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Saccadic suppression relies on luminance information

Received: 3 March 1995 / Accepted: 16 June 1995

Abstract To determine whether saccadic suppression of image displacement uses information from luminance channels, we measured spatial displacement detection thresholds with equiluminant and non-equiluminant targets during saccades. We compared these saccadic thresholds with displacement thresholds measured during fixation by making ratios of saccadic thresholds to fixation thresholds. Ratios were lower in the equiluminant condition than in the non-equiluminant. This surprising result indicates that detection of equiluminant target displacements during saccades was better than detection of nonequiluminant targets, compared with the detection abilities during fixation. Thus, saccadic suppression of image displacement, which should increase displacement thresholds during saccades over fixation thresholds, was more effective with nonequiluminant targets. Because of target flicker, displacement thresholds were anisotropic in the nonequiluminant condition; thresholds were greater when target and eye moved in the same direction than when they moved in opposite directions, consistent with earlier results. These two effects (flicker-induced anisotropy and greater suppression in nonequiluminance) canceled when the eye moved opposite the displacement, yielding equal thresholds, and summed when eye and target moved in the same direction, yielding large threshold differences. We conclude that saccadic suppression of image displacement uses mechanisms sensitive to luminance contrast.

Introduction

How do we perceive space to be stable despite motion of an image of the world across the retinas with each saccadic eye movement? Saccadic suppression is an important feature of the visual system's ability to maintain space constancy (Dodge, 1900, 1905; Holt, 1903). One aspect of saccadic suppression is an elevation of spatial displacement detection thresholds measured during saccades (Zuber & Stark, 1966; Latour, 1966). This rise in displacement threshold called *saccadic suppression of image displacement* (SSID), has a magnitude of up to one-third the size of the saccade (Bridgeman, Hendry, & Stark, 1975; Stark et al. 1976; Ilg & Hoffmann, 1993).

Retinal and extraretinal signals individually or additively mediate SSID. The classical extraretinal component, called *efference copy* or *corollary discharge*, is a feedforward copy of the eye movement's motor signal. Sent to the visual system, it subtracts from the retinal motion signal caused by a saccade (von Holst & Mittelstaedt, 1950; Sperry, 1950; Teuber, 1960). Efference copy does not compensate for the entire eye movement, however; its gain is less than one (Yasui & Young, 1975a, b; Grüsser, Krizic, & Weiss, 1987; Holtzman, Sedgwick & Festinger, 1978; Pola & Wyatt, 1989). Another extraretinal component, extraocular muscle proprioception, has an even lower gain (Gauthier, Nommay, & Vercher, 1990). Indeed, these two extraretinal signals studied additively have a combined gain of less than one (Bridgeman & Stark, 1991). Thus, other mechanisms must contribute to space constancy.

The mechanism underlying SSID may include an inhibitory backward masking process, similar to metacontrast, that inhibits perception by using the present retinal sample to mask the previous sample (Grüsser, 1972; Matin, Clymer, & Matin, 1972; Macknik, Fisher, & Bridgeman, 1991). In these conceptions, the retinal image of the target just before the eye stops is inhibited by the adjacent image

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during fixation. However, Bridgeman (1983) found that displacement detection during fixation was better than during saccades even when retinal displacement of the target was equated during fixation and saccades. While this experiment did not disprove a backward-masking process, it did show that the visual component underlying SSID must include a mechanism other than simple spatial masking. Thus, the contribution of visual inputs to SSID remains unclear. We continue the study of visual inputs to SSID by asking which of the early visual-information channels is sampled by the mechanism that mediates SSID.

