# Elevation of Visual Threshold by Displacement of Retinal Image

THERE have been many reports that the threshold for perception of a test flash is raised during a saccadic eye movement[1-4]. Even with a flash brief enough to eliminate any blurring of its retinal image during the saccade, an elevation of threshold by half a log unit is common[3], although there have been significant exceptions[5]. Of particular interest is the finding that this reduction in visibility may apply to flashes occurring as much as 40 ms before the onset of a saccade. Not unnaturally, this has been widely interpreted as evidence of some central inhibitory process, set in motion as part of the preparation of a voluntary eye movement.

An ingenious alternative advanced recently by Richards[6] attributes the inhibition to mechanical strains set up in the retinal layers by the rapid acceleration suffered during a saccade. To support this hypothesis he has shown that a similar reduction in sensitivity can be brought about by externally imposed impulsive rotations of the eyeball; and has argued that signals arriving at the receptors 40 ms before acceleration might still be in transit at the ganglion cell layer when it suffered the mechanical insult.

My purpose is to report evidence in favour of a third possibility that seems to have been overlooked. The displacement of the retinal image that occurs during a saccade is itself something of an insult to the dynamic balance of the visual nervous system. Could not the ripples of neural disturbance set up by such sudden displacements be sufficient to account for any observed reduction in sensitivity to transient signals, including those generated earlier but still in course of analysis when the disturbance arrives centrally? If so, a similar elevation of threshold should be found with the eye held stationary and the visual field displaced in saccadic fashion. The experiments described here have shown that it is, and that its time course closely parallels that found with active saccades.

The stimulus display was chosen to be fairly typical of those used by other investigators such as Richards[6]. On a projection screen 1 m in front of the subject, a uniformly illuminated area $A$, 18 cm (10°) in diameter and 1 log foot Lambert in luminance, can be rapidly displaced from position $X$ to position $Y$ by an electronically controlled mirror system in the light path of a projector. The subject fixates a black dot $F$ subtending 15 minutes of arc, and tries to detect a superimposed test flash that illuminates a circular area 3·5 cm (2°) in diameter and lasts for less than 100 ms. The flash intensity was adjusted in each of the conditions to be described so as to allow the frequency of seeing to range between 0 and 1.
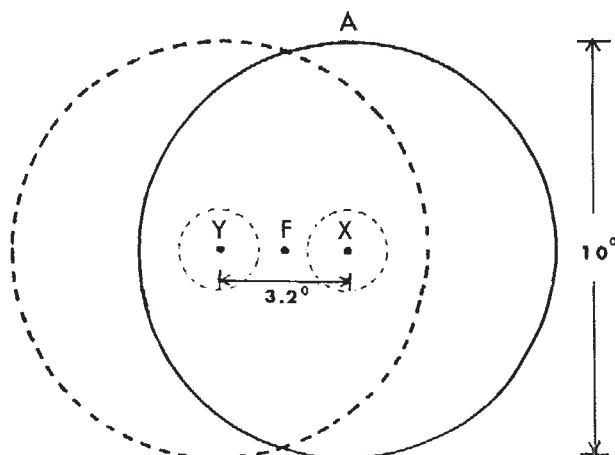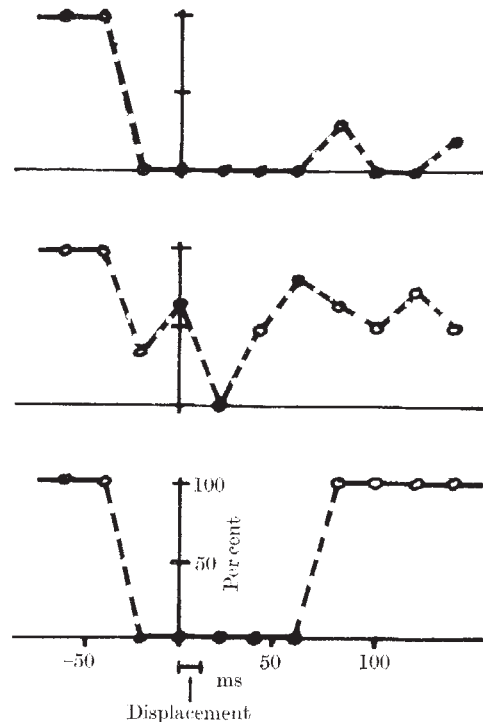


Fig. 2. Frequency-of-seeing curves with fixation at $F$, and flash stationary at $X$ (upper curve) $F$ (middle curve) and $Y$ (lower curve). Time origin at onset of displacement.

