Saccadic Suppression*†

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A shift of the peak of the Stiles–Crawford effect suggests that saccades shear the retina. This action appears to lead to an increase of the retinal activity of a real-light background. Thus, thresholds following a saccade are raised the most for test wavelengths which are most similar to the adapting-field wavelength. If the adapting field is eliminated, saccadic suppression is reduced. Saccades also affect the customary rises of thresholds found near the onset and extinction of the adapting field. This effect is as if the retinal feedback loop underlying adaptation is disrupted by the saccade.

INDEX HEADING: Vision.

Vision is generally impaired during rapid eye movements. This impairment, however, is not due entirely to optical smearing of the retinal image, for two reasons. First, the visual threshold has been shown to be altered for microsecond flashes[1,2] and, second, the maximal suppression effect often occurs just prior to the eye movement.[1–3] Thus, neural factors are apparently involved in the visual suppression associated with saccadic eye movements.

Because of the presence of elevated thresholds prior to the actual eye movement, most investigators have attributed the suppression effect to central factors.[2–4] For example, the expectancy of making an eye movement could lead to a central command coordinated with the command for eye movement, i.e., a "corollary discharge,"[5] which would attenuate the incoming

[1] P. L. Latour, Vision Res. 2, 261 (1962).
[2] B. L. Zuber and L. Stark, Exptl. Neurol. 16, 65 (1966).
[3] F. C. Volkmann, A. M. L. Schick, and L. A. Riggs, J. Opt. Soc. Am. 58, 562 (1968).
[4] P. L. Latour, "Cortical Control of Eye Movement," thesis, Institute for Perception RVO-TNO, Soesterberg, The Netherlands (1966).
[5] H.-L. Teuber, in *Handbook of Physiology, Vol. III, Neurophysiology*, J. Field, Ed. (American Physiological Society, Washington, D. C., 1960), p. 1595.

blurred visual signal arising during the actual eye movement.[6]

Recently, however, this view has been questioned by the observation that visual suppression may occur during passive eye movement.[7] Based upon this evidence, an alternate explanation of the suppression effect is proposed: that the origin of the effect is in the retina, which is disrupted as a consequence of the eye movement.[8] Because the neural effect of a light flash is still residing in the retina several tens of milliseconds following the flash, it is possible that an eye movement might affect the threshold for a flash delivered prior to the actual movement.

Consider the eye as a rigid sphere containing a gelatinous material. If this sphere is subjected to high rotary acceleration, then shearing forces will act with different magnitudes at different distances from the center of the sphere. Like a bowl of jelly suddenly made to rotate, in which the greatest forces occur at the wall of the container, the retina will be subject to shear. The shear in the neighborhood of the vitreous-scleral boundary might conceivably cause displacements within the retina itself which would lead to an increase of the threshold for detecting the neural signal arising from a light flash. In order to decide whether or not the retina might be sheared during eye movement, measurements of the Stiles–Crawford effect were made both before and following eye movements. Following an affirmative result, further experiments were performed which suggest that eye movement affects adaptation mechanisms in the retina.

APPARATUS

A two-channel maxwellian-view system (2-mm pupil) was used to provide the test and background fields, as shown in Fig. 1. An 11° diam adapting field was provided by a tungsten source (S_1) plus various Kodak Wratten filters (F). The 1° test field was formed
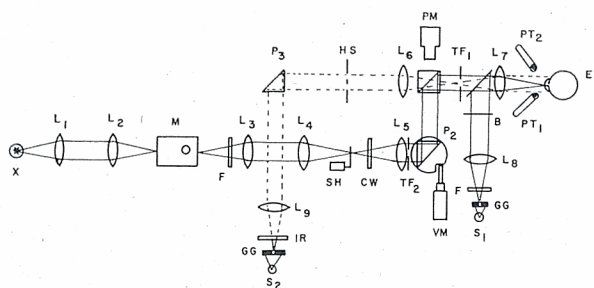

FIG. 1. Schematic diagram of the apparatus: B, background field; CW, circular wedge; E, eye; F, Wratten filter; GG, ground glass; HS, horizontal slit; IR, infrared filter; L, lens; M, monochromator; P, prism; PM, photomultiplier; PT, phototransistor; S, tungsten source; SH, shutter; TF, test-field stop; VM, vernier micrometer; X, xenon arc.

