different rates one can readily obtain a curve relating modulation sensitivity to temporal frequency, both when the flickering field is stabilized (as described above) or unstabilized, in which case the background and test fields (both now 5.3 deg diameter) are viewed without any bleached annulus.

Figure 2 shows, for P.L. and M.H., how modulation sensitivity varied with temporal frequency. When the field had a stabilized edge (unfilled circles),

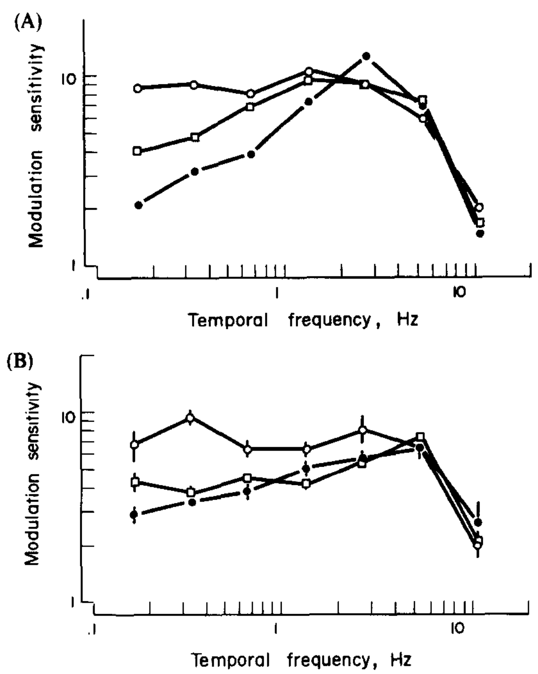


Fig. 2. Modulation sensitivity curves for a 483 nm flickering test field superimposed upon a 483 nm steady background. (A) Observer P.L., mean illumination 0.3 scot. td. Unfilled circles: background and test both 9.1 deg diameter superimposed upon a concentric annular bleach (inner dia 5.3 deg, outer dia 11.8 deg) that confines effective rod stimulation to a 5.3 deg disc with a stabilized edge. Filled circles: test and background fields both 5.3 deg diameter, with no bleached annulus. Unfilled squares: test and background fields both 9.1 deg diameter, with annular bleach to confine rod-visible field to 5.3 deg. A dark annular ring (inner dia 5.3 deg, outer dia 5.8 deg) fell across the inner edge of the bleached annulus. (B) Observer M.H. Conditions as for (A) except: unfilled squares are for test and background fields both 5.3 deg dia, together with an annular bleach of inner dia 5.5 deg that left an unbleached ring approximately 5 min wide around the test field.

sensitivity was almost uniform between 0.17 Hz and 5 Hz, and for all frequencies in this range was appreciably higher than when the field was viewed normally (filled circles). Between sessions repeatability was better than 0.1 log units for P.L. and for M.H. is indicated by the vertical bars in Fig. 2b. The advantage of the BWS condition was greater the lower the temporal frequency. This finding is surprising, in view of the plentiful evidence that well-stabilized images quite rapidly fade to invisibility.

The observations of Fig. 2 were made at a level of illumination below cone threshold. At higher levels of illumination the test field became visible to cones, but even then it was easy to explore rod flicker sensitivity because only rods can see the *discontinuity* between the bleached annulus and the spared window. At high levels of illumination the flicker seen by cones makes it subjectively difficult to set rod thresholds upon blue backgrounds, so although the logic of our technique does not require it, we generally employed a red background to reduce the photopic visibility of the flickering test, when using higher levels of illumination. Figure 3 shows that at levels of illumination above cone threshold rod sensitivity to a flickering test with a stabilized edge (unfilled circles) was appreciably higher than when the same field was viewed normally (filled circles). The following experiments explore the generality of the paradoxical increase in sensitivity shown in Figs 2 and 3 and attempt to elucidate its mechanism.

*Is the paradoxical increase in sensitivity an edge effect?*

One possibility suggested by our observations on criteria for threshold is that the time-modulated signal elicited by the flicker is in normal viewing counteracted by the effects of random signals that are

