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RESEARCH NOTE

VOLUNTARY NYSTAGMUS, SACCADIC SUPPRESSION, AND STABILIZATION OF THE VISUAL WORLD

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Abstract—Voluntary nystagmus, a series of rapidly alternating saccadic eye movements accompanied by a failure of subjective stabilization of the visual world, was used to test the strength of relationship between subjective stabilization and saccadic suppression. Suppression of a full-field flash was similar during voluntary nystagmus and during voluntary saccades of the same magnitude (about 0.5 log unit threshold increase in each case) despite the difference in stabilization experienced in the two conditions. In a second experiment, the failure of subjects to perceive movement of a stabilized retinal image during voluntary nystagmus showed that no extraretinal signal was influencing apparent stimulus position. The results contradict the hypothesized role of saccadic suppression in subjective stabilization. The similarity of saccadic suppression during voluntary nystagmus and voluntary saccades (experiment 1) points out a significant similarity between the two types of eye movement, while the difference in subjective stabilization (experiment 2) reveals a significant distinction between them.

INTRODUCTION

It has been widely assumed that saccadic suppression, the increase of visual thresholds during saccadic eye movements, may aid in the subjective stabilization of the visual world during saccades (E. Matin, 1974; L. Matin, 1972). Masking of images during saccades is necessary to complete the stabilization process because the shifting of visual coordinates occurs more slowly and with different dynamics than the eye movement itself (Bichof and Kramer, 1968; Matin and Pearce, 1965; Matin, Matin and Pearce, 1969; Matin, Matin and Pola, 1970). At the peak of saccadic velocity the retinal image is sweeping the receptors so fast that no pattern information can be transduced. At the beginning and end of the movements, however, the eye is moving more slowly, resulting in the formation of images during the saccade. Some suppression of vision during saccades is felt to be necessary so that the inaccurately localized image which occurs near the beginning and end of a saccade will not be perceived.

E. Matin (1974) proposes a dual mechanism, with both saccadic suppression and compensatory extraretinal signals contributing to the subjective stabilization of the world. This idea can be tested empirically by examining conditions in which saccadic eye movements are not accompanied by the normal subjective stabilization. An investigation of saccadic suppression under these conditions would yield insights into the strength of the relationship between the two phenomena.

A saccadic eye movement unaccompanied by subjective stabilization has recently become available for study with the discovery by Shults, Stark, Hoyt and Ochs (1977) and Stark, Shults, Ciuffreda, Hoyt, Hsu, Kenyon and Ochs (1977) that voluntary nystagmus has a saccadic structure. Voluntary nystagmus is a rapid (about 20 Hz) pendular oscillation of the eyes, usually horizontal and conjugate (Blair, Goldberg, and Von Noorden, 1967; Goldberg and Jampel, 1962; Lipman, 1972; Westheimer, 1954; Wist and Collins, 1964). Voluntary nystagmus is invariably accompanied by oscillopsia, a rapid apparent jiggling of the visual world (Blair *et al.*, 1967; Goldberg and Jampel, 1962; Lipman, 1972; Westheimer, 1954; Blumenthal, 1973; Coren and Komada, 1972; Rosenblum and Shafer, 1966). Our own informal surveys of several hundred undergraduates have found that voluntary nystagmus can be performed by about 5% of the normal population, and that those capable of voluntary nystagmus have no pattern of ocular deficits or other unusual abilities.

Saccadic eye movements are ballistic in nature (their dynamics are not influenced by patterns or motions in the ambient visual array) and are defined by their dynamics in an invariant main sequence which relates the sizes of the movements to their durations and magnitudes (Bahill, Clark and Stark, 1975). All types of saccades fall on the same main sequence. Using these definitions, Shults *et al.* (1977) have shown that voluntary nystagmus consists of a rapid series of normal saccadic movements alternating in direction. This conclusion was reached by several methods: first, durations and peak velocities of the movements of voluntary nystagmus were plotted against their magnitudes in a main sequence diagram