[6] E. B. Holt, Harvard Psychol. Stud. I, 3 (1903).
[7] W. Richards, J. Opt. Soc. Am. 58, 1159 (1968).
[8] Note also the phosphene of quick eye motion reported by B. Nebel, Arch. Ophthalmol. 58, 236 (1957).
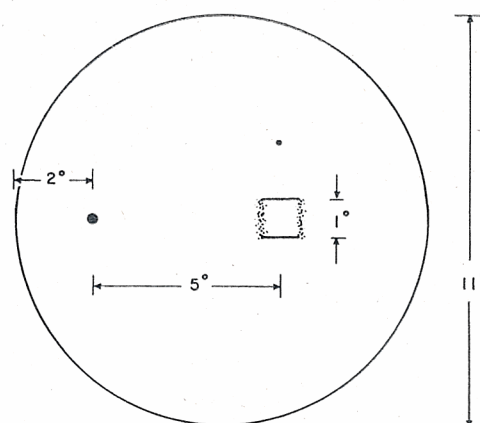
FIG. 2. Stimulus configuration used for most of the experiments.

by a xenon source (X) whose beam passed through a monochromator (M) with a 4.4-nm half-width, and then through Wratten neutral-density filters (F), a circular inconel wedge (CW), and two field stops (TF 1, TF 2). At one focal point in this path was a high-speed shutter (SH) which could be triggered to present the test flash for approximately 2 msec. Also in this same path was a prism (P_2) which could be rotated by turning a vernier micrometer (VM). Rotation of this prism (P_2) caused the focal point of L_7 seen by the eye (E) to move laterally, causing the test-field stimulus to enter the observer's pupil eccentrically for measurements of the Stiles–Crawford effect.

Eye positions were monitored using the method developed by Stark and members of his laboratory.[9] The beam from the ir source (S_2) had a second focal point near the plane of the test-field stop (TF_1), which thus created a slightly diverging, invisible beam after passing through lens L_7. This ir beam illuminated the iris-scleral boundary with two horizontal lines of flux; the two lines were projected onto opposite sides of the iris. Lateral eye movements altered the amount of reflecting surface of the eye illuminated by the lines. These changes in total flux reflected from each side of the eye were monitored by two LS-400 photo transistors (PT). To minimize the effects of fluctuations in flux not related to horizontal eye movements, the output from these phototransistors was fed to a differential amplifier and a Schmidt trigger, which, in turn, activated an electronic timer. This timer provided a variable delay between the firing of the Schmidt trigger and the activation of the high-speed shutter in the path of the test-field beam. A second timer in this circuit prevented the shutter from being activated during the following two seconds.

Figure 2 shows the stimulus configuration seen through a reduction tube by the subject, who held his head in position with a bite board. The ir illuminant

[9] L. Stark, G. Vossius, and L. R. Young, IRE Trans. HFE-3, 52 (1962).

was not visible. To the right of a black fixation spot ($\frac{1}{4}°$ diam) was a 1° test field, which appeared as a 2-msec flash superimposed upon a background of 3 cd/m² (color temperature 2500 K). The horizontal sides of the test field were in sharp focus at an effective accommodation distance of 50 cm. The vertical boundaries of this test field were intentionally blurred, however, by placing the appropriate field stop (TF 2) beyond the focal point of the objective. Thus, detection of the brief flash was based principally on the appearance of its upper and lower horizontal borders, which are in sharp focus, and not upon the vertical borders whose sharpness might be affected slightly by residual horizontal movements following a saccade.