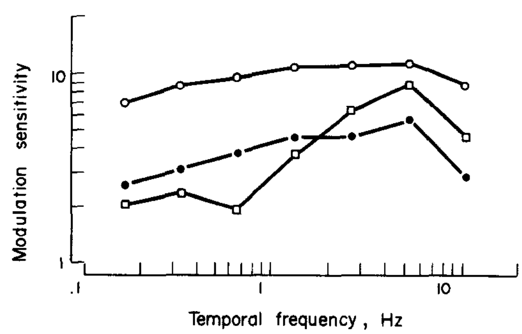


Fig. 3. Modulation sensitivity of rods measured with fields visible to cones. Test and background fields both 483 nm, mean illumination 20 scot. td. Unfilled circles: 9.1 deg dia test and background fields superimposed upon bleached annulus (inner dia 5.3 deg, outer dia 11.8 deg) that rendered invisible all but a 5.3 deg disc with a stabilized edge. Filled circles: test and background fields 5.3 deg dia, viewed without bleached annulus. Squares: test and background fields both 9.1 deg dia, with an annular bleach to confine the rod-visible field to 5.3 deg. A dark annular ring (inner dia 5.3 deg, outer dia 5.8 deg) fell across the inner edge of the bleached annulus. Observer P.L.

created at the edge of the test field by small eye-movements. Several simple controls bear upon this possibility.

*Addition of an edge inside the bleached boundary.* If the stabilized edge is critical, we ought to be able to reproduce the results obtained in normal viewing by making measurements under stabilized conditions (as above) but with the addition to the test beam of a thin opaque unstabilized ring (inner dia just less than 5.3 deg, outer dia 5.8 deg) that covers the inner edge of the bleached annulus.

This procedure had a substantial effect both upon the appearance of the test field and upon the subjective difficulty of setting threshold. After the cones had recovered from the bleach sufficiently for the background to appear uniform, the display appeared as if a bleach had never been given, and the observer found it correspondingly difficult to set thresholds.

The addition of the dark ring changed modulation sensitivity commensurately with the appearance of the fields: the open squares in Fig. 2a show that sensitivity to low temporal frequencies was substantially lower than it had been in the stabilized condition. Results of the same experiments undertaken at a higher level of illumination are shown by the unfilled squares in Fig. 3. In a variant of this experiment the ring was withdrawn, the diameter of the flickering disc (and background) was set to 5.3 deg, and the inner diameter of the bleach was fixed at 5.5 deg, so leaving an unbleached ring approx. 5 min wide enclosing the patch. The unfilled squares in Fig. 2b show modulation sensitivity measured under this condition. Except at the very lowest temporal frequency, sensitivity was as if the patch had been viewed normally, without the bleached annulus. The slightly higher sensitivity for the lowest frequency may be the result of eye-movements bringing the disc on to the bleached area, and thus producing a partially stabilized image.

*Sensitizing effects of large backgrounds?*

The bleached surround clearly enhances sensitivity to low frequency flicker. In the following experiments we consider whether it merely produces some sensitizing effect that could equally well be brought about by an annulus of steady light.

In the first experiment, the test field was 5.3 deg in diameter and was viewed normally against a larger uniform background, 8 deg in diameter, that also was viewed either normally, or with its boundary defined by the inner edge of a bleached annulus. Modulation sensitivity curves obtained under these conditions, and under the conditions used previously (Fig. 2), are shown in Fig. 4. Unfilled and filled circles show, respectively, sensitivities for BWS and normal viewing, as in Fig. 2. Enlargement of the background (filled squares) abolishes the sharp loss of low-frequency sensitivity found when coextensive test and background fields are viewed normally (an observation first reported by Kelly, 1959) and impairs sensitivity

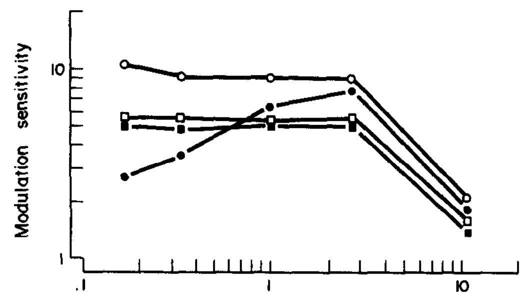


Fig. 4. Effect of background size upon modulation sensitivity. Unfilled and filled circles show bleach-stabilized surround and control conditions, as for Fig. 2B. Filled squares: 5.3 deg test field (483 nm) superimposed upon an 8 deg dia background (483 nm) viewed normally. Unfilled squares: same as filled squares except that outer edge of background now falls on an annular bleached area (inner dia 6.4 deg, outer dia 11.8 deg). Between-sessions standard errors were about 0.03 log units. Mean illumination 0.3 scot. td. Observer D.M.

to high frequencies. It clearly does not affect sensitivity in the same way as does a bleached stabilized surround. Stabilizing the border of the background (unfilled squares) improves sensitivity marginally, if at all, and certainly not by an amount comparable to that obtained in the BWS condition we have used so far. The results in Fig. 4 were obtained from observer D.M. Similar results were obtained from M.H.