Some visual tasks can use purely chromatic cues, while other tasks rely upon luminance cues (Ramachandran & Gregory, 1978; DeValois & Switkes, 1983; Cavanagh, Tyler, & Favreau, 1984; Livingstone & Hubel, 1987, 1988; Lennie & D'Zmura, 1988). Can the visual component of SSID use purely chromatic cues or does it rely upon the presence of luminance information in the target? To study this question, we measured the difference in threshold detection of displacements with equiluminant and nonequiluminant stimuli during saccades and fixation. We also examined whether these results confirm earlier findings that the visually driven component of SSID includes a process other than simple spatial masking.

Method

Subjects. The subjects were 4 undergraduate students naive to the hypothesis and 1 experienced psychophysical observer, all of whom had normal color vision of red-green contrasts, confirmed with flicker photometry, as is detailed below. All subjects had either 20/20 acuity or were corrected to 20/20 with contact lenses.

Apparatus. Stimuli were presented on an IBM 8513 RGB monitor with a vertical refresh rate of 70 Hz. An IBM PS/2-70 computer with an 8-bit color interface board controlled the experiment. Horizontal eye movements were monitored with an infrared photoelectric sensor that consisted of an infrared emitting diode and two infrared photocells. The sensor was placed about 0.5–1.0 cm below the pupil of the right eye; the left eye was covered with an eye patch. A G+W Eye-Trac (Model 200) differentiated and amplified the output from the sensor. The computer sampled the analog signal at 1 kHz.

Procedure. The relative luminance of the red and green was equated with minimal flicker photometry for each subject. A 2° by 2° square changed from red to green and back at a rate of 23.3 Hz. Subjects varied the luminance of the red square while the luminance of the green square remained constant. We defined the equiluminant point to be the red-luminance value at which the red and green alternating square seemed to flicker least. The luminance value of the red square for each subject was used in the subsequent experimental and control conditions. The green luminance was identical for all subjects and conditions, while the red luminance was different for each subject.

Saccadic condition. Two 1° squares, their centers separated by 20° , served as saccade initiation and goal areas. The target was a similar square, centered between these areas (Figure 1).

In the equiluminant condition, the red target square was presented on a $41^\circ \times 31^\circ$ green background. In the nonequiluminant condition, the target was a black square on the same green background.

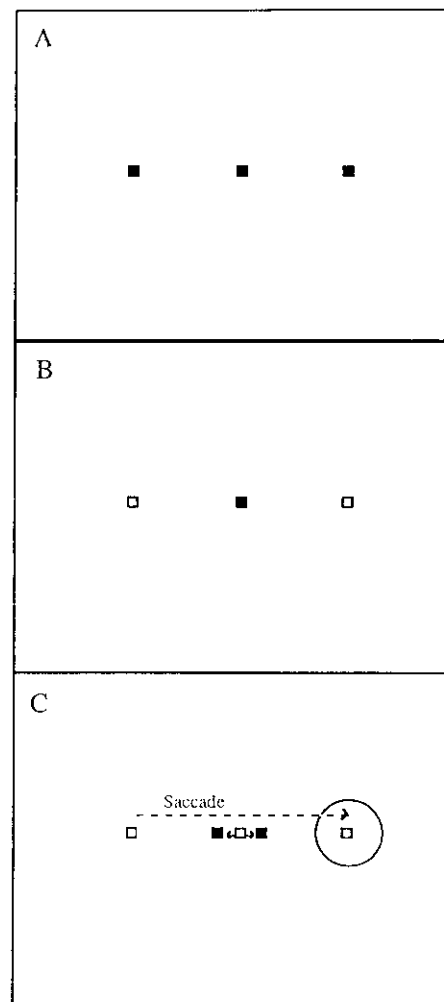


Fig. 1 Stimulus conditions during a trial. Black squares represent visible stimuli. The background is green. At the start of a trial, 3 squares appear on the screen (panel A). The target (center) and the left and rightmost squares were equiluminant red in the equiluminant conditions and black in the nonequiluminant conditions. Subjects practiced saccades between the left and rightmost squares. When the subject was ready to start a trial, the subject fixated the leftmost square and pressed a button. The left and rightmost squares were then extinguished (filled in with green) (outline squares in panel B). Midway through the saccade, the target, the only visible contour on the screen, was displaced either in the same direction as the saccade or in the opposite direction (panel C). Circle represents acceptable error limits in the eye movement (panel C)