PROCEDURE

The task of the subject was to make a voluntary saccade to the region of the background field where the test flash appeared and then, immediately to make a return saccade, back to the fixation point. As can be seen from Fig. 2, the test flash appeared below a small spot which served as a cue to the correct distance for the first saccade. After some practice, both subjects could make consistent saccades to the region of the test flash even though the cuing spot was located above the flash. The second return saccade back to the initial fixation position was always delayed by about 200 msec. Thus, following the first saccade to the right, the eye continued to be oriented toward the position of the test flash for another 200 msec or so before returning to the initial fixation position. This delay is seen clearly in Fig. 3 for the two observers who were used for the following studies. After the first saccade, there is a dead time of about 250 msec for WW and 150 msec for WR, before the return saccade. Note also that each observer shows hardly any consistent overshooting following the first saccade.

The advantage of making two successive saccades is that the dead time preceding the second saccade can be used to present flashes with fairly reliable time intervals prior to a saccade. Thus, the first saccade triggers a delayed flash which will precede the second saccade by an interval which depends upon the length of the dead time. This period of no movement was found to be roughly constant for each observer, varying by no more than 20% during a session. As will be seen by the results, this stationary period is sufficient to permit a decision whether the first or second saccade has principally altered the threshold. For long delays, to insure that the test flash occurred prior to the second saccade, the eye movement record was displayed on a cathode-ray tube, and monitored by the experimenter.

All threshold settings were made by the observer, who manipulated the circular neutral-density wedge (CW) which was placed in the path of the test flash. Observer WR was accustomed to this method, but WW, a naive observer who previously had no experience
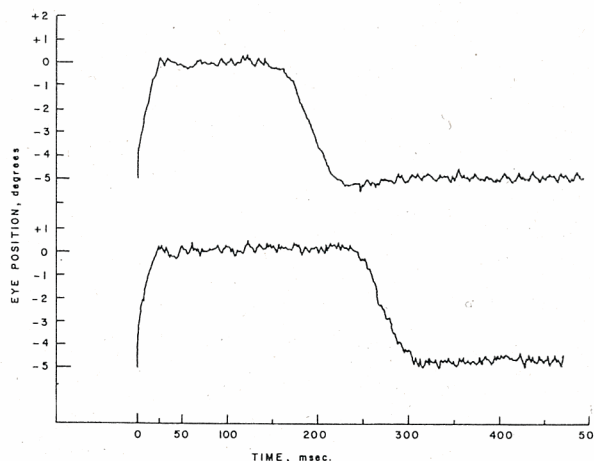

FIG. 3. Averages of 25 double saccades made by the two observers. Upper trace: WR; Lower trace: WW. Note the absence of any consistent overshooting once the eye reaches the target area, and the subsequent stability of the eye for 150 or 200 msec prior to the beginning of the return saccade.

making such judgments, needed several practice sessions before he could make consistent settings. These practice sessions were run before beginning the entire series of experiments.

SACCADES AND THE STILES–CRAWFORD EFFECT

The hypothesis under examination is that saccadic suppression takes place in the retina, and is an indirect result of shear in the retina due to eye acceleration. As previously discussed,[7] the suppression prior to the beginning of eye movement may be due to delays of phototransduction and transmission that occur in the neural chain preceding the site of suppression. Such delays would require the stimulus to be presented prior to the eye movement in order for the delayed neural activity to occur when the neural components of the retina are subject to shear.

Even though it is clear that acceleration of the eyeball must result in shear in the retina during rapid eye movements, apparently there has not been any direct confirmation of this. The Stiles–Crawford effect is one method that can be used to measure the extent of shear in the retina. If the sclera is moving faster than the vitreous, then the resultant shear should cause the photoreceptors to be tilted away from the direction of movement. Thus, the optimal path of entry for the photoreceptors will change by the angle of tilt. To demonstrate this tilting, the Stiles–Crawford effect immediately following a rapid eye movement may be compared with similar measurements made without preceding eye movements.

