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Increment-threshold spectral sensitivity during saccadic eye movements in uniform visual field

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Abstract

We measured increment-threshold spectral sensitivity functions during saccades, immediately after saccades and during fixation. A uniform white background field which covered observer's whole visual field prevented any retinal masking effects. Visual sensitivity was degraded during saccades or after saccades. The reduction in sensitivity depended upon the wavelength of the test stimulus. The spectral sensitivity function during fixation produced a broad smooth curve in the middle and long wavelength region, while saccades caused a prominent dip around 570 nm. This finding indicates that saccadic suppression, which cannot be attributed to retinal masking, has more effect on the achromatic channel than the chromatic channel. The role of central and retinal processes dealing with the perceptual clearness and stableness across saccades will be discussed. © 1999 Published by Elsevier Science Ltd. All rights reserved.

Keywords: Saccade; Saccadic suppression; Masking; Spectral sensitivity; Magnocellular pathway

1. Introduction

Saccadic suppression refers to an inhibitory effect occurring with saccadic eye movements (Volkmann, 1962; Matin, 1974; Volkmann, 1986). It has been shown that several factors produce saccadic suppression. MacKay (1970) demonstrated that the displacement of retinal images was one of them. Campbell and Wurtz (1978) found that clear images displayed right after saccades played an important role to eliminate smeared images during saccades. Although these retinal effects were significant, saccadic suppression can not be completely attributed to these effects because threshold elevation was found when no retinal effects could occur (Riggs, Merton & Morton, 1974; Riggs & Manning, 1982). Riggs and Manning measured detection thresholds for a decrement stimulus under 'whiteout' conditions. Translucent plastic diffusers were fitted about the observer's eyes to provide a visual field without any distinguishable contours. They found visual sensitivity was impaired 0.7–1.1 log units during saccades. These results suggest that central inhibition occurs during saccadic eye movements.

Recent studies have indicated that saccadic suppression had more impact on the achromatic channel than the chromatic channel (Sato & Uchikawa, 1992; Burr, Morrone & Ross, 1994; Uchikawa & Sato, 1995). Sato and Uchikawa (1992) and Uchikawa and Sato (1995) measured increment-threshold spectral sensitivity functions during saccades and during fixation. Spectral sensitivity functions during fixation demonstrated a broad peak in the middle and long wavelength region with a small peak around 440 nm. Sensitivity during saccades was generally lower than fixation and sensitivity reduction was wavelength dependent. Sensitivity reduction was largest around 570 nm. Spectral sensitivity functions during saccades illustrated a prominent dip in this region. The shape of the spectral sensitivity function is determined from the relative contribution of both the chromatic and achromatic channels for stimulus detection (King-Smith & Carden, 1976). Our results indicate that the contribution of the chromatic channel for stimulus detection becomes relatively larger during saccades. In other words, sensitivity reduction is larger in the achromatic channel than in the chromatic channel.

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Schwartz and Godwin (1996) reported the influence of masking stimulus on increment-threshold spectral sensitivity functions. They found that a decremental masking stimulus caused a transformation of spectral sensitivity function similar to saccadic suppression. Schwartz and Godwin suggested that saccadic suppression might reflect, at least in part, a masking effect of the magnocellular pathway.

Were the transformations of spectral sensitivity functions during saccades reported in the previous papers due to masking effects or a central inhibition? Sato and Uchikawa (1992) and Uchikawa and Sato (1995) used a white background field subtending 43° × 62° where observers made 6° saccades. In the experiment of Burr et al. (1994), the screen subtended 53° × 67° and was surrounded by a white card with mean luminance and chromaticity that subtended 118° × 136° where observers made 40° saccades. Masking effects seem to be already minimized in these conditions. However, Brooks, Impelman and Lum (1980) reported that the displacement of a white background field in a saccadic manner caused substantial threshold elevation when observer kept steady fixation. Their background field subtended 43° × 45° and the simulated saccadic amplitude was 15°. This suggests that retinal effect might play a role in the previous experiments of saccadic suppression.

This study was attempted to clarify the extent of transformation of spectral sensitivity functions caused by saccadic eye movements under conditions where no masking effects could occur. In the present study, we used a uniformly illuminated white background field covering the observer's whole visual field, instead of a 43° × 62° background field used in the previous study (Sato & Uchikawa, 1992; Uchikawa & Sato, 1995).