The subject initiated a trial by fixating the leftmost square (saccade initiation area). One second after the beginning of a trial, saccade initiation and goal areas, the leftmost and rightmost squares respectively were extinguished. This was the signal for the subject to saccade to the saccade goal area (the remembered position of the rightmost square). Saccades were always from left to right. The target was displaced horizontally during the portion of the saccade in which the target was near the fovea. In order to displace the target during or near foveation, we triggered the displacement of the target when the eye was 3.5° to the left of the target. Assuming a saccadic velocity of about 500° per second (typical of a 20° saccade) and with a vertical refresh rate of 70 Hz, this technique ensures that the target displacement occurred not more than 3.5° from foveal center, and on average displacement would occur when the fovea crossed the

target. The target was displaced in either the same or the opposite direction as the saccade, in a random order. At the saccadic goal area, the subject fixated for 400 ms before the end of the trial.

Each saccade was analyzed on line, and improper saccades rejected. Undershoots were saccades less than 19° in length, overshoots were more than 23° , and double saccades either stopped in the target area before continuing to the saccadic goal area, or reversed into the target area after arriving in the saccadic goal area. Subjects received immediate undershoot, overshoot, or double saccade messages respectively on the screen. If the saccade was accurate, the subject responded, via button box, "yes" if he saw the target displacement, or "no" if no displacement was seen.

Using the Modified Binary Search "yes/no" MOBS staircase technique (Tyrrell & Owens, 1988), we determined thresholds for four conditions: equiluminance and nonequilibrium, each with target displacement in two directions. The MOBS algorithm, a staircase with adjustable step size, determined the size of the target displacement, within a range of 0.1 to 3.0° , for the next trial of each condition. The algorithm sets displacement size at the expected threshold on each trial, based on performance in previous trials. The threshold was the point at which there had been at least five reversals of the staircase and the 95% confidence interval of the threshold was 5% or less. The number of trials for each subject and condition was decided by the MOBS algorithm based on this criterion.

Matched-pairs student's *t*-tests were used to compare threshold target displacements in a series of orthogonal planned comparisons.

Fixation condition. We measured sensitivity to target displacements during fixation. To make the minimum jump size as small as possible, we moved the display to four times its previous distance from the subject. In the equiluminant condition, the 1° target was red on a $10.3^\circ \times 7.8^\circ$ green background. The subject signaled the computer upon fixation of the target and remained fixated for 4 s. From 1 to 4 s (randomly determined) into this period, the target was displaced horizontally by 0.016° to 0.31° (in steps of one pixel, 0.016°) to the left or right. All other aspects of the control experiment were identical to the methods in the experimental condition.

Results

Fixation

Figure 2 displays the average displacement thresholds measured in the fixation condition for equiluminant and nonequilibrium displacement sensitivity. Because target-displacement direction in the equiluminant condition and the interaction between contrast type and displacement direction were nonsignificant, $t(9) = .83$, $p = .428$, $r = .38$, we collapsed the data over displacement direction. Consistent with the literature (Cavanagh et al., 1984; Livingstone & Hubel, 1988), the displacement-detection threshold in the equiluminant condition was 1.47 times higher on average than in the nonequilibrium condition, $t(4) = 2.98$, $p = .041$, $r = .96$.