Figure 4 shows the results of two such sets of measurements made using a 2-mm exit pupil, with a natural pupil diameter of about 6.5 mm. Each point indicates the mean relative sensitivity (reciprocal of the threshold
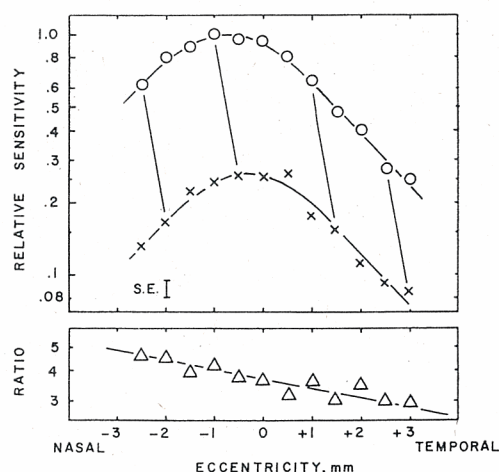
FIG. 4. The change of the Stiles–Crawford effect following a saccade. The circles show the customary attenuation versus eccentric entry; the crosses show the new sensitivities 40 msec following the beginning of a 5° saccade. Note the slight temporal displacement of the curve, as well as the reduced sensitivity. This shift of the curve is also shown more clearly by the declining ratios between the crosses and circles, plotted below with triangles. (Observer WW.)

luminance) estimated from four separate threshold determinations made on different days. The approximate standard error of these means is given on the figure. The data were collected using a haphazard sequence, except that at any given eccentricity each threshold for steady fixation was always followed (or was preceded by) a similar threshold determination for the same 1-deg flash delivered 40 msec after the beginning of the saccade. The circles indicate the relative sensitivities obtained with steady fixation of the background field (equivalent luminance of 3 cd/m²) at the position where the 575-mm test flash was presented. The crosses show how the visual sensitivity is reduced when the test flash is presented 40 msec after a saccade from the left fixation mark to the same position on the background field. As expected because of the saccadic suppression effect, the sensitivity following the saccade is attenuated by about 0.5 log units, even though the eye was then stationary. However, Fig. 4 also shows that if one smooth curve is to fit both sets of points, then this curve must be displaced toward the temporal side of the pupil in order to fit the crosses. This shift is also shown in the lower portion of the figure, where the ratios between the crosses and circles are compared at each eccentricity.

The average shift in the Stiles–Crawford effect following a 5° saccade is about 0.6 mm for this observer, corresponding to about a 2° angular tilt on the retina. As can be seen from Fig. 3 for observer WW, it is unlikely that this effect of the prior eye movement is due to the eye overshooting the target. The simplest explanation for this shift following an eye movement is that the photoreceptors have been tilted slightly. According to the data, the direction of tilt suggests

that 15 msec after the eye is stationary, the position of the retina still trails that of the sclera.

EFFECT OF BACKGROUND LUMINANCE

In order to investigate the visual effects of saccadic suppression in more detail, it seemed worthwhile to examine the magnitude of suppression as a function of the luminance of the background. If central factors were the principal source of brightness attenuation associated with saccades, then the suppression effect might reasonably be expected to be more dependent upon brightness than upon background luminance. On the other hand, the luminance of the adapting field, rather than brightness, might be the more important variable if suppression occurred in the retina.

Figures 5 and 6 show the dependence of the suppression effect upon background luminance. The black circles show the average thresholds for the 1-deg test flash of 575 nm for steady fixation. The crosses show the thresholds also for a stationary eye, but 40 msec following the onset of a 5° saccade.

The threshold curves obtained following the saccade (crosses) cannot be approximated by merely vertically shifting the customary threshold curves (circles).
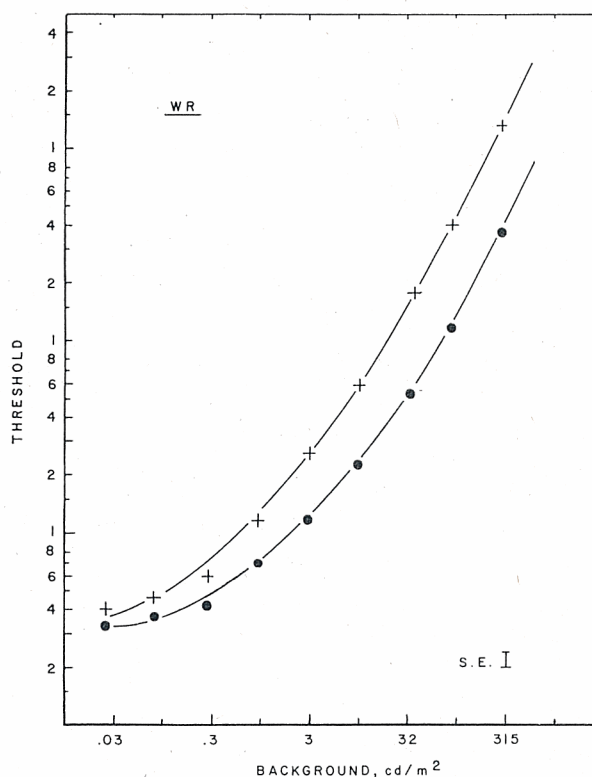