2. General methods

2.1. Apparatus and stimulus

We used a three-channel optical system with a 500 W xenon-arc lamp to provide a white background field and a monochromatic test stimulus. A rear screen, made of a white plastic board, was placed in front of an observers eye, shown as in Fig. 1. Two white channels illuminated the screen constantly to make a white background field. The white background field covered observer's whole visual field. The CIE 1931 (x, y) chromaticity coordinates of the background field were (0.359, 0.353) with a luminance of 62 cd/m^2 at the centre of the field. We measured the distribution of luminance all over the screen with 10° steps to confirm the uniformity of the background field. The luminance was almost constant (variation was less than 5%) from 60° in the nasal field to 80° in the temporal field. The incremental test stimulus was projected for 10 ms within the area indicated by a dotted line in Fig. 1. The test stimulus was made with an interference filter with an 11 nm half-band width. The diameter of the test stimulus was 28 mm and subtended more than 100° in visual angle.

Eye position was derived from a limbus-tracker, which consisted of two infrared light emitting diodes and two photo diodes. It was placed in front of the eye which did not view the stimulus and the eye was covered with black cloth. Observers usually perceived a white uniform field, however, the occluded black field sometimes became dominant. When this occurred, the experiment was paused for a while. To acquire eye position, we subtracted and amplified the output voltages from the two photo diodes. We differentiated the eye position signal to obtain eye velocity. The duration of a saccade was defined as a period when the eye velocity exceeded 90 deg/s. The onset of a saccade was used as a trigger signal for the stimulus presentation in experiment 1.

2.2. Subjects

Four males, KH, MS, SN and HS served as subjects for experiment 1. MS, SN, HS participated in experiment 2. All subjects had normal color vision. Their age ranged from 22 to 25 years.

3. Experiment 1. Spectral sensitivity functions

We conducted five experimental conditions. The first was fixation condition. The test stimulus was presented while observer fixated at the screen. The others were saccade conditions. The test stimulus was presented when observer made voluntary saccades. Delay of test stimulus from the onset of a saccade was varied to

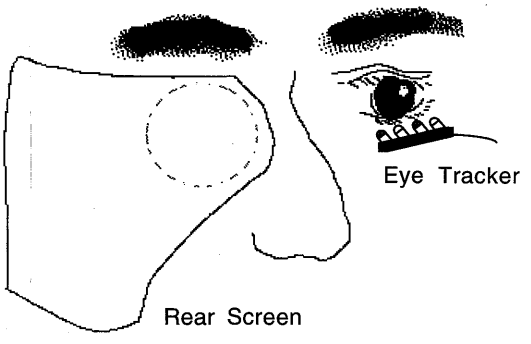

Fig. 1. A white plastic board was placed in front of an observer's eye and illuminated by white light constantly to provide a uniform background field. A monochromatic test stimulus was presented within the area indicated by a dotted circle. An eye tracking device was placed in front of the other eye. This eye was covered with black cloth.

derive the time course of saccadic suppression. The delay was either 10, 50, 100 or 200 ms.

3.1. Procedure

In the fixation condition, the observers fixated at the center of the visual field. Subjects pressed a stimulus presentation button to initiate each trial. After 0.4 s delay, the test stimulus was presented for 10 ms. In the saccade conditions, observers made a voluntary saccade horizontally to the left. Any fixation markers were not presented in both conditions to prevent the masking effects. The experimenter monitored every saccade with an oscilloscope. If the duration of a saccade was less than 30 ms or more than 55 ms, the trial was rejected. The average of the duration of saccades was 45 ms. Our preliminary measurement indicated that a 12° saccade needed that duration: The test stimulus was presented for 10 ms after a delay (10, 50, 100 or 200 ms) from the saccade onset. The observer indicated whether the test stimulus was detected or not verbally.

The method of limits was implemented to determine the detection threshold of the test stimulus. At the beginning of a descending series, the test stimulus was presented at a supra-threshold level and the intensity of the test stimulus was decreased by 0.02 log-unit step until the observer could not detect the test stimulus. When subject could not detect the test stimulus for two trials successively, the intensity of the test stimulus from the last trial was defined as a descending threshold. In the next sequence of trials, the intensity of the test stimulus was increased by the same step from a sub-threshold level. An ascending threshold was determined in the same manner. The average of these two thresholds was defined as a threshold for that session. In these descending and ascending series of trials, the wavelength of the test stimulus was fixed. Trials were repeated for nine wavelengths: 421, 444, 481, 505, 538, 569, 600, 633 and 667 nm. The wavelength of the test stimulus was selected in a random order.

