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We measured spectral-sensitivity functions during saccadic eye movement by the increment-threshold method to test whether saccades selectively suppressed achromatic or chromatic responses. A circular monochromatic test stimulus of 12-deg diameter was presented for 10 ms on a 62 deg × 43 deg white background, and observations were made under three conditions: during fixation, during 6-deg saccades, and immediately after saccades. In two additional conditions the test stimulus was made to move during fixation and during 6-deg saccades at the same speed and in the same direction as the saccades. The during-fixation spectral-sensitivity function was found to resemble the relative luminous efficiency $V(\lambda)$ function in shape except for the case of short wavelengths, whereas the during-saccade spectral-sensitivity function showed lower sensitivity for all wavelengths and had three prominent peaks at approximately 440, 530, and 600 nm. These characteristics did not depend on whether the stimulus was stationary or moving. These results indicated that saccadic suppression was greater for achromatic than for chromatic response. A possible suppression mechanism was discussed involving the magno and parvo pathways.

1. INTRODUCTION

It is well known that visual perception is degraded during saccadic eye movements. This visual degradation, called saccadic suppression, has been investigated in many visual dimensions, e.g., light detection,[1–3] increment threshold,[4] contrast sensitivity,[5,6] motion,[6,7] and shape.[2] These findings have revealed characteristics of saccadic suppression in detail, but there is still disagreement concerning its determinants.[8] Recently the achromatic and chromatic pathways have been considered as basic separate channels from the retina to the visual cortex. These channels may correspond to the magno and the parvo pathways, respectively, which were physiologically found in the primate visual system.[9–12] It is of interest and importance to investigate whether saccadic suppression is selective to either the achromatic or the chromatic response, because such selectivity would reveal a significant feature of saccadic suppression.

Richards reported wavelength dependencies of saccadic suppression.[4] When the background of a test flash was a white field of 2500 K, saccadic suppression was greatest for the test flashes near 575 nm. It decreased for the stimuli near the short- and the long-wavelength ends of the spectrum. Richards concluded that the greatest saccadic suppression occurred when the colors of the test wavelengths were similar to that of the background. It can be noticed in his results that the saccadic-suppression function resembles the reciprocal of the saturation function of spectral light.[13] His results may suggest that saccadic suppression has a greater effect on the achromatic component than on the chromatic component of the test flashes. Lederberg studied color recognition of monchromatic lights during saccades and showed that saccades impaired color recognition of red (632-nm), green (549-nm), and blue (488-nm) lights.[14] It was found that maximum impairment occurred during the saccade for a red flash and a green flash but 20–60 ms after the saccade for a blue flash.

Spectral-sensitivity functions for increment thresholds have three peaks at approximately 440, 540, and 600 nm when a large stimulus is presented for a long duration on a relatively high-intensity white background.[15,16] It is generally accepted that the middle- and long-wavelength peaks reflect the red–green opponent mechanism and that the short-wavelength peak reflects the blue mechanism. When small and brief stimuli are used, these peaks become less prominent, and the increment-threshold spectral-sensitivity function is similar in shape to the $V(\lambda)$ function, that is, to the spectral-sensitivity function of the luminance mechanism. It seems reasonable that increment-threshold spectral sensitivity is determined by the relative contribution of chromatic (opponent) and achromatic (nonopponent, or luminance) responses and that a large and long stimulus is more favorable to the chromatic mechanism than to the achromatic mechanism.

For estimation of the relative degree of saccadic suppression of achromatic and chromatic responses, it is useful to compare the increment-threshold spectral sensitivity obtained during fixation and that obtained during saccade. In fact, in a binocular-rivalry experiment, Smith III *et al.*[17] showed that increment-threshold spectral sensitivities altered markedly during the suppression phase of binocular rivalry. The three peaks of the sensitivity function disappeared, and the spectral-sensitivity function exhibited a single peak near 555 nm, which was similar to the $V(\lambda)$ function. These results indicated that binocular rivalry suppressed the chromatic response to a greater extent than the luminance response.

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In the present study we investigated whether saccades differentially suppress chromatic and achromatic responses. We measured increment-threshold spectral sensitivity during fixation, during saccade, and immediately after saccade. Further, we added two more conditions to make it clear that the retinal smear of the stimulus was not the cause of the saccadic suppression. In the first additional condition, when the observer fixated his eyes the stimulus was moving at the same speed as the saccade. In the second additional condition, when the eye moved during saccade the stimulus was moving at the same speed so that the retinal image of the stimulus was fixed at the fovea.

