

adjacent rhodopsin molecules, or between rhodopsin and other membrane proteins present in much smaller amounts. Such cooperative interactions could be involved in either of the two mechanisms currently suggested to account for visual excitation: that light causes an increase in the resistance of the outer segment membrane system, or that light activates an electrogenic pump which utilizes metabolic energy to move ions across the membrane¹⁶. If the 10^7 – 10^9 rhodopsin molecules present in an outer segment's membrane system were equally involved in maintaining its resistance to an observed dark current of approximately one to two cations/rhodopsin/second¹⁷, then the alteration of just one of these molecules by photoexcitation could not cause the net movement of 10^5 cations within milliseconds, which Penn and Hagins have observed in rat outer segments¹⁷. Any change in resistance would have to be a cooperative phenomenon, with the excited rhodopsin molecule influencing adjacent areas of the photoreceptor membrane. Activation of an electrogenic pump, unless the pump were rhodopsin itself, would also require cooperative interaction between rhodopsin and the presumed pump molecules. Sodium-potassium activated adenosine triphosphatase activity in outer segments, which might be involved in active ion movements, is not greater than 10^{-1} moles ATP hydrolysed/mole rhodopsin/minute (D. B., in preparation), and no effect of illumination has been observed on this activity.

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Interocular Transfer of Suppressive Effects of Retinal Image Displacement

WHEN the retinal image of the visual field is suddenly displaced by a saccadic eye movement, perceptual sensitivity to a weak test flash at the time of displacement is reduced. Flashes presented from 40 ms before until at least 100 ms after the displacement may be affected. I have discovered¹ that visibility is similarly reduced when the visual field is displaced as a whole before a stationary (fixating) eye. This throws doubt on the idea that either oculomotor activity² or mechanical acceleration of the eyeball³ is required to account for such effects. It suggests

rather that the surge of neural activity caused by the rapid displacement of the retinal image has side-effects that interfere with processing of the signals generated by the test flash, and so raise the perceptual threshold¹.

If such interference between the two signals took place only at the retina or in the early stages of the visual pathway before signals from the two eyes were combined, then with dichoptic presentation, exposing only one eye to the moving visual field and presenting the test flash to the other, one might expect to find no corresponding suppressive effects. A reduction of visibility in these circumstances would imply that the interference had a more central origin.

I have now found that interference is not abolished when the two stimuli are presented dichoptically. On the contrary, the frequency of seeing drops quite as convincingly as when both the flash and the moving field were presented to the same eye; and once again the time range over which flash visibility is reduced begins about 40 ms before onset of displacement of the field presented to the other eye.

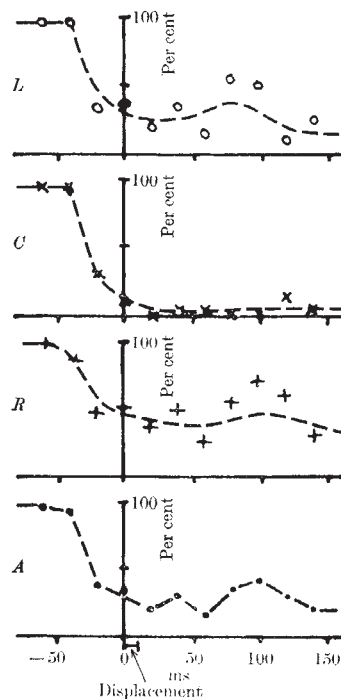


Fig. 1. Typical frequency-of-seeing curves for fixation to left (L), right (R) and on centre (C) of test spot. Abscissa shows time from onset of image displacement in right eye to onset of test flash to left eye. Average for L, R, C combined is shown at A.

The same sizes and dispositions of field and test spot were used as in the previous experiment¹; but the 2° test flash, now controllable in duration, was presented via a mirror to the subject's left eye only. The right eye viewed the 10° circular field, which was displaced by 4° in 10 ms from right to left about the time of each flash, at intervals of 1 s, returning 0.5 s later. Both eyes viewed a fixation field of three luminous red dots, optically superposed via a semitransparent mirror. The dots formed a horizontal row, their separation being equal to the diameter of the test spot. The subject was instructed to fixate each dot in turn in a pseudo-random order, so as to reduce the effects of retinal adaptation in the eye exposed to the faint test flash.

The time interval between flash and field displacement was also varied at random, and the frequency of seeing was calculated separately for each interval and fixation position. Typical results on a coarse time-scale are shown in Fig. 1, for the same subject as in the previous report¹.

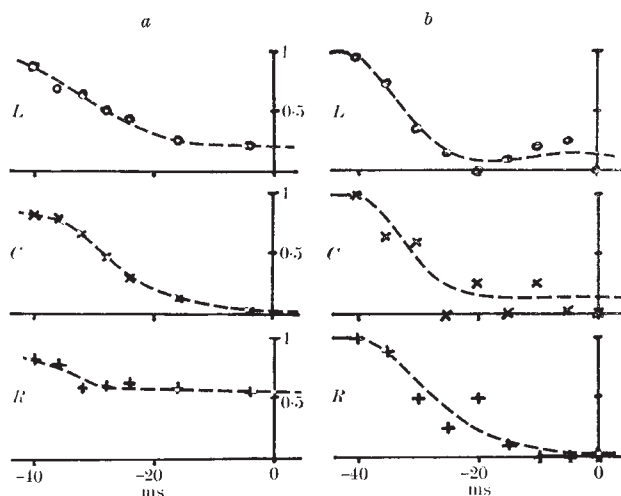


Fig. 2. *a*, Cumulative frequency-of-seeing curves for five experiments, expanded time-scale, dichoptic condition. Notation as in Fig. 1. *b*, Corresponding curves obtained when both stimuli were presented to both eyes (see ref. 1).