FIG. 5. Thresholds obtained for a 1° foveal test flash for steady fixation (solid circles) and for fixation 40 msec following the beginning of a 5° saccade (crosses). As the background luminance is decreased, the effect of the preceding saccade on the threshold is reduced. However, the change of the logarithm of the equivalent background luminance following the saccade appears to be independent of the luminance level. (Observer WR.)

Instead, the threshold curves for the eye movement condition are displaced laterally toward lower levels of luminance of the background. Thus, the effect of the eye movement appears to be to amplify the equivalent background level[10] rather than to attenuate the test flash. For the naive observer WW, this increase of equivalent background level is almost tenfold.

It is conceivable, but unlikely, that such an amplification of equivalent background luminance could be brought about by central factors. The principal difficulty is to conceive of a central effect which increases the brightness of background, but not that of the test stimulus. However, retinal mechanisms associated with adaptation are already known to be present which might bring about similar changes of equivalent backgrounds without affecting the test-flash activity.[11–13]

EFFECT OF DELAY

As luminance level is reduced, the photoreceptor delays increase.[14] Thus, another possible interpretation of the reduced attenuation near absolute threshold is
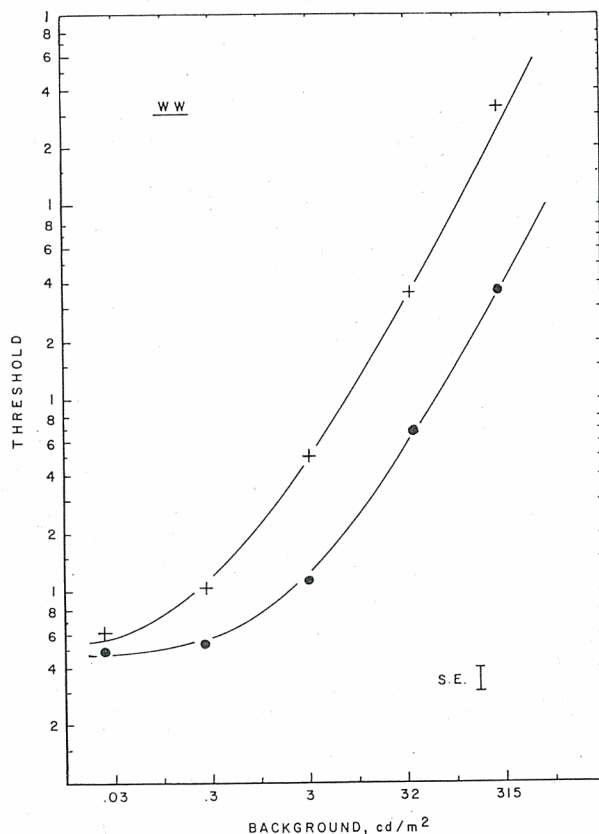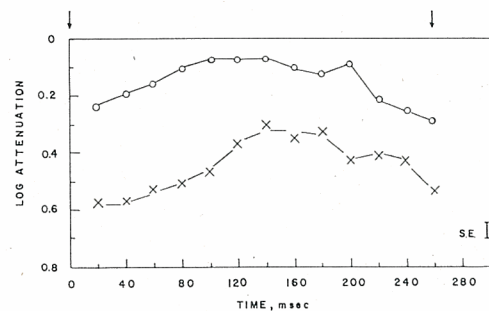