The "equivalent background luminance" of the bleached annulus used in our BWS condition was, during the time measurements were being made, substantially higher than the background illumination used in the experiment of Fig. 4. It is therefore possible that any sizeable sensitizing effect depends upon the annular region being substantially brighter than the coextensive background. We checked this, for D.M., in an experiment where the coextensive test and background fields (viewed normally) were enclosed by a 658 nm annulus (inner dia 5.3 deg, outer dia 8.0 deg) at a at a luminance of 13 scot. td (1.64 log units above the background), which was "equivalent" to the bleached annulus at 5 or 6 min after the bleach. At all temporal frequencies sensitivity was lower than for normal viewing, and more than 0.6 log units lower than sensitivity in the corresponding BWS condition.

*Is the paradoxical increase in sensitivity an artefact of bleaching?*

The bleached surround clearly affects low-frequency sensitivity in a way that real light does not, so the question arises whether some special lateral sensitizing influence spreads from the bleached region. Our "ring" experiment (Fig. 2) suggests not, but we have examined this possibility in an experiment on Troxler fading through voluntary fixation. Persistent steady fixation leads to the sporadic fading of peripherally viewed targets. Using the usual test and background fields (normally viewed), D.M. made measurements of flicker sensitivity by finding the modulation required to revive the field after it had been caused to fade by steady fixation. Using a temporal frequency of 0.33 Hz, sensitivity was 0.23 ± 0.066 SEM higher during this condition than when the measurements were made with the fields initially visible.

*Is the paradoxical increase in sensitivity peculiar to rod vision?*

We were able to use the BW technique to measure the flicker sensitivity of the cone system during the first few minutes after a bleach. For about the first 30 sec following a bleach the threshold for flicker in the window falls very rapidly as the cones there recover their full sensitivity. Threshold then remains stable for about a minute before rising rapidly as the spared area becomes progressively more difficult to distinguish from the larger surrounding region where cones are recovering. The rise in threshold continues until the modulation in the spared area is sufficient to make it visible to rods. Figure 5 shows curves of modulation sensitivity of the cone system obtained with the stabilized field (unfilled circles; measurements made during the period when threshold was stable) and when viewed normally, with the background and test coextensive and the same diameter (5.3 deg) as the window (filled circles), or with the 5.3 deg test superimposed upon a background 9.1 deg in diameter (unfilled squares). As was the case for flicker detected by rods, low-frequency sensitivity to the field with the stabilized edge is appreciably greater than sensitivity to a field viewed normally.

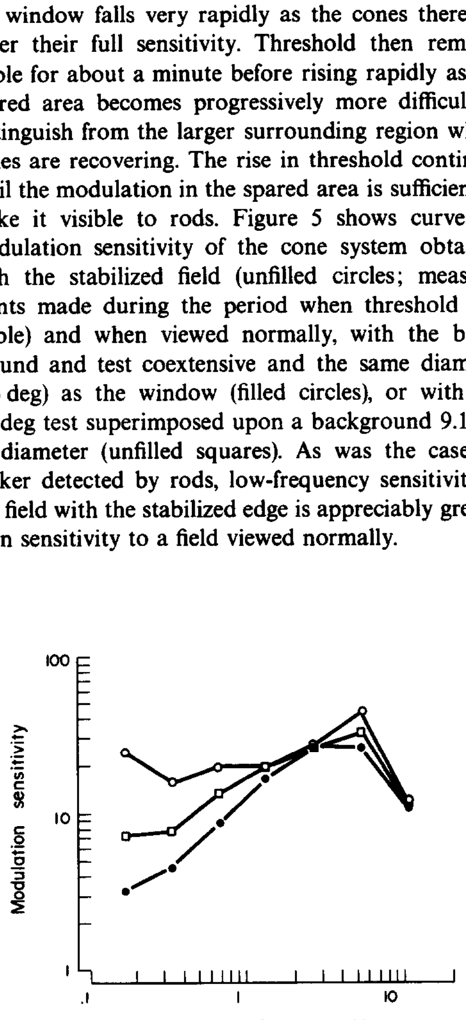


Fig. 5. Modulation sensitivity in cone vision. Test and background fields both 483 nm, mean illumination 1.5 phot. td. Open circles: 9.1 deg dia test and background fields superimposed upon a bleached annulus (inner dia 5.3 deg, outer dia 11.8 deg) that reduced the visible field to a 5.3 deg disc with a stabilized edge. Filled circles: test and background fields both 5.3 deg dia, viewed without bleached annulus. Squares: test field 5.3 deg dia superimposed on a uniform background 9.1 deg dia. Between-sessions standard errors less than 0.08 log units. Observer P.L.