Saccades

The thresholds from the two directions for target displacement in the equiluminant condition were com-

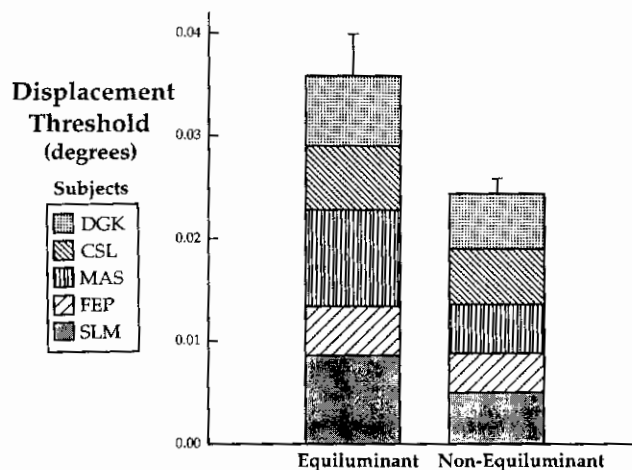


Fig. 2 Target displacement thresholds in degrees during fixation, averaged across displacement direction, for both equiluminant targets and nonequilibrium targets. Patterns of shading represent the proportional contribution of an individual subject to a given threshold, indicated in the framed legend

pared for further analysis because there was no significant difference between them (same direction 1.27° ; opposite direction, 1.24° ; $t(4) = .361$, $p = .74$; $r = .18$). Threshold-target displacement in the nonequilibrium condition (same direction, 1.86° ; opposite direction, 1.25°) was on average 50% greater than in the equiluminant condition when eye and target moved in the same direction, while thresholds were similar when target and eye moved in opposite directions.

The purpose of this study was to identify the information stream most important to the saccadic-suppression system by comparison of sensitivity to displacements of targets with various visual attributes during saccades and fixation. To compare changes in sensitivity between fixation and saccadic conditions with respect to the chromatic and luminant attributes of the targets, ratios of the saccadic thresholds and fixation thresholds (saccadic threshold/fixation threshold) were calculated within each condition, and the yields tested statistically (Figure 3). The nonequilibrium same-direction ratio was significantly greater than the combined equiluminant ratios, $t(4) = 7.70$, $p = .0015$, $r = .97$. This high ratio in the nonequilibrium same-direction condition indicates that thresholds were high during saccades (Figure 3), but low during fixations (Figure 2), in comparison with the combined equiluminant conditions. Thus, saccadic suppression works best under nonequilibrium conditions in which the target moves in the same direction as the saccade. In the against direction, the nonequilibrium threshold was not significantly different from the equiluminant value, $t(4) = .59$, $p = .59$, $r = .28$. This anisotropy is expected and will be discussed further in the next section.

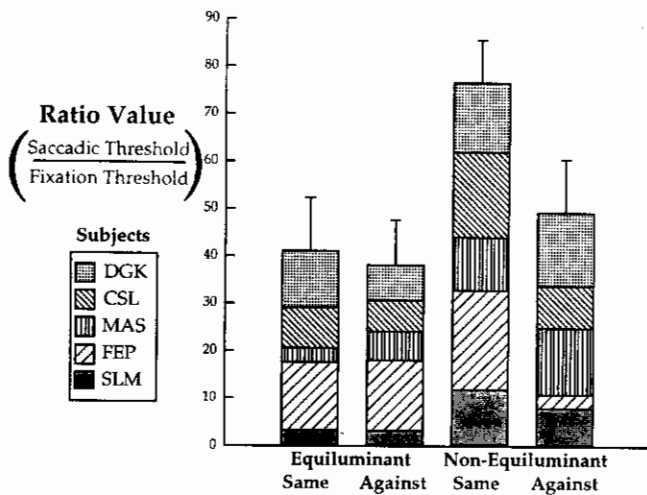


Fig. 3 Ratios of the saccadic and fixation thresholds (saccadic thresholds fixation thresholds), from both equiluminant and nonequiluminant conditions. Each pattern of shading represents the proportional contribution of an individual subject to a given ratio, indicated in the framed legend

Discussion

These results are consistent with the interpretation that saccadic suppression of image displacement fails, or nearly fails, in equiluminant conditions. We conclude that retinal information from luminance channels is crucial for proper SSID. This is a reasonable feature of SSID because suppression must act very quickly and thus luminance channels are better suited to processing such information than channels sensitive to equiluminant contours.