2. METHODS

A. Apparatus

We used a three-channel optical system with a 300-W xenon-arc lamp to provide a white background and a test stimulus. The background subtended 62 deg × 43 deg of visual angle and was projected on a rear screen by two white channels (Fig. 1). The CIE 1931 (x, y) chromaticity coordinates of the white background were (0.361, 0.360), and luminance was 109 cd/m^2. The circular test stimulus of 12-deg diameter, made with a monochromatic channel, was projected onto the center of the background. This monochromatic light was produced by an interference filter of 11-nm half-band width. In some experimental conditions a small mirror, controlled by a galvanometer, was inserted into the test channel so that the test stimulus on the screen could move horizontally.

Five pairs of fixation markers were placed on the screen: five in the top row (1–5) and five in the bottom row (1′–5′), as shown in Fig. 1. We made the contrast of these fixation markers 1.2%, which was just barely visible in order to avoid any masking effect by the fixation markers during saccade. When the observer made a saccade, he moved his fixation from the center position of a pair of top and bottom markers to the center of another pair of markers. For example, the observer moved his eyes from the center of 2 and 2′ to the center of 4 and 4′. This was done so that no fixation marker moved across the center of the visual field.

We used the limbus-trucker method to measure eye movement. An eye-movement detection device, consisting of an infrared LED and two phototransistors, was placed in front of the observer's left eye. The left eye was occluded by a large black cover. The observer used his right eye to see the stimulus. We subtracted and amplified the output voltages from the two phototransistors and then differentiated them to obtain the speed of the eye movement. We could then take an appropriate value of the speed as a trigger for presenting the stimulus during a saccade.

B. Stimulus

We used five stimulus conditions in the present experiments. The test stimulus was presented for 10 ms in all conditions. Condition 1 was a control condition, in that the test stimulus was presented while the observer fixated at the center of positions 3 and 3′. In condition 2 the observer made a 6° horizontal saccade from the center of 2 and 2′ to the center of 4 and 4′. The test stimulus was presented 5 ms after the saccade started. In condition 3 the observer made a saccade from the center of 1 and 1′ to the center of 3 and 3′. The test stimulus was presented just after the saccade finished. We set the saccade speed of 90°/s as the threshold of the saccade. The experimenter monitored all saccades, using an oscilloscope to ensure that the shutter opened at the correct timing. Because the test stimulus always appeared at the center of 3 and 3′, the observer saw the test stimulus in the fovea for all conditions.

In condition 4 the mirror, which reflected the test stimulus onto the screen, oscillated sinusoidally at 12.5 Hz along a horizontal line. The test stimulus was moving between the center of 2 and 2′ and the center of 4 and 4′. The observer fixated at the center of 3 and 3′. The shutter opened for 10 ms when the test stimulus passed through the center of 3 and 3′. The speed of the test stimulus was 220°/s at the center. This speed was set to simulate the 6° saccade speed. In condition 5 the test stimulus moved at a constant speed of 220°/s from the left to the right on the screen. The observer made a saccade from the center of 2 and 2′ to the center of 4 and 4′. The observer's saccade triggered the beginning of the stimulus movement. The test stimulus was presented for 10 ms at the same speed as the saccade when the observer's eye passed through the center of the stimulus field. Thus in this condition the retinal image of the test stimulus was always stationary when the eye was moving.

C. Procedure

We used the method of limits to determine the detection threshold of the test stimulus. In a trial a test stimulus of a fixed wavelength was presented at a suprathreshold level. The observer responded "yes" or "no" by the forced-choice method, depending on whether he could detect the test stimulus. As long as the observer continued to make a yes response, the intensity of the stimulus decreased in 0.008-log-intensity steps. When the observer made a no response twice consecutively, the intensity of the stimulus for the second no response was defined as the descending threshold. In the next trial the stimulus in-