## DISCUSSION

*An effect of stabilization or of bleaching?*

The unexpected improvement in sensitivity by up to 0.5 log units in the BWS condition is our main result. How can we explain it? If the critical thing about the surround bleach is that it stabilizes the retinal boundary of the stimulated region this would be the only known instance of a substantial *improvement* in sensitivity with stabilization of the retinal image. The improvement could occur if sensitivity in normal vision is significantly impaired because of masking by the transient excitation that results from eye-movements. The alternative interpretation that needs to be considered is that a sustained signal is emitted by the insensitive surrounding rods as a consequence of their having been bleached (Penn and Hagins, 1972). The persisting signal due to the bleach might interact with signals from the center in some way so that modulation sensitivity is enhanced. This kind of lateral interaction may well have an influence on sensitivity in the BWS condition, but there are a number of reasons for suspecting that it is not a critical one.

First, the improvement in sensitivity due to surround bleaching could be prevented by preserving a ring of sensitive retina only 5′ wide around the 5.3 deg illuminated test region (Fig. 2). Moreover observers reported the same difficulty in setting threshold in this "thin ring" condition as in normal viewing, in contrast to the ease of making settings in the BWS condition. The critical importance of this narrow zone around the border of the test region is to be expected if the surround bleach improves sensitivity by abolishing signals generated by eye movements, since fixational eye movements are of such small amplitude (Ditchburn, 1974, p. 98) that the 5′ margin would be enough to make the bleach ineffective in this respect. The result is hard to explain on a lateral interaction hypothesis, however, because "sensitizing" interactions observed at this retinal eccentricity in rod vision extend over a radius many times greater than 5′ (Westheimer, 1965). Second, though lateral interactions of appropriate polarity (albeit of inappropriate spatial range) may occur in steady state light adaptation (and comparison of the filled circles and unfilled squares in Fig. 4 provides an example of this in the low frequency range), no such effects have been reported when surrounding rods are bleached rather than illuminated. On the contrary, numerous studies (e.g. Westheimer, 1968; Hayhoe, 1979a) have shown that bleaching of surrounding rods does not affect incremental sensitivity to flashed test stimuli. The different behaviours of bleaches and backgrounds with respect to sensitization has strengthened suspicion that the rod vision phenomena ascribed to lateral interactions may themselves be due to masking by transients evoked by eye movements (Lennie and MacLeod, 1973; Hayhoe, 1979b). Third, even if it were true that backgrounds and bleaches are equivalent with respect to lateral interaction, the equivalent background intensities for the bleached surrounds in our experiments were initially extremely high relative to the intensity of the test field and they decrease enormously as recovery progresses, yet sensitivity is stable during the recovery period until the unstabilized contour of the test field becomes visible.

Despite these arguments we cannot rule out a role for lateral interaction, especially because our results with "pure" stabilization of the retinal image and with Troxler fading have been inconclusive, showing smaller improvements in sensitivity than BWS (but with imperfect stabilization). Keesey (1970) found no difference in flicker sensitivity when the retinal image was stabilized, but she worked with cone vision and did not examine the very low frequencies where our BWS improvement in sensitivity was largest; and perhaps infrequent but probably inevitable disruptions of stabilization by blinks or large eye movements could obscure an effect at very low modulation frequencies.

Further evidence on the role of lateral interactions is obviously desirable but it seems clear that at least some of the effect must be attributed to stabilization *per se*.

*Speculations about mechanism*

Stabilization could benefit sensitivity in either of two related ways. One is by removing variability or "noise" generated by more or less random fixational eye movements. With normal steady fixation a test field tends to fade from view due to Troxler's effect, but fixational eye movements sporadically revive it so that its apparent brightness fluctuates. Externally imposed intensity modulation (especially modulation at low frequencies) might be more difficult to discern against such a variable baseline. A related hypothesis might invoke a compressively nonlinear response to increased input in cells sensitive to changes in intensity produced either by modulation of the test stimulus or by eye movements. When eye movements elevate the baseline firing rate in such cells (whether or not they also add variability), the modulation of the test stimulus would be less effective in exciting them.

To determine the physiological locus of the effect an obvious approach would be to deliver the test stimulus and the steady adapting field to different eyes. Such experiments were done by Lipkin (1962a, b) who found that the presence of a normally viewed steady field in one eye could greatly reduce sensitivity to slow flicker in the other eye. This could mean that the masking process invoked here operates after the convergence of signals from the two eyes, but it may only reflect binocular rivalry effects absent in the monocular situation.