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(Bahill *et al.*, 1975), and it was found that the movements of voluntary nystagmus matched well with the main sequence of normal saccades. Only the pulse-step control signal characteristic of saccadic eye movements is capable of accelerating the eye to saccadic peak velocities within the limitations of saccadic durations. The above authors confirmed this with a mathematical model of the eye movement control system, where it was shown that the nearly sinusoidal wave form of eye movement typical of voluntary nystagmus could be reproduced with a series of rapidly alternating normal saccadic control signals. The analysis of Shults *et al.* (1977) and of Stark *et al.* (1977) therefore shows that voluntary nystagmus is a series of saccadic eye movements, even though the nystagmus has the superficial appearance of a sinusoidal rather than a square wave pattern.

The saccadic nature of voluntary nystagmus in otherwise normal subjects provides a tool to test the relationship between saccadic suppression and subjective stabilization of the world. If these two pnenomena are closely linked, voluntary nystagmus without subjective stabilization should be free of saccadic suppression as well. Thus a test of saccadic suppression during voluntary nystagmus will reveal whether the suppression is influenced by the subjective stabilization or by the saccade itself.

In our first experiment, saccadic suppression during voluntary nystagmus was compared with the suppression obtained in the same subjects during voluntary saccadic eye movements of the same magnitude.

EXPERIMENT 1

Method

The observer sat in front of a hemicylindrical, uniformly illuminated (34.25 cd/m^2) screen, with the head restrained at chin and forehead. The observer's horizontal eye movements, monitored by paired infrared-sensitive photocells mounted from below, were displayed on an oscilloscope. The blurry contours of the photocells and the infrared light source were obscured by a baffle below the observer's line of sight. There was so little contrast in the visual field that observers complained that the ganzfeld faded out. Full-field 10 msec flashes were presented a four intensities: 0.3, 0.4, 0.7 and 0.9 log units above threshold. The sampling of the 0.9 log unit condition was limited when it was found that subjects always detected a flash of this intensity. Threshold was determined by a staircase method, and was defined as that intensity at which the flash was detected during fixation on 50% of the trials.

Before each session the average amplitude of each observer's voluntary nystagmus was measured and fixation points were arranged so that voluntary saccades of the same mean amplitude could be made. This was done in order to directly compare the amount of suppression found during the two kinds of eye movements.

Each subject was run in a block of sixty trials. Seventy-five percent of the trials were randomly assigned to be flash trials, while no flash occurred during the remaining twenty-five percent of the trials. On a given ten-trial series the observer was asked to make either a voluntary saccade or voluntary nystagmus while one of the strobe intensities was randomly assigned on each flash trial. After each trial the observer indicated with a forced choice whether or not a flash had been presented.

Results

The amplitude of the voluntary nystagmus produced by our six observers varied between observers and within observers, though it was possible to establish a mean magnitude of nystagmus in each subject. The frequency of oscillation was about 20 Hz; this corresponds to 40 saccades per second, since each cycle consists of two saccades. The character of the movement remained unchanged when observers performed nystagmus in the dark. Some of our observers used convergence to initiate their nystagmus, while others did not; there was no difference in results for the two types of initiation. Because our stimulus was a full-field flash, differences in accommodation or eye position would not be expected to change the detectability of the stimulus.

The main result is that saccadic suppression occurred during voluntary nystagmus (Fig. 1, left). The visual threshold for a diffuse stimulus flashed against a uniform dim background, conditions designed to reduce the effects of masking, was 0.53 log units above the corresponding threshold for each subject during fixation.

The suppression found during voluntary nystagmus did not differ significantly from that found during horizontal voluntary saccades of the same amplitude (Fig. 1, right). Values averaged over subjects and sessions were 0.45 log units of threshold elevation for voluntary saccades and 0.53 log units elevation during saccades of voluntary nystagmus. This difference is not statistically significant (two-tailed Sandler's $A = 0.93$, $0.2 < P < 0.5$). The variability between observers is indicated in Fig. 1. It is similar in both cases and is in agreement with the literature, where a saccadic suppression of about 0.5 log units is usually found (Volkman , Schick and Riggs, 1968; Zuber and Stark, 1966). Figure 2 compares the nystagmus and saccade results for pooled observers.