The drop from 100 per cent in the neighbourhood of -40 ms (that is, when the flash occurred 40 ms before displacement) is marked in every case. The detailed form of the curves in the region from -40 to 0 ms was explored in a separate series of experiments, spread over 5 successive days. The general features (though not the mean sensitivity level) were remarkably consistent from day to day, and the cumulative results shown in Fig. 2*a* are typical.

The sensitivity curves with dichoptic presentation are very similar in form and timing to those obtained when the same eye viewed both stimuli¹. For ease of comparison, the curves of Fig. 3 in ref. 1 are re-drawn as Fig. 2*b*, on the same scale. The maximum elevation of threshold measured was of the order of 3 dB; but to avoid unduly prolonging experiments this measurement was made only in a few typical cases. It should be noted that any tendency to interocular rivalry would have had the effect of raising the "threshold" as statistically defined, quite apart from the interference between signals from the two stimuli, which is our present concern.

Significant differences were found between results for different fixation points. Visibility was lowest overall with foveal presentation of the test spot (curve *C*). This is to be expected, for the left eye is in scotopic condition (see below). More interesting is the marked and consistent contrast between response frequencies with fixation left (*L*) and right (*R*) of the test flash. Subjects reported the flash to be "much easier to see" when presented to the left of the fixation point.

In control tests with the moving field occluded, no comparable asymmetry was found between the thresholds with *L* and *R* fixation. In a total of 123 trials, using a flash duration close to scotopic threshold, the frequencies of seeing were 0.7(8), 0.7(7) and 0.1 with fixation on left, right and centre respectively. This confirms that the difference in scotopic sensitivity between extra-foveal and foveal areas is more than enough to account for the difference between curves *L* and *C* in Fig. 2; indeed, it suggests that the interference effects may be stronger with fixation on *L* than with central fixation. It also, however, shows clearly that the difference between curves *R* and *L* cannot be put down to a bias in scotopic sensitivity.

It remains to be seen whether this difference reflects a weakening of the interference process, or whether a flash in the left half-field of the left eye is "helped over the threshold" at some central stage by the breakthrough of signals from the corresponding half-field of the right eye. Because the area of the right eye-field actually corresponding to that of the test flash in the left eye does not change

in luminance (the 10° field is displaced by only 4°), it seems more likely that it is the asymmetry of the disturbance caused by the displacement which accounts for the bias in favour of signals from the left half-field.

In any case, the results suggest that the effects of a moving field on the visibility of a test flash depend mainly on central rather than purely peripheral physiological interactions.

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Effect of Presenting Novel Verbal Material during Slow-wave Sleep

THE topic of sleep learning has come increasingly to the fore during the past decade, partly because of the considerable scientific interest that has been shown in the Soviet Union, where a number of unusual claims have been made¹⁻³, and also because of the growing commercial interest in marketing devices designed to enable individuals to make use of the supposedly "waste periods" of sleep by storing useful, if perhaps dull and repetitive, material while in a state of unconsciousness. In principle the idea is attractive, but it depends on at least two assumptions: (1) that during sleep no other important process is taking place which would be disrupted by input of data; (2) that it is indeed possible for the brain to store (and subsequently extract) information fed in during those periods of sleep known as levels *C* to *E*⁴, during which consciousness is generally believed to be absent. The function of sleep is still largely not understood, but present evidence suggests that important information processing may be taking place at frequent periods throughout the night. Experimental evidence for the second assumption is contradictory⁵⁻⁷ and often obscure. Fox and Robbin⁵, for example, seem to have obtained clear-cut evidence for "sleep learning" (of Chinese-English equivalents) but their experiment is open to criticism because the subjects were not actually observed while the material was being fed in and it is possible that the learning took place when the subjects were at least partially awake.

It is now generally agreed that there is no reliable way of monitoring the state of sleep other than by the use of the electroencephalogram (EEG). This precaution was taken by Emmons and Simon^{6,7} in their series of experiments, and the result was a clear correlation between fall in cerebral vigilance and fall in the amount of retention or learning as indicated by subsequent recall and recognition tests. For example, with the exception of those cases where the subject had been drowsy and immediately aroused by the signals, subjects who had had words repeatedly played to them during sleep showed no evidence of recall and were no better than control subjects in selecting the test words from a list of fifty. Although the experimental techniques were more satisfactory in the Emmons and Simon study, it is still possible to raise objections on the grounds of inadequate control. For example, in each experiment the tests of recall or recognition were carried out the next day. It is therefore possible to argue that learning might have taken place during the sleep presentations but have been vitiated by the retroactive interference effect of experiences intervening between presentation and test.