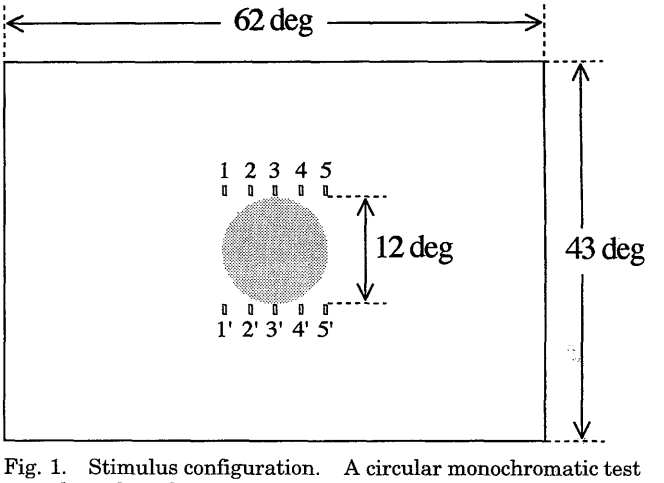

Fig. 1. Stimulus configuration. A circular monochromatic test stimulus of 12-deg diameter was presented at the center of the 62 deg × 43 deg white background. Five pairs of fixation markers were placed along lines above and below the test stimulus field.

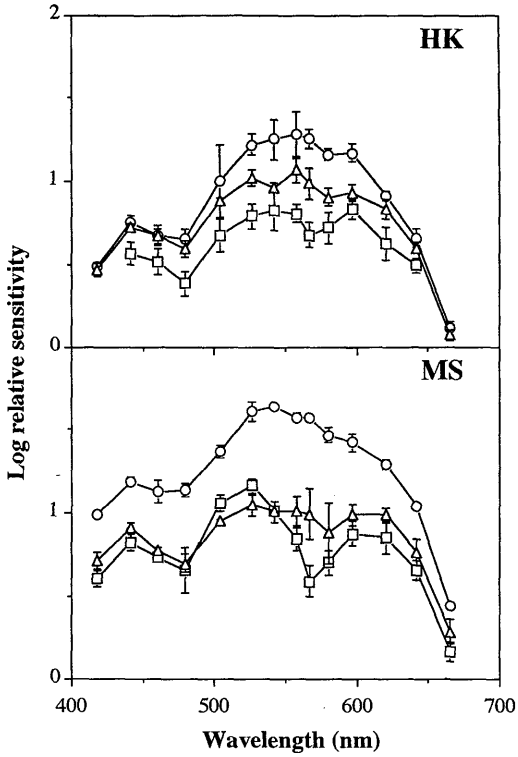

Fig. 2. Log relative-sensitivity functions obtained in conditions 1, fixation (open circles); 2, during saccade (open squares); and 3, after saccade (open triangles) for observers HK and MS. Error bars represent the standard deviations.

tensity increased from a subthreshold level to determine an ascending threshold in a similar way. Trials were repeated until all wavelengths were tested in a session.

In a session the wavelength of the test stimulus was randomly selected among 14 wavelengths: 418, 441, 461, 479, 504, 526, 542, 558, 567, 580, 597, 621, 642, and 665 nm. The observer participated in three sessions for each stimulus condition. Three ascending and three descending thresholds were averaged to produce a final threshold for a wavelength.

We conducted conditions 1, 2, and 3 at the same time in order to compare relative threshold differences for the same wavelength in different conditions. However, conditions 3 and 4 were carried out in separate periods in the experiments, because the apparatus was partially modified for insertion of the mirror in the test channel. To determine relative threshold differences obtained in conditions 1, 2, 4, and 5, we repeated these four conditions using four wavelengths: 479, 526, 567, and 597 nm in the same sessions.

D. Observers

Two males, HK and MS, 27 and 23 years of age, respectively, served as observers in all experiments. Both had normal color vision.

3. RESULTS

Figure 2 shows the log relative sensitivities, defined as reciprocals of thresholds, in conditions 1, fixation (open circles); 2, during saccade (open squares); and 3, after saccade (open triangles) for observers HK and MS. Error bars represent the standard deviations. The sensitivity functions obtained in condition 1 are relatively smooth in shape in middle- and long-wavelength regions for both observers. These functions resemble the luminance $[V(\lambda)]$ function in shape except in the short-wavelength region. On the other hand, the sensitivity functions obtained in condition 2 have three clear peaks at 440, 520–540, and 600 nm and two dips at 480 and 570 nm. The sensitivities during saccade are lower than those at fixation for all wavelengths. The maximum and the minimum log differences in sensitivity between fixation and saccade conditions turned out to be 0.57 and 0.15 for HK and 0.95 and 0.27 for MS, respectively. The sensitivity functions obtained in condition 3 are located between the fixation and the saccade sensitivity functions for HK but are closer to the saccade sensitivity function for MS.