In the first group of experiments the test flash was presented, at regular intervals of 1 s, in a fixed position relative to the fixation point $F$. The circular adapting field $A$ was displaced by 5·5 cm from right to left at about the time of each flash, the interval from flash to onset of motion being varied at random between +60 and −120 ms. Displacement was complete approximately 10 ms after onset. In this condition (with a stationary eye) the retinal image sequence is similar to that produced by a saccadic rotation of the eye when the adapting field is stationary but the test flash is moved with the eye so as to maintain its retinal position.

Flashes were presented in three different positions in successive experiments: (1a) to the right of $F$, (1b) centred on $F$ and (1c) to the left of $F$. Results for a typical subject are shown in Fig. 2. In each case a clear-cut drop in frequency of seeing began between 20 and 40 ms before the onset of displacement of $A$. In (1a) the "suppression" effect was longer lasting than in (1c). This may have been because in (1a) the closer approach of the dark edge of $A$ created more disturbance than in (1c). For (1b) the flash fell on the central fovea and was more visible throughout; but the reduction of visibility was still marked and long lasting.

In each case the time course of onset of suppression was studied in more detail by repeating the experiment with a shorter range of time intervals, varied in 5 ms steps. Fig. 3 shows that there were no significant differences between the times of onset of the drop in frequency of seeing for (1a), (1b) or (1c): all were at about 40 ms before onset of displacement.

In a second group of experiments, the test flash was presented in a fixed position relative to the adapting field $A$ (actually at its centre) so that its retinal position varied in relation to that of the fixation point $F$ according to its time of occurrence. In this condition (with a stationary eye) the retinal image sequence is similar to that produced by a saccadic rotation of the eye when both the test flash and adapting field are fixed in position.
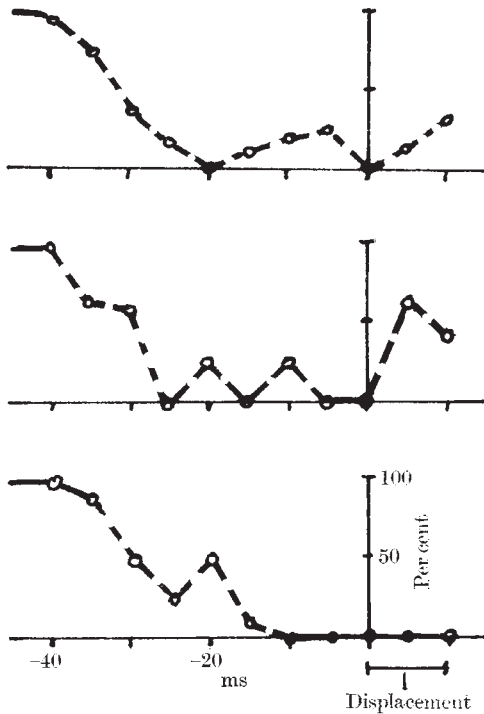


Fig. 1. Stimulus configuration (see text).

Fig. 3. Details of initial drop in frequency of seeing in similar conditions to those for Fig. 2.

In this case three different fixation points were used in successive experiments: (2a) at centre of test spot in position X, (2b) midway between positions X and Y and (2c) at the centre of the test spot in position Y. Results are shown in Fig. 4. Again there was a clear-cut drop in frequency of seeing at or before the onset of displacement, which persisted for 40–80 ms. Because of the time that elapsed between experiments 1 and 2, too much significance should not be attached to a detailed comparison with the curves of Fig. 2. A small increase in flash intensity (by approximately 0·1 log units) yielded the dotted curve of Fig. 4, showing that the degree and range of suppression depend critically on relative intensities as well as on the condition of the subject. Further experiments, in which the subject will adjust the intensity of the flash for visibility, are in progress to determine finer details of the time course of suppression. For our present purpose it is sufficient that there was retrospective suppression in both conditions. In other words, the phenomenon is not simply the consequence of a change in location of test flash relative to adapting field, as in condition (1).

Repeat runs in condition (2) with an expanded time scale showed that here also the onset of suppression was quite rapid, the frequency of seeing decreasing from 100 per cent to zero in 10 ms.

Because natural saccades may take as long as 40 ms, experiments (1a), (1b), (1c) and (2b) were repeated with the transition time from X to Y increased to 40 ms. Results were quite similar, except that the shoulders of the visibility curve were less steep. The responses for (1b) (flash centred on F), however, revealed a strikingly consistent recovery of sensitivity for flashes occurring between +20 and +60 ms after onset of motion, flanked by regions of complete invisibility from −40 ms to +20 ms and from +60 ms to +120 ms or so (Fig. 5). Increasing the displacement of the adapting field also enhanced suppression. Further experiments on the effects of the speed and magnitude of image motion will be reported separately.