Figure 3 shows that displacement-direction sensitivity in equiluminant conditions is isotropic throughout all conditions, while nonequiluminance sensitivity is anisotropic only during the saccadic condition; nonequiluminant targets displaced in the direction opposite to the saccade are easier to detect. This is expected, since Macknik, Fisher, & Bridgeman (1991) previously found a similar anisotropic SSID threshold for luminance-defined targets flickering at rates similar to those used here. They showed that by varying target-flicker rate and displacement direction (i.e., retinal-smear contiguity during a saccade) one varied SSID, concluding that the SSID mechanism relies upon a high degree of retinal contiguity of the stimulus. The isotropic displacement thresholds at equiluminance found in the saccadic condition serve as further evidence that SSID did not contribute to threshold elevations during saccades.

Subjects frequently detected a displacement of a single pixel (about 1' arc) in the nonequiluminant fixation condition, despite the small amount of inevitable blur associated with VDT screens. The angular size of a pixel could have been reduced by moving the

screen even further from the subject and increasing the area of the screen occupied by the target, but this would have reduced the proportion of green background field size to target size and might have distorted, relative to saccadic conditions, the adaptation state of the retina in the neighborhood of the target. Thus the thresholds measured for luminance-defined targets in the fixation condition may overestimate the true thresholds of the subjects. This would have the result of reducing the apparent difference between displacement thresholds obtained in the fixation and saccadic conditions, making our conclusions overly conservative. Our results should therefore be interpreted as a minimum effect size, not as a quantitative estimate of the amount of saccadic suppression relative to fixation.

Afferent chromatic information channels may have one of three relationships with the saccadic suppression system. (1) Chromatic channels may be disassociated completely from the neural structures responsible for SSID (i.e., saccadic suppression may use only luminance channels); (2) chromatic channels may provide an input, but saccadic suppression is not activated by it alone (i.e., SSID may have selective or gated response properties); (3) chromatic channels may be associated with saccadic suppression mechanisms, but the slow temporal properties of chromatic channels cause retinal chromatic displacement information to arrive too late at the suppression site to initiate suppression.

These results add further evidence against the hypothesis that the visual component of SSID is due solely to lateral inhibition or spatial masking (Brooks & Fuchs, 1975). If this were the case, all displacement-detection thresholds would be expected to be isotropic (or identically anisotropic across all conditions if other factors caused the anisotropy). Figure 3, however, shows anisotropy in only the nonequiluminant saccadic condition. Furthermore, if SSID were simply spatial masking, then the relationship found between equiluminant and nonequiluminant displacement thresholds during fixation would not change during saccades. Against this prediction, we found that during saccades displacements in equiluminant conditions become more easily detectable than in nonequiluminant conditions, reversing the ratio of equiluminant to nonequiluminant thresholds found during fixation (Figure 3). Thus, the perceptual phenomenon of SSID is not due solely to spatial masking.

It is unlikely that subjects are simply comparing the position of the target before and after the saccade rather than failing to detect displacements during saccades. If this were true, target displacements in the same direction as the saccade would be more easily detected because target position after the saccade would be slightly closer to the fovea and would thus be more precisely localized. As can be seen in Figure 3, the nonequiluminant conditions show the opposite trend. In addition, this mechanism would apply equally to

equiluminant targets, yet Figure 3 shows that displacement detection in these conditions is isotropic with respect to saccade direction. The amplitude of the SSID effect here is smaller than that seen in some other studies (Bridgeman et al., 1975) because in the current experiments we did not optimize either the timing of the target displacement in relation to saccade onset or the retinal locations of the targets.