The observers participated in at least four sessions for each condition. Measurements were done for both the right eye and the left eye.

3.2. Results and discussion

Figure 2 shows the spectral sensitivity functions obtained for fixation condition (□), saccade condition with 10 ms delay (■), 50 ms delay (▲), 100 ms delay (●) and 200 ms delay (◇).

The spectral sensitivity functions during fixation have a small peak in short wavelength region and a broad peak in middle and long wavelength region. This broad curve was similar to the typical luminous efficiency function obtained by the heterochromatic flicker photometry, although our curve was slightly broader. The broad curve may result mostly from the achromatic channel with partial contribution of the chromatic channel for stimulus detection. The small peak in short wavelength region may result from the yellow–blue opponent channel.

The spectral sensitivity functions obtained in the saccade conditions were generally lower than the fixation condition. The amplitude of sensitivity reduction depended upon the wavelength of the test stimulus. A trough appeared at 569 nm when sensitivity was reduced. These results indicate that the visual system is inhibited under the condition of uniform visual field which prevents any retinal masking effects and that the suppression is more effective to the achromatic channel than the chromatic channel.

The amplitude and the time course of saccadic suppression were found to be different among individuals and between the right eye and the left eye. Fig. 3 is a replot from the results of experiment 1. Open squares show sensitivity of the right eye and closed squares show sensitivity of the left eye. The wavelength of the test stimulus was 569 nm.

In KH's left eye, large sensitivity reduction occurred during saccades. However, in his right eye, sensitivity during saccades was not as low. The maximum suppression occurred when saccades were near completion for his right eye. Same tendency can be seen for observer SN. In SN's right eye, suppression was the largest at the end of saccades, while suppression was the largest during saccades for his left eye. For MS, the largest suppression occurred during saccades for his both eyes. Sensitivity was slightly higher in MS's right eye than in his left eye for both the fixation condition and two saccade conditions. The amount of sensitivity loss (the difference of sensitivity between the saccade condition and the fixation condition) seemed to be the same for MS's both eyes. In HS's right eye, sensitivity reduction was the largest when the stimulus was presented with a 100 ms delay from the saccade onset. His left eye demonstrated that substantial suppression occurred during saccades. Previous research has shown the time course of saccadic suppression (Latour, 1962; Volkmann, Shick & Riggs, 1968; Brooks et al., 1980; Shioiri & Cavanagh, 1989). Generally, sensitivity reduction began slightly before saccades and reached maximum during saccades. Sensitivity gradually recovered after saccades. The time course of sensitivity reduction for HS's right eye seems to be unusual. This finding will be assessed further in experiment 2.

4. Experiment 2. Time course of saccadic suppression

In experiment 1, we measured the spectral sensitivity functions during and after saccades and during fixation. Results show that saccadic suppression was more effec-