It seems clear from these results that the displacement of the retinal image during a saccade can in some cases

produce suppressive effects without any assistance by postulated corollaries of the activation of eye muscles or mechanical shearing of the retina. This is not to deny that these other agencies might also operate, but only to question to what extent existing evidence requires us to invoke them. The range of suppression typically reported with natural or imposed eye movement (40–60 ms before saccade to 80 ms after) is so similar to that found here as to suggest that similar processes are at work in all three cases. Obviously any suppression found during eye movements in total darkness could not be attributed to the same cause as that reported here; but it may be significant that in at least one case where saccadic suppression was absent or undetected, the background was dark[5]. Most investigators seem to have used adapting fields or illuminated fixation marks which would generate considerable transient signals on the occurrence of saccadic motion. One possible linking hypothesis is that the motion of contours over the retina generates a disturbance in the input to the comparator of the servo system that normally maintains fixation by feedback to the eye muscles. If natural saccades originate in this same system, the central factor common to all three cases of suppression would be a disturbance of the oculomotor comparator, which could be supposed to lead to an increase in internal background activity and consequent failure to detect weak signals.

The difference found between results with foveal and parafoveal presentation of the test flash brings out a
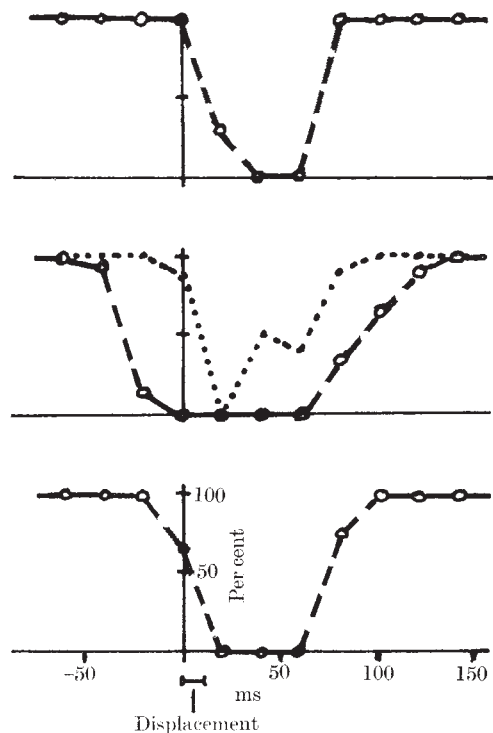


Fig. 4. Frequency-of-seeing curves for test flash locked at centre of moving field A, with fixation at X (upper curve), F (middle curve) and Y (lower curve).
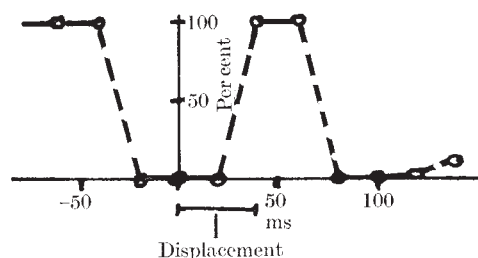


Fig. 5. Anomalous "rebound" of visibility in condition (1b) but with transit time from X to Y increased to 40 ms.

further complication in interpreting the results of experiments on visibility during large saccades. Where changes in relative timing of flash and saccade affect the retinal position of the flash, the effects of flash position (shown in Fig. 2) will be confounded with those of relative timing as such. In trying to correlate experiments on saccadic suppression, the spatial relation of the flash not only to the fovea but also to any background features of the field may be a crucial factor.

It is tempting to link these results with the finding[7] that the acceleration of a previously stationary retinal image gives rise in man to an evoked occipital potential which is characteristically biphasic, and comparable in strength with that evoked by a bright flash of light. The suppressive effects of a bright flash are well known[8,9], and so it may not be unreasonable to expect other transient stimuli that produce large cortical evoked potentials to have similar side effects. This hypothesis is further strengthened by the recent discovery by Wurtz[10] that certain units in the monkey visual cortex show a "suppression response" to rapid displacement of a textured stimulus before a stationary eye. It will be interesting to discover whether any periodicities in the time course of the human visual threshold are mirrored in the occipital potential evoked by image displacement.

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## Electrophysiological Correlate of Binocular Depth Perception in Man

It is known that within the visual pathway of the brains of anaesthetized animals single units can be found which respond optimally when both eyes are simultaneously stimulated with light[1-3]. The characteristics of such binocular units are consistent with psychophysically observed features of binocular depth perception[4-6]. At present, human subjects have important advantages over animals in studies of stereopsis because with human subjects the critical binocular fusion and subjective reports of depth perception can easily be obtained. With human subjects, however, any electrophysiological information must be obtained by the analysis of scalp evoked potentials (EPs). This communication reports the finding of an EP correlate of binocular depth perception in man.