Fig. 7. Change of thresholds associated with a 5° saccade for two test-field wavelengths. Circles: 460 nm; crosses: 580 nm. Time scale is with respect to the beginning of the first saccade, indicated by the left-hand arrow at the top of the figure. The right-hand arrow indicates the approximate beginning of the return movement. (Observer WW.)

that the test flash has been presented too late. Because of the increased receptor latency at low luminance levels, the test stimulus should be presented well before the saccade for the optimum effect. This possible explanation for Figs. 5 and 6 has not yet been explicitly tested as a function of luminance level. However, evidence will be presented later which suggests that increased photoreceptor delays do not cause the principal effect shown in these two figures.

Nevertheless, it is true that photoreceptor delays will influence the temporal relationships needed between the saccade and the test flash for optimal suppression. This effect is seen in Fig. 7 for test flashes of two different wavelengths, 580 and 460 nm. For this observer (WW), the 580-nm test flash is maximally attenuated for about 50 msec following the beginning of the first saccade and also just prior to the beginning of the second saccade.[15] The attenuation of the 460-nm flash follows a similar time course, except perhaps displaced 40 msec earlier, with maximal suppression now clearly prior to the beginning of the saccade. The shift of the 460-nm curve with respect to that obtained with 580-nm flashes suggests that the blue-sensitive process has a slightly longer latency under our test conditions using a 3 cd/m² background (color temperature 2500 K).

In addition, it is also clear from Fig. 7 that the shorter-wavelength test flash is always suppressed less than the 580-nm flash. One possible explanation for this effect is that the thresholds obtained following the saccade were not foveal but slightly parafoveal owing to imperfect eye movements which either exceeded or fell short of the true position of the test flash. However, measurements made with parafoveal test flashes of 460 nm yielded similarly reduced attenuation, suggesting a true wavelength dependency for the saccadic suppression effect.

Fig. 6. Same as Figure 5. (Observer WW.)

[10] B. H. Crawford, Proc. Roy. Soc. (London) **B134**, 283 (1947).
[11] H. B. Barlow and J. M. B. Sparrock, Science **144**, 1309 (1964).
[12] W. A. H. Rushton, Proc. Roy. Soc. (London) **B162**, 20 (1965).
[13] J. E. Dowling, Science **155**, 273 (1967).
[14] R. M. Chapman, Vision Res. **2**, 89 (1962); R. A. Cone, J. Gen. Physiol. **47**, 1089 (1964).

[15] Note also the characteristic secondary decrease of the threshold near 180 to 200 msec equivalent to 50 or 70 msec prior to the beginning of the return saccade. This decrease has also been reported by others.[1–4] We propose that the peak and valley preceding the eye movement reflect neural disinhibition or the Broca–Sulzer phenomenon, whereas those decreases that occur after a single eye movement are due to retinal (or vitreous) oscillations.

WAVELENGTH DEPENDENCIES

Figure 8 presents further data showing the decrease of the suppression effect at short wavelengths. For both observers, the test flashes were delivered 40 msec following the saccade, when the eye was stationary (see Fig. 3). Maximal suppression occurs for test flashes near 575 nm.

We might infer from this result that the red- and green-sensitive processes are suppressed more than the blue-sensitive process. Thus, suppression might be increased still more if the relative sensitivities of the red- and green-sensitive systems are raised at short wavelengths by depressing the activity of the blue-sensitive process with a blue adapting field.

The triangles in Fig. 9 show that this increase is not observed. The background field of 471 nm at 3 cd/m^2 has decreased the suppression at longer wavelengths, shifting the maximum effect toward a region near 470 nm—the wavelength of the background. To confirm that the 471-nm background decreased the suppression effect of a long wavelength, another series was run using a 645-nm background. The squares in Fig. 9 show increased suppression at longer wavelengths and a marked decrease of suppression at short wavelengths. The effect of the background, therefore, is just the opposite of what would be predicted if the activity of the suppressed receptors had been decreased by the background field. Rather, the greatest saccadic suppression occurs when the test wavelengths are roughly the same as the wavelengths comprising the background.