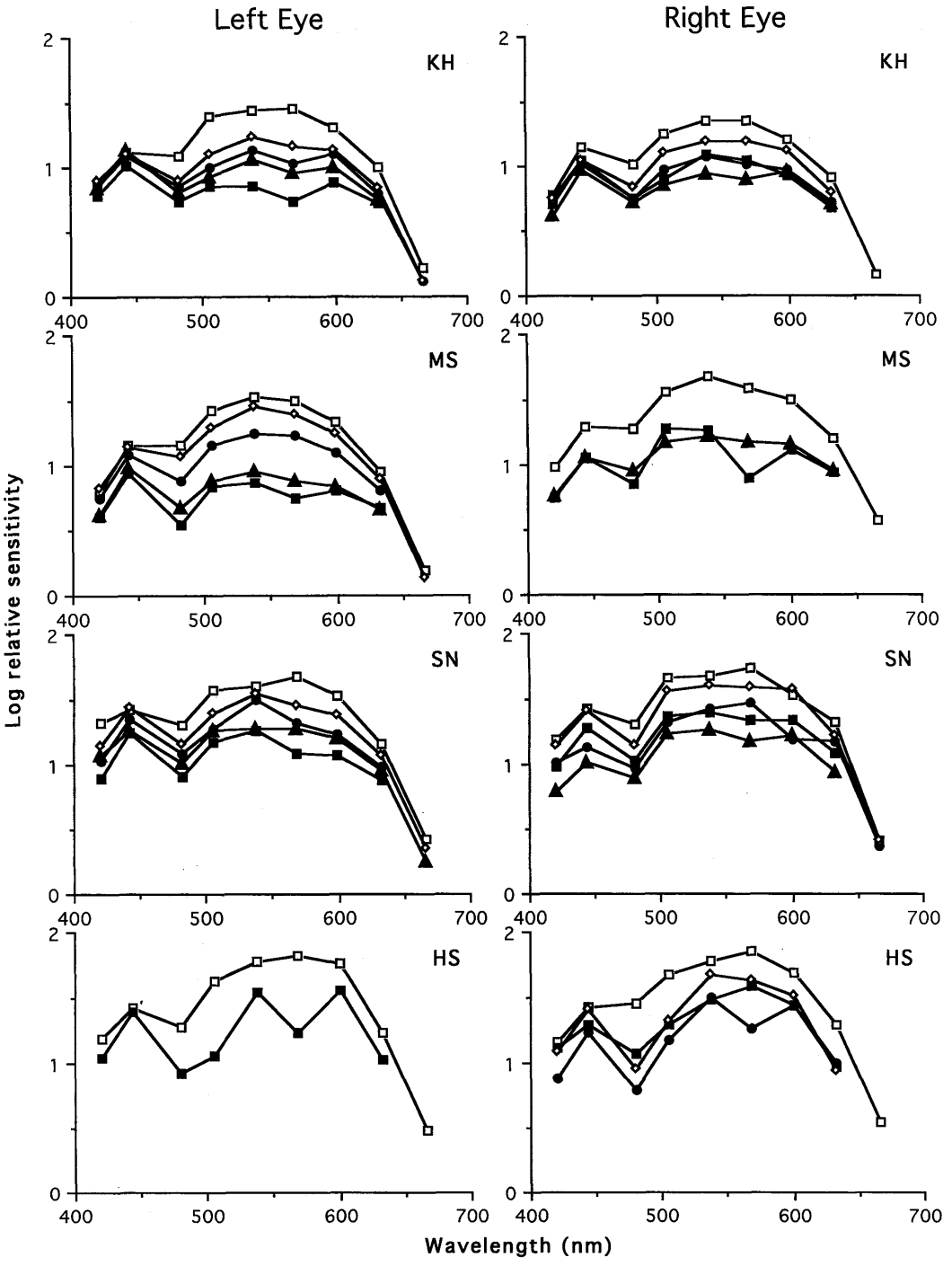

Fig. 2. Spectral sensitivity functions obtained during fixation (□), during saccades (■), immediately after saccades (▲), under the condition where the stimulus was presented with a delay of 100 ms from the beginning of a saccade (●), under the condition of 200 ms delay (◇). The average of standard errors of mean for all data points was 0.045.

tive on the achromatic channel either during saccades or after saccades. However, the spectral sensitivity functions before saccades is still unknown. We could not measure spectral sensitivity functions before saccades in experiment 1 because the saccade onset triggered the stimulus presentation. The chromatic channel may be strongly and exclusively suppressed before saccades because of the difference in temporal properties between chromatic and achromatic responses (Kelly & van Norren, 1977; Bowen, 1981; Schwartz & Loop, 1983; Uchikawa & Yoshizawa, 1993). Experiment 2 was designed to measure the time course of saccadic suppression for chromatic and achromatic responses.

4.1. Stimulus

Four wavelengths: 444, 505, 569 and 633 nm were selected as test stimuli. Results from experiment 1 indicated that a test stimulus of 444 nm should be detected by the yellow–blue opponent channel around threshold level and that a test stimulus of 569 nm should be detected by the achromatic channel. Both the chromatic and achromatic channels should contribute to detect a test stimuli of 505 and 633 nm. Four wavelengths were tested to observer MS. The 444 and 569 nm stimuli were tested to observers SN and HS. Two stimulus intensities were selected from a pilot study where the detection probability changed from 0 to 1 along the time course of a saccade. For MS, the intensity values of the test stimuli were 0.22 and 0.33 log unit above threshold determined in experiment 1 at 444 nm, 0.41 and 0.55 at 505 nm, 0.43 and 0.58 at 569 nm and 0.35 and 0.46 at 633 nm. For SN, those were 0.22 and 0.46 at 444 nm and 0.42 and 0.57 at 569 nm. For HS, those were 0.06 and 0.22 at 444 nm and 0.29 and 0.39 at 569 nm.