It might be argued that our findings could be explained by the lowpass spatial nature of chromatic channels versus the higher spatial-frequency characteristics of luminance channels. Following this argument, one would suppose that during a saccade the target is blurred (which is similar to being passed through a low-pass filter) and equiluminant target displacements would be more easily discerned than nonequilibrium target displacements because blurred images would be expected to be relatively more attenuated in the luminance channels.

This is not a likely explanation of our results, however, because the target in the nonequilibrium condition contrasts with the background not only in luminosity, but also in chromaticity. Given this, the color channels isolated in the equiluminant condition should pass on chromatic information about the nonequilibrium stimuli just as they did for the equiluminant stimuli. This would be shown even more clearly by psychophysically equating the chromatic and luminant contrast of the stimuli. However, Ilg and Hoffmann (1993) have shown that decreasing blur (i.e., using a target with higher-band spatial information) increases saccadic-suppression thresholds, just as we have shown. Thus, it seems unlikely that the blurring of the stimulus during a saccade can explain our results.

The question of the spatial frequency of the targets was also addressed by Burr, Concetta Morrone, and Ross (1994), who measured saccadic suppression of the detectability of a target briefly flashed under either equiluminant or nonequilibrium conditions. They found suppression only for targets of low spatial frequencies. Their results on flash suppression are complementary to ours on displacement suppression: both studies conclude that magnocellular channels are selectively affected.

One might argue that relative chromatic, as against luminance, contrasts went uncontrolled in our experiment and so our findings do not show a difference in displacement detection between chromatic and luminant channels so much as a difference in sensitivity to high and low relative contrasts. However, in the fixation condition, in which displacement thresholds were measured for the same targets as in the saccadic condition, nonequilibrium target displacements were more easily detected, as was expected from the literature on motion detection (Figure 2).

Our findings show that the retinal component of SSID relies upon luminance information to produce its

role in suppression. The results also confirm that decreasing the spatial contiguity of retinal samples in nonequilibrium conditions (displacing the target in the direction opposite the saccade) reduces the visual component of saccadic suppression just as it does in the equiluminant conditions (Macknik, Fisher, & Bridgeman 1991).

We can use these data to estimate the gain of the visual component of SSID. We assume first that an optimum gain was achieved in the nonequilibrium condition in which the target was displaced in the same direction as the saccade; target displacements were suppressed as well as possible. Second, we assume that the visual component of SSID completely failed in the equiluminant conditions; only extraretinal signals contributed to suppression. Now we can calculate the gain of the visual component of SSID. This value is derived by subtracting the combined equiluminance conditions, ratio values (or the conditions in which SSID was weak and presumably had no visual component; average ratio value = 39.99) from the ratio value from the nonequilibrium, same-direction condition (the condition in which SSID presumably had both visual and extraretinal components in full effect; ratio value = 76.39), and then dividing the difference by the full-effect value (i.e., the nonequilibrium condition, same direction; ratio value 76.39). Solving this equation results in a gain of 0.49, meaning that about half of normal saccadic suppression of displacement is due to extraretinal signals.

Acknowledgements These results were reported at the Association for Research in Vision and Ophthalmology Conference in Sarasota, Florida, May 4, 1991 (Macknik, Switkes, & Bridgeman, 1991). Results that confirm ours showing a decrease in threshold in equiluminant conditions were presented at the Advances in Color Vision Topical Meeting of the Optical Society of America in Irvine California, January 31–February 1, 1992, (Ishida, Shinoda, & Ikeda, 1992). This research was supported by a University of California President's Undergraduate Fellowship to SLM, AFOSR grant 95-0095 and a faculty research grant from the University of California, Santa Cruz, to BB.

We thank Mark Goettsche for his excellent technical assistance. We also thank Dr Richard Born, Dr Robert Desimone, Dr Brian Fisher, Dr Margaret Livingstone, Peter Nelson, Dr Philip Nelson, and Dr Mark Tramo for their comments on the early manuscript.

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