The sensitivity functions obtained in conditions 4, moving stimulus (filled circles) and 5, moving stimulus during saccade (filled squares) are shown in Fig. 3 for both observers. The moving-stimulus sensitivity functions in condition 3 resemble the fixation sensitivity functions (open circles in Fig. 2) in shape. The moving-stimulus-during-saccade sensitivity functions obtained in condition 5 have three peaks that are similar to the saccade sensitivity functions (open squares in Fig. 2).

To compare the spectral sensitivity functions obtained in conditions 1, 2, 4, and 5, we adjusted the functions' relative heights as follows. We performed supplementary experiments to obtain the thresholds for four wavelengths near two dips and two peaks: 479, 526, 567, and 597 nm, in all conditions. We averaged these thresholds across the four wavelengths in each condition to deter-

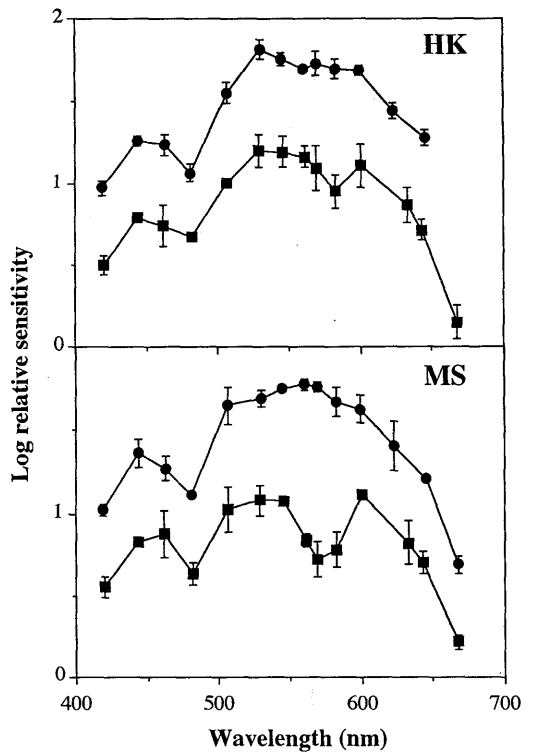

Fig. 3. Log relative-sensitivity functions obtained in conditions 4, moving stimulus during fixation (filled circles) and 5, moving stimulus during saccade (filled squares) for observers HK and MS. The vertical positions of these spectral-sensitivity functions are arbitrary. Error bars represent the standard deviations.

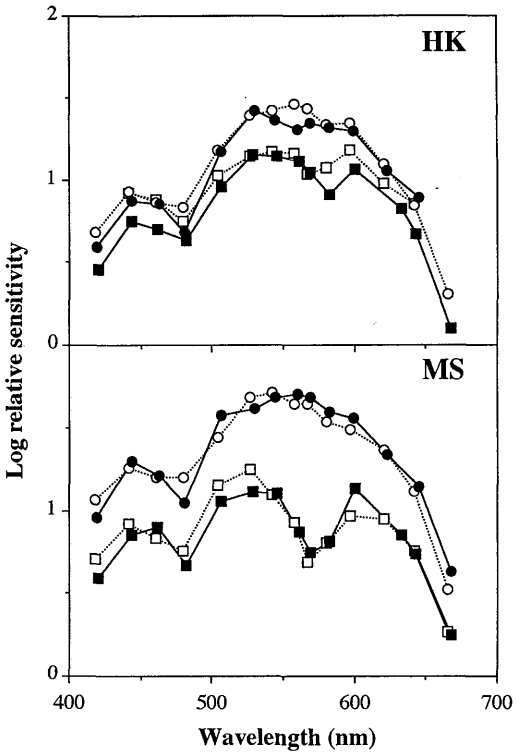

Fig. 4. Final log relative-sensitivity functions determined for conditions 1, fixation (open circles); 2, during saccade (open squares); 4, moving stimulus during fixation (filled circles); and 5, moving stimulus during saccade (filled squares) for observers HK and MS.

mine the relative level of each sensitivity function. The thresholds that had been obtained in the main experiments for the same four wavelengths were also averaged. Then the whole spectral-sensitivity function in each condition was shifted up or down to fit its four-wavelength average to its relative level.