4.2. Procedure

Observer pressed a stimulus presentation button and made a voluntary saccade leftward. Half second after the stimulus presentation button was closed, a test stimulus was presented for 10 ms. The observer attempted to saccade at the same time as the test stimulus. The actual delay of a saccade after the stimulus presentation button varied for every trial. As a result, the test stimulus was presented before the saccade or after the saccade. The observer responded whether the test stimulus was detected. The right eye was tested for this experiment. The duration and delay of the saccade along with the observer's response were noted. If the duration of the saccade was less than 30 ms or more than 55 ms, the trial was rejected. Forty one trials were completed for each session.

In 30% of trials, the intensity of the test stimulus was either 0.1 log unit greater than the upper intensity value or 0.1 log unit lower than the lower intensity value. These modifications to the stimulus range acted as an experimental control which ensured that subjects were actually responding to the detection task and not using any other response strategy.

Three subjects, MS, SN and HS participated in 29, 16 and 12 sessions for each test wavelength, respectively.

4.3. Results and discussion

Fig. 4 indicates the detection probability of a test stimulus as a function of the stimulus-presentation time from the saccade onset. Each data point was calculated in a 20 ms bin and reflecting the results of four trials at least. The number of trials in each 20 ms bin varied along time. It reached to the maximum around time 50 ms and was approximately 80, 30 and 20 for subjects

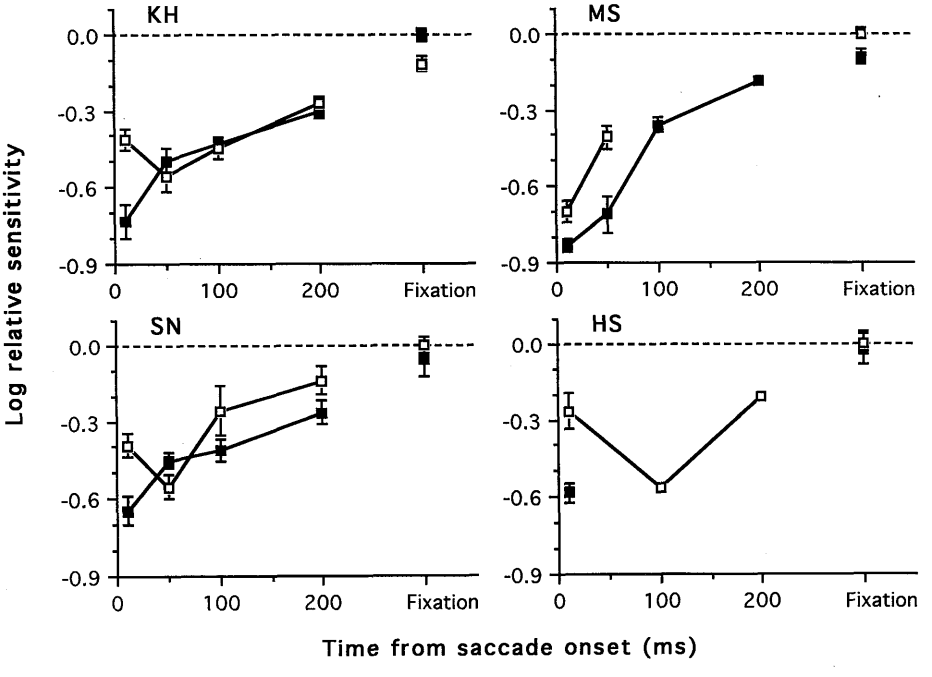

Fig. 3. Log relative sensitivity (defined as a reciprocal of threshold intensity) as a function of stimulus presentation time from saccade onset. Replot from Fig. 2. The wavelength of the test stimulus was 569 nm. Open squares shows the results for the right eye and closed squares for the left eye. Error bars show the standard errors of mean.