A perception of depth can result when one eye views a random pattern (for example, of small squares or dots), and the other eye views a second pattern which is identical with the first, except that a region has been bodily displaced to one side[7,8]. With binocular fusion, the displaced region appears to be located either in front or behind the rest of the pattern, and this illusion is often very striking. We used such patterns for the simplification afforded by the absence of familiar shapes or of any other clues for depth perception other than binocular retinal disparity.

Three projectors, matched for brightness, threw images of the above patterns onto a screen placed 4 m in front of
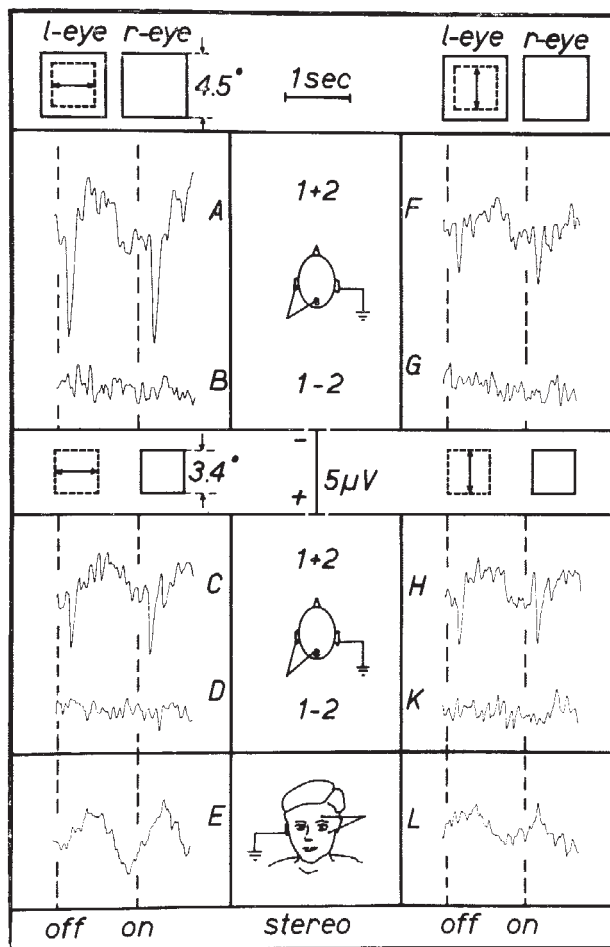


Fig. 1. Scalp potentials evoked by stereoscopic stimuli and control stimuli. The right eye viewed a static random pattern of small black and white squares. The left eye alternately viewed a pattern identical to that viewed by the right eye, and a pattern in which the central region had been bodily shifted a short distance to one side (dotted line at top of figure). The alternation frequency was 0·45 per s. In these conditions the central dotted area appeared to jump rhythmically forward out of the plane of the paper and then return. A, Potential evoked when retinal disparity of central area changed horizontally and gave rise to a stereoscopic percept (1 and 2 are two separate sessions of 200 counts); B, difference 1–2 showing variability and noise; F, as A except that the retinal disparity now changed vertically and no stereoscopic perception resulted; this is a typical response. It was sometimes possible to align the movement relative to the head so that responses were very small and the response to appearance of depth was near noise level; G, difference between responses to two sets of 200 stimulus repetitions showing variability and noise for a constant stimulus alignment. Lower half of the figure shows responses to displacements of the retinal image similar to the displacements used in the upper half of the figure, but with the stationary border of the field removed by placing black velvet on the screen so that there was no stereoscopic perception; C and H show that similar potentials were evoked by horizontal and vertical displacements of the retinal image; D and K, differences showing variability and noise; E and L, electro-oculograms recorded 4 cm from the centre of the eye showing none of the characteristic brisk responses in A, F, C or H. EEG amplifiers 0·1–200 per s (−3 dB). Stimulus repetition frequency 0·45 per s; 2 s sweep; electrode 3 cm above midline, left earlobe reference. Electrodes 3 or 5 cm to left or right of midline electrode and on vertex showed similar but smaller responses; total angular subtense of stimulus 4·5°; angular subtense of central area 3·4°. Brightness of light areas 0·4 log foot lamberts.

the subject. A fixation mark was located at the centre of the screen. Projectors 1 and 3 carried the reference pattern, and projector 2 carried a pattern identical except for a central square which was displaced 2, 4 or 8 pattern elements (10′, 20′ and 40′). Shutters periodically cut off the light from projector 2 and simultaneously switched on projector 3, so that the left eye alternately viewed the reference pattern and the pattern with the displaced central region. Projector 1, viewed by the right eye, remained on throughout. By viewing through suitably orientated polaroids the subject had the illusion that a centrally located square abruptly changed in depth forward and back. This stimulus arrangement ensured that