Figure 4 shows the spectral-sensitivity functions that were finally obtained in the four conditions for two observers. The fixation (open circles) and the moving-stimulus (filled circles) sensitivity functions are very similar in both shape and relative height. The saccade (open squares) and the moving-stimulus-during-saccade (filled squares) sensitivity functions fit quite well. These results clearly indicate that the determining factor for saccadic suppression in the present experiments is not whether the stimulus was moving but whether the observer made a saccade.

4. DISCUSSION

It was clearly shown in the present experiments that, when the observer fixated, the spectral-sensitivity function resembled the $V(\lambda)$ function except for the case of short wavelengths and that, when the observer made a saccadic eye movement, the spectral-sensitivity function had three peaks at approximately 440, 530, and 600 nm.

The log spectral-sensitivity function for condition 1, fixation (open circles) was subtracted from each of those for conditions 2, during saccade (open squares); 4, moving stimulus (filled circles); and 5, moving stimulus during saccade (filled squares) shown in Fig. 4 to produce the log ratio functions. They are shown in Fig. 5 for both observers. The log ratio for condition 4 (filled circles) is almost constant across all wavelengths for both observers, which indicates that the moving stimulus in condition 4 does not have any effect on the sensitivity. The log ratio for conditions 2 (open squares) and 5 (filled squares) turned out to be a V-shaped function with the minimum at approximately 570 nm. This function resembles the spectral-saturation function,[13] which indicates that saccadic suppression is less responsive to more-saturated monochromatic stimuli. These results imply that the saccade selectively suppresses the achromatic or the luminance response relative to the chromatic response.

It is generally accepted that the short-wavelength peak at 440 nm of the increment spectral-sensitivity function reflects the short-wavelength-sensitive- (S-) cone mechanism and that the two peaks at 530 and 600 nm reflect the red–green [long–middle-wavelength-sensitive-(L–M)-cone] opponent chromatic mechanism. It is likely that the broadband spectral sensitivity, which appears in the fixation condition, reflects the luminance system, although there are some arguments that the broad unimodal spectral-sensitivity function does not unambiguously define an achromatic mechanism.[18,19] We determined relative contributions of the chromatic and the achromatic components to the spectral-sensitivity function for the fixation and the saccade conditions by fitting the (L + M)-, (L − M)-, and S-cone spectral sensitivities. We used the Smith–Pokorny L-, M-, S-cone spectral sensitivities for calculations.[20] Our model of stimulus detection hypothesizes that the maximum sensitivity of the three subsystems (the red–green opponent

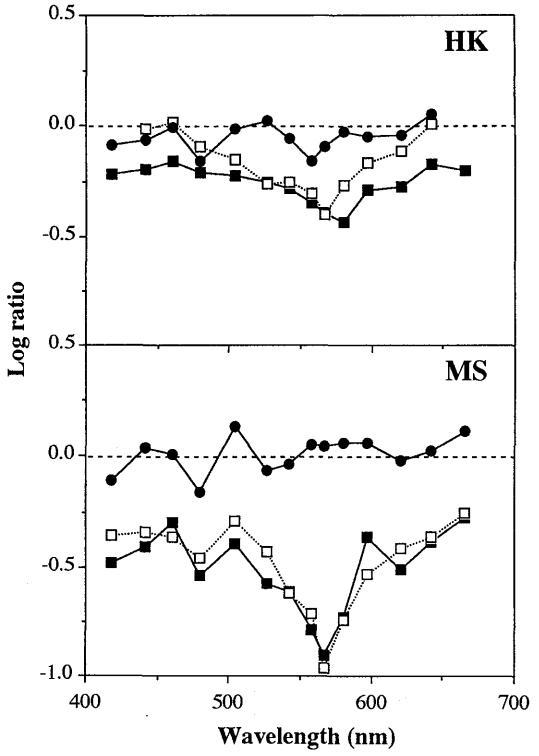

Fig. 5. Log ratio of the spectral sensitivity obtained in each of conditions 2, during saccade (open squares); 4, moving stimulus during fixation (filled circles); and 5, moving stimulus during saccade (filled squares) to that obtained in condition 1, fixation, for observers HK and MS.