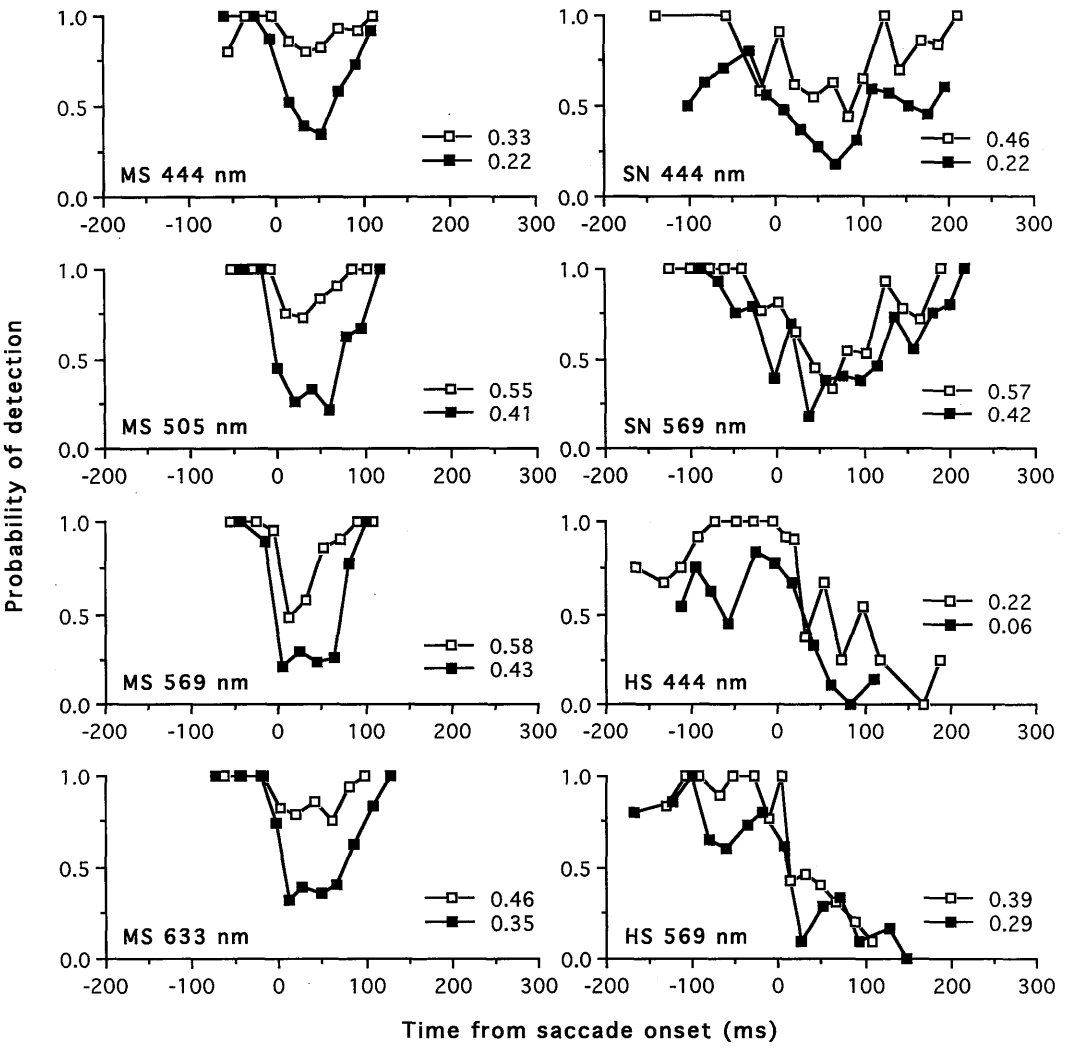

Fig. 4. Detection probability as a function of stimulus presentation time from saccade onset. The stimulus was presented to the right eye. Open squares shows the results for the more intense stimuli and closed squares for the less intense stimuli. Log intensity values of the test stimulus above threshold are shown in each panel.

MS, SN and HS, respectively. The average of saccadic duration was approximately 41 ms. This is corresponding to a 10° saccade according to our preliminary measurements. The log intensity values of the test stimuli above thresholds determined in the experiment 1 were shown for each panel. The results showed that the detection probability to the stimulus with greater intensity (□) was generally higher than that to the less intense stimulus (■). This tendency was common to the other two intensity values. This supports that the subjects responded to appearance of the stimulus directly, not using other response strategy.