This finding of the dependence of saccadic suppression upon the spectral composition of the background suggests again that the principal effect of eye movements is upon the neural activity associated with the background. This hypothesis was previously mentioned as an explanation for the displaced threshold curves in Figs. 5 and 6. Now, the results of Fig. 8, obtained with a background color temperature of 2500 K, together with the two curves of Fig. 9, demonstrate the importance of the background activity more forcefully. Thus, the greater the background activity at any
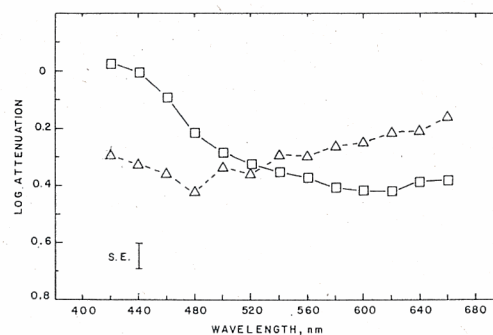
Fig. 9. Saccadic suppression for WR as a function of wavelength for two differently colored adapting fields. Triangles: dominant wavelength of background is 471 nm; squares: background dominant wavelength is 645 nm.

given wavelength, the greater will be the resultant suppression at these wavelengths.

TRANSIENT BACKGROUND

If saccadic suppression is due to an increase of the background activity, then elimination of the background should eliminate the suppression effect associated with rapid eye movements. In order to test this hypothesis, a background of 645 nm at 50 cd/m^2 was presented for only 1.0 sec in a total cycle of 3.0 sec, and thresholds were obtained at instants close to the lighting and extinction of the background.

Under these conditions, when the background was off for most of the inter-cycle interval, an additional luminous fixation mark was needed. This extra fixation mark was provided by a pin point of light introduced at the right-most edge of the background field (whose configuration had been altered to 7.5° vertical by 11° horizontal). The observer's task was to make a single 4.5° saccade from the region of the test flash to this luminous fixation point. As before, the beginning of this saccade then triggered the test flash after a 40-msec delay. Thus, for the following measurements, all thresholds were obtained for test flashes presented approximately 4° to the left of the fovea. The test-flash wavelength was 580 nm.

As for all of the previous measurements, thresholds were obtained for steady fixation of the luminous mark, as well as 40 msec following the beginning of a saccade to the same fixation point. For this series, however, thresholds were to be obtained at various delays with respect to the onset and extinction of the 645-nm background field. For the steady fixation position, these temporal positions with respect to the background were obtained easily by merely resetting a timer which delayed the test flash. In the case in which the flash was triggered by the saccade, however, correct temporal positioning of the test flash was more difficult. Our final method was to use an auditory click, which served as a cue to make the saccade. The experimenter then adjusted the click delay in order to control the
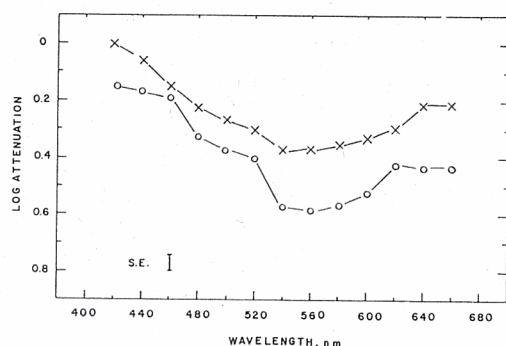

Fig. 8. Saccadic-suppression effect for two subjects as a function of wavelength of the test stimulus. Crosses: WR; circles: WW. Background color temperature is 2500 K.

average temporal position of the flash with respect to the lighting of the background. Because the latency between the click and the saccade was variable, the experimenter had to track the temporal position of the test flash on a cathode-ray tube, attempting to keep the delivery of the flash within ±25 msec of the desired temporal position. Threshold judgments were made only if the flash appeared within this tolerance. As before, all threshold settings were made by the observer WR, who manipulated the circular neutral density wedge placed in the path of the test flash.