The elimination of low frequency attenuation by enlarging the steady background with normal viewing (Fig. 4) is suggestive of a sensitizing lateral interaction that may be independent of eye movement transients. The fact that the effect occurs only at low frequencies suggests a different mechanism from that of the sensitization effect observed with brief flashes. As MacLeod (1974, Chap. 8) suggests, a retinal grain control might reduce sensitivity to slow intensity modulation by compensating for intensity changes, as they occur, with a reciprocal adjustment of sensitivity. However, in cells with receptive fields near the border of the test field, adding a steady light in the surround would tend to prevent this loss of sensitivity by holding the gain relatively constant. This hypothesis requires only that there be some temporal and spatial integration (not necessarily any centre-surround antagonism) in the control of sensitivity*.

Leaving specific conjectural explanations aside, it is clear that conditions near the border of the test patch are critical for sensitivity. This is most clearly revealed by the "thin ring" experiments. Also relevant is the fact that the surround effect was as great for large test fields as for smaller ones. Since cells with receptive fields in the middle of the 5.3 deg test patch would be little affected by conditions at its border, the cells critical for modulation sensitivity must be the ones with receptive fields near the edge of the patch, a conclusion urged by Lennie (1979) on the basis of light adapted ganglion cell behaviour.

*Dynamics of fading*

The unexpected improvement in sensitivity in the BWS condition invalidates this experiment in its originally intended role as a quantitative indicator of the dynamics of the fading process, but the high sensitivity observed in the BWS condition down to 0.17 Hz suggests that the fading process is not rapid enough to track this or higher frequencies efficiently. This is quite consistent with the integration time of 2.5 sec proposed by King-Smith *et al.* (1977) which would predict that modulation sensitivity would be maintained down to frequencies as low as 0.067 Hz (at which frequency an RC differentiator with a 2.5 sec integration time would attenuate output amplitude by only 0.15 log units). The dynamics of such a fading process would assert themselves mainly at still lower frequencies, where measurements of modulation sensitivity are extremely difficult.

*Acknowledgement*—This work was supported by NIH Grant EY 01711.

*There is little to indicate what spatial properties such a process might have, or whether or not bleaches and backgrounds could be expected to act equivalently on it. Most of the arguments raised against lateral interaction earlier in the Discussion are therefore not applicable to this conjectured form of it. It should be noted however that even if surround bleaching does produce, by lateral interaction, as much sensitization as was observed by enlarging the background, there still remains in the BWS condition an additional improvement in sensitivity most reasonably explained in terms of masking by eye movement transients.

## REFERENCES

Barlow H. B. and Sparrock J. M. B. (1964) The Role of afterimages in dark adaptation. *Science* **144**, 1309–1314.

Ditchburn R. W. (1973) *Eye movements and visual perception.* Clarendon Press, Oxford.

Hayhoe M. M. (1979a) Lateral interactions in human cone dark adaptation. *J. Physiol.* **296,** 125–140.

Hayhoe M. M. (1979b) After-effects of small adapting fields. *J. Physiol.* **296,** 141–158.

Keesey U. T. (1970) Variables determining flicker sensitivity in small fields. *J. opt. Soc. Am.* **60,** 390–398.

Kelly D. H. (1959) Effects of sharp edges in a flickering field. *J. opt. Soc. Am.* **49,** 730–732.

King-Smith P. E., Riggs L. A., Moore R. K. and Butler T. W. (1977) Temporal properties of the human visual nervous system. *Vision Res.* **17,** 1101–1106.

Lennie P. (1979) Scotopic increment thresholds in retinal ganglion cells. *Vision Res.* **19,** 425–430.

Lennie P. and MacLeod D. I. A. (1973) Background configuration and rod threshold. *J. Physiol.* **233,** 143–156.

Lipkin B. S. (1962a) Monocular flicker discrimination as a function of the luminance and area of a contralateral steady light. I. Luminance. *J. opt. Soc. Am.* **52,** 1287–1295.

Lipkin B. S. (1962b) Monocular flicker discrimination as a function of the luminance and area of a contralateral steady light. II. Area. *J. opt. Soc. Am.* **52,** 1296–1300.

MacLeod D. I. A. (1974) Signals from rods and cones. PhD Thesis, University of Cambridge.

Penn R. D. and Hagins W. A. (1972) Kinetics of the photocurrent of retinal rods. *Biophys. J.* **12,** 1073–1094.

Westheimer G. (1965) Spatial interaction in the human retina during scotopic vision. *J. Physiol.* **181,** 881–894.

Westheimer G. (1968) Bleached rhodopsin and retinal interaction. *J. Physiol.* **195,** 97–105.