For MS, reduction of detection probability began slightly before saccades. Sensitivity fell rapidly during saccades and recovered soon after saccades. This was similar across the various wavelengths of the test stimuli. Experiment 2 was to clarify whether large sensitivity reduction occurred before saccades for a particular wavelength. This was not the case. It is difficult to compare the extent of sensitivity reduction quantitatively among different test wavelengths in this condition, however, the largest sensitivity reduction seemed to occur at 569 nm because quite a large sensitivity drop can be seen immediately after the beginning of saccades for this wavelength although the intensity value of 0.58 was even greater than other wavelengths. This was consistent with the results from experiment 1.

For SN, the change of sensitivity was more gradual than MS. Detection probability began to fall earlier and recovered slowly. However, the time course of saccadic suppression for each wavelength was similar. Large sensitivity reduction before saccades could not be seen. Detection probability was lowest when the test stimulus was presented at the end of a saccade. This was also consistent with the results from experiment 1.

For HS, the time course of sensitivity reduction was different from the other subjects. Sensitivity began to fall at the onset of a saccade and continued to fall after the end of a saccade. About 60 ms after the end of a saccade (i.e. time 100 ms), sensitivity was still low. We could not acquire enough data to formulate the complete time course for HS's sensitivity recovery. However, substantial sensitivity loss at time 100 ms was consistent with the results from experiment 1. According to experiment 1, sensitivity was supposed to be higher around time 200 ms. There was no large sensitivity reduction before saccades and time course of sensitivity reduction was similar among different test wavelengths.

Observer HS's unusual characteristics of suppression may reflect his anisotropic vision. Since his right eye is myopic (-2.25 D) and his left eye is slightly hyperopic ($+0.25$ D), he may use his left eye to view distant objects and his right eye for closer objects. Defocused image from the eye he does not use must be suppressed to produce clear perception. We speculate this special inhibition caused HS's unusual temporal property of suppression.

5. General discussion

We measured spectral sensitivity functions during saccadic eye movements and fixation, using a uniformly illuminated white background field that covered the observer's whole visual field. We demonstrated that visual sensitivity was degraded and that the sensitivity functions were transformed to chromatic type during or immediately after saccades while those were achromatic type during fixation. This indicates that saccadic suppression had more effect on the achromatic than the chromatic channel and that this inhibition was not due to any retinal masking effects.

Several inhibitory mechanisms have been proposed other than retinal masking. For instance, Richards (1969) suggested that mechanical force from eye rotation sheared retina and that this raised visual thresholds during saccades. In our experiments, Richards shearing force may apply, however, it seems to be difficult for such a mechanical force to cause the transformation of spectral sensitivity functions.

Another possible explanation for selective suppression of the achromatic channel during saccades could be that the apparent selectivity was due to the difference in temporal property between the chromatic and the achromatic channels. If chromatic responses have a longer latency than achromatic responses, chromatic stimuli should be presented earlier to be suppressed optimally. Experiment 2 rejected this hypothesis. The time course of sensitivity loss was almost the same among different test wavelengths. Richards' (1969) experimental condition was similar to present design except that the background and the test stimulus were small. He found that the largest suppression to a 460 nm test stimulus occurred when presented slightly before saccades while optimal inhibition occurred to a 580 nm test stimulus during saccades. It was not clear why results differed from ours. However, Richards also showed that sensitivity reduction was larger for a 580 nm than a 460 nm test stimulus even though the time course of sensitivity reduction was slightly different. This result supports our primal finding: saccadic suppression had more effect on the achromatic than the chromatic channel.