Figure 10 shows the thresholds obtained for both the steady fixation (circles) and the saccadic condition (crosses). As expected from previous determinations,[10,16,17] the thresholds obtained during steady fixation are slightly elevated near the lighting and extinction of the background field. These transient effects are believed to reflect the underlying "on" and "off" bursts of neural activity.[17,18] The thresholds obtained following the saccade (crosses) do not show these transients. Instead, the threshold following a saccade appears to continue to rise beyond the peak of the on burst and then to reach a plateau that remains flat until the extinction of the background light. At this time, the saccadic threshold then falls more sharply than the thresholds for the steady fixation condition, leading to an enhanced detection of the test flash close to the time of extinction of the background. As expected from the previous data (Figs. 5–9), the saccadic suppression effect is minimal in the absence of the background.

DISCUSSION

The results of Fig. 10 further reinforce the hypothesis that the visual suppression associated with saccades is due to an amplification of the background activity following an eye movement. Such an increase must almost certainly be retinal.[11,12] However, a further inference may be drawn from the behavior of the transients at the beginning and extinction of the background. Figure 10 suggests that the saccade has eliminated the neural component that customarily lowers the threshold, by counteracting the initial surge of activity associated with the first appearance of a light. Thus, the effect of the saccade is as if a feedback loop has been broken, perhaps the synaptic loop suggested by Dowling[13] which may underlie the mechanisms of adaptation and lateral inhibition. Disruption of this same loop could also be responsible for the sharp
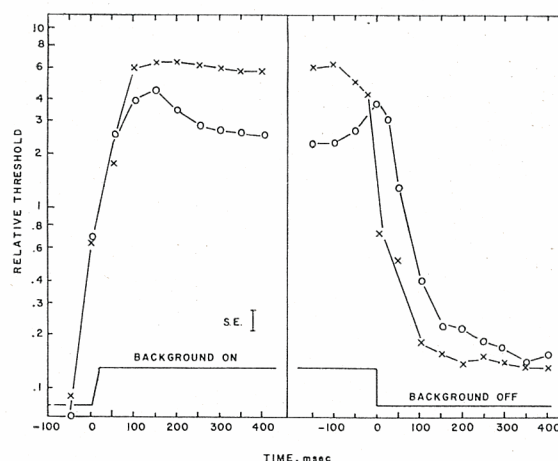

Fig. 10. Comparison of thresholds obtained with steady fixation (circles) and 40 msec following a 4.5° saccade (crosses). Test-field wavelength: 580 nm; background wavelength: 645 nm. The background was on for 1.0 sec every 3.0 sec.

decrease of threshold at the instant of extinction of the background field, providing the residual activity in this loop originated from the presence of the real background field. If this explanation is valid, then the effects of saccades are being felt at the level of the bipolar and amacrine cells of the retina. In addition, we can also predict that rapid eye movements should alter the increment thresholds measured according to Westheimer's technique.[19] Thus, if the effect of the saccade is to eliminate (or reduce) lateral interactions in the retina, then a preceding saccade should cause the incremental threshold for a small brief flash to remain at its maximum value as the diameter of a background field is further increased. The effect of the saccade on spatial interactions should be analogous to the temporal effects seen in Figure 10.

Finally, if the customary increases of thresholds at the lighting and extinction of an adapting field are correlates of "on" and "off" bursts, then elimination of these transients by the saccade also provides information about the site of saccadic suppression. If the effect of the saccade occurred at the second or a later "off" burst, then the activity of the first such burst would still mask the test-flash activity, causing the threshold to increase in this period. The elimination of a subsequent, higher-order transient could not recover the signal which had already been masked. Hence, the saccadic effect must have occurred at or prior to the site of the first "off" burst. Because these are found in the optic nerve, the site of saccadic suppression must be in the retina.

[16] H. D. Baker, J. Opt. Soc. Am. **39**, 172 (1949); **53**, 98 (1963).
[17] R. M. Boynton, Arch. Ophthalmol. **60**, 800 (1958).
[18] F. Ratliff, H. K. Hartline, and W. H. Miller, J. Opt. Soc. Am. **53**, 110 (1963).

[19] G. Westheimer, J. Physiol. (London) **190**, 139 (1967).