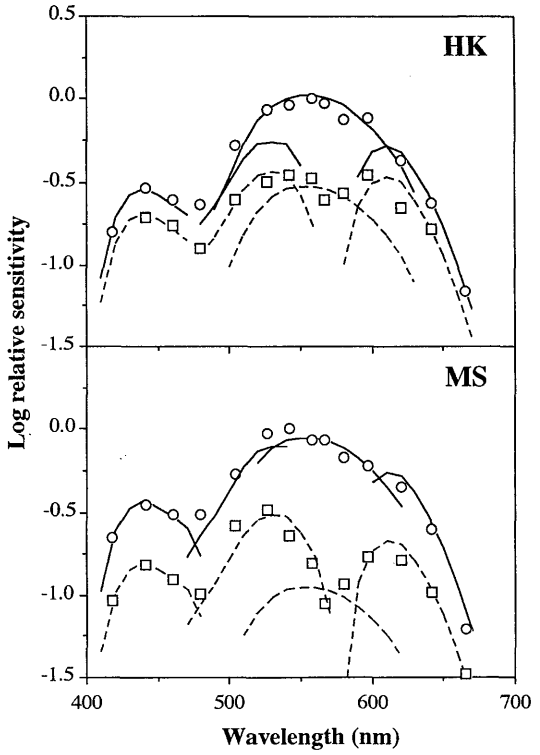

Fig. 6. Achromatic component, defined as log (L + M); the red–green opponent component, defined as log (L − 2.1 M) for observer HK and log (L − 2.3 M) for observer MS; and the S-cone component, defined as log S, best fitted to the data points. L, M, and S represent the Smith–Pokorny cone spectral sensitivities. Solid curves, fixation condition; dashed curves, saccade condition.

mechanism, the luminance mechanism, and the S-cone mechanism) defines the sensitivity of the total system. Figure 6 shows that the achromatic component, defined as log (L + M), and the red–green opponent component, defined as log (L − 2.1 M) for observer HK and log (L − 2.3 M) for observer MS, and the S-cone component defined as log S, can fit the experimental data well. The coefficient of the M cone in the L–M system and the relative sensitivities of the three subsystems were determined with the least-squares method. The solid curves indicate the fixation condition, and the dashed curves indicate the saccade condition. For observer HK the log difference of the achromatic component, log (L + M), between the fixation and the saccade conditions is 0.54; and those of the chromatic components, log (L − 2.1 M) and log S, are 0.18 and 0.15, respectively. For observer MS, log differences of log (L + M), log (L − 2.3 M), and log S between the fixation and the saccade conditions are 0.90, 0.41, and 0.37, respectively. In this model the achromatic component, log (L + M), is more strongly suppressed than the chromatic components, log (L − 2.1 M) or log (L − 2.3 M) and log S, during saccade.

Our results also revealed that the retinal smear was not a determining factor of saccadic suppression but that central inhibition, caused by the saccadic eye movement, played an important role. Masking effects were almost eliminated in these experiments, because the edges of the background field appeared in the far peripheral retina and the contrast of the fixation points was very low.

The pavocellular and the magnocellular pathways seem to be two basic subdivisions of the visual pathway from the retinal to the visual cortex.[10,12] The magno pathway has better temporal resolution and no chromatic selectivity. These characteristics correspond well to properties of the achromatic channel, which has been psychophysically determined.[11] The parvo pathway corresponds to the chromatic channel. Our results suggest that saccades selectively suppress the magno pathway. This view can be supported by the fact that saccadic suppression was selective for the low spatial frequency of luminance gratings,[5,6,21] because the magno system has larger receptive fields than the parvo system.

Shioiri and Cavanagh[7] showed that short-range motion could not be detected during saccades, indicating that saccadic suppression was involved in motion perception. Since motion perception is mediated mainly by the luminance channel,[9,22] our experimental results may support the visual-integration theory that saccadic suppression eliminates a retinal smear image that occurs during saccade in order for the visual system to produce a unitary, stable visual field by comparing or integrating two retinal images before and after saccade.

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