The subjects usually perceived a white uniform field, however, the black field in the occluded eye sometimes became dominant. This indicates that an inhibition which usually suppressed the occluded eye could affect the eye to see the stimulus. A subtle or incomplete suppression could affect the results even though the subject paused the experiment when the black field was dominant. What was the influence of this suppression on the spectral sensitivity functions? Smith, Levi, Harwerth and White (1982) measured the spectral sensitivity functions during the dominance and suppression phases of binocular rivalry. The functions obtained during the dominance phase exhibited three peaks at approximately 440, 530 and 610 nm, however, the functions during suppression showed a single broad peak near 555 nm. This indicates that the suppression of binocular rivalry has more effect on the chromatic channel than the achromatic channel. Ooi and Loop (1994) confirmed this results. They further investigated permanent suppression and flash suppression. The results showed that permanent suppression was more effective to blue sensitivity than luminance sensitivity, but flash suppression showed opposite spectral selectivity. This indicates that this kind of binocular inhibitory interaction is not produced by a single mechanism but multiple mechanisms that have different spectral characteristics. It is interesting that flash suppression and saccadic suppression appeared to have a similar spectral selectivity. These inhibitory effects may have a common process. However, it should be stressed here that saccadic suppression obtained in the present study can not be explained without saccadic eye movements because retinal inputs were always constant in the saccade and fixation conditions.

We conclude that central inhibition does work when saccadic eye movements occur and that it has more impact on the achromatic than the chromatic channel.

We found that there was a difference in the amplitude of inhibition between the right eye and the left eye. This may indicate that saccadic suppression occurs at low level in the visual pathway as low as where the right eye information and the left eye information are well segregated. Burr et al. (1994) measured the effect

of saccadic suppression on masking effect. The mask was presented during saccade and the test was presented 90 ms later. Sensitivity to the test stimulus was improved when compared to the control condition where the mask and the test stimulus were presented during fixation. This indicates that the site of saccadic suppression is lower than the masking effect at least. Burr et al. suggested that the lateral geniculate nucleus (LGN) was a likely candidate as the site for saccadic suppression. The LGN has a suitable structure for saccadic suppression which has the characteristics revealed here: (1) magnocellular layers of the LGN are considered to be color blind, while parvocellular layers show clear color opponency; (2) information from the right eye and the left eye is well segregated; and (3) the LGN is affected by the superior colliculus which is related to the initiation of saccade. Central inhibition may occur at the magnocellular layers of the LGN and have slightly different magnitude to the right eye and the left eye in some individuals.

The amplitude of threshold elevation (the difference of log sensitivity value between the saccade condition and the fixation condition) revealed here was 0.44 (KH, right eye), 0.73 (KH, left eye), 0.70 (MS, right eye), 0.74 (MS, left eye), 0.55 (SN, right eye), 0.59 (SN, left eye), 0.58 (HS, right eye), 0.58 log unit (HS, left eye) for the 569 nm test stimulus where the maximum suppression was measured. These values were typical when compared to previous studies (Matin, 1974; Volkmann, 1986).

What is the role of this 0.5 log unit suppression? The simple notion that suppression accompanied saccades inhibits smeared retinal images during saccades and removes them from perception cannot be true. This magnitude of suppression seems to be too week to cause such an effect. Actually, Campbell and Wurtz (1978) demonstrated that the observers could see smeared images when the illumination of the room was restricted during saccades. Central inhibition must have been involved in such a situation. Although central inhibition has been demonstrated by the present and previous studies, this does not deny other inhibition processes such as retinal masking. It seems to be quite reasonable to assume that the clear images immediately after saccades serve as a visual mask. As Campbell and Wurtz (1978) reported, retinal masking is very important to remove the smeared images during saccades from perception. Central inhibition may have a different meaning if it has a meaning for visual perception. The selectivity of saccadic suppression to the achromatic channel suggests that suppression is useful to build stable perception across saccades (Burr et al., 1994). Motion is considered to be a fundamental dimension in human perception (Nakayama, 1985). It has been shown that motion perception depends primarily upon luminance information (Ramachandran & Gregory, 1978; Cavanagh, Tyler & Favreau, 1984; Mullen & Boulton, 1992). We usually do not perceive the movement of visual field when making saccades, although the change of retinal image is the same as that when the visual field itself moves during steady fixation. Central inhibition may have an important role to reduce this motion perception.

However, ordinary scenes we encounter in daily life are rich in luminance contrast. Human motion detectors are sensitive to luminance contrast (Cavanagh et al., 1984; Mullen & Boulton, 1992). Saccadic suppression is not enough to block all information of luminance contrast across saccades, even though it is selective to the achromatic channel. In order to test the hypothesis that saccadic suppression works to inhibit motion perception during saccades, it should be explored further how motion perception is affected by the luminance modulation caused by saccadic suppression.

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