Of interest is a small increase in suppression with larger movements for subject KK with both types of saccades. An increase in suppression with larger saccades was also found by Bridgeman, Hendry, and Stark (1975) and by Mitrani, Yakimoff and Mateeff (1970).

Discussion

These results clearly show the simultaneous occurrence of both saccadic suppression and oscillopsia,

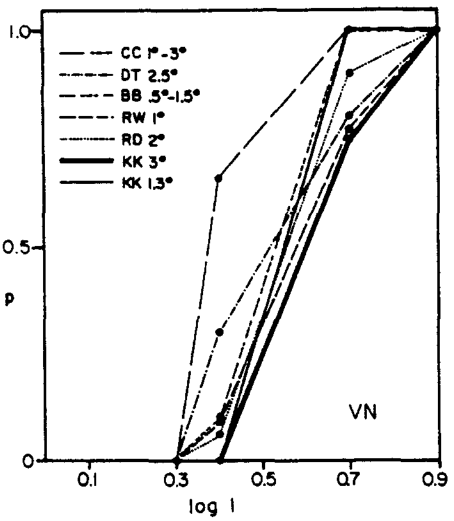

Fig. 1. The probability (p) of detecting a flash of light during voluntary nystagmus (vn) and voluntary saccades (vs) as a function of the intensity of the flash.

implying that saccadic suppression and the stabilization of the visual work are not tightly linked.

It is possible, however, that the subjective stabilization mechanism, whatever its nature, is still fully operative in the nervous system during voluntary nystagmus but is simply overloaded by the very rapid sequence of saccadic eye movements. In this case the operation of the stabilization mechanism, even if unsuccessful, could lead to saccadic suppression. (We thank N. Nelken for suggesting this possibility.) We tested this hypothesis by measuring the subjective stability of a stabilized retinal image on a blank background during voluntary nystagmus. Any mechanism which generates a new local sign should induce an apparent shift of an image which maintains a constant position on the retina.

EXPERIMENT 2

Methods

In order to ascertain whether an extraretinal signal was influencing apparent localizations along with eye movements we tested for apparent movement of an afterimage during voluntary nystagmus. After the observer dark adapted for 20 min, a strobe illuminated a black screen with a vertical white stripe. A small spot of luminous paint at the center of the stripe served as a fixation point in the dark. The infrared photocell system enabled us to monitor the nystagmus in complete darkness. When the observer had a stable positive afterimage, he performed voluntary nystagmus.

Each session consisted of ten trials: after each trial the observer was asked to describe the apparent movement of the stripe and to compare it with his oscillopsia in the light condition. If an extraretinal signal were influencing the apparent position of the stripe, the observer should report apparent movement of the afterimage; in the absence of such a signal the image should appear to remain stationary.

Results

None of the observers reported any movement of an afterimage during voluntry nystagmus. In fact, the afterimage was so stable that some of the observers, lacking the usual visual feedback of oscillopsia, expressed doubt about the success of their attempts to induce voluntary nystagmus. This lack of apparent movement is in striking contrast to the dramatic oscillation of the world and the mild disorientation usually experienced during voluntary nystagmus. It is the reverse of the situation with voluntary saccades, where afterimages are perceived to jump with the eye while normal images remain subjectively stable. Thus it seems unlikely that any extraretinal information about eye movement during voluntary nystagmus is used to cancel out or substract the effects of the nystagmus on retinal signals. Even if an extraretinal mechanism were only partly successful in cancelling

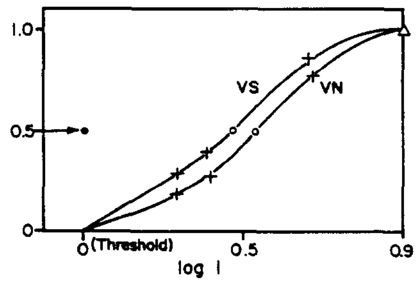

Fig. 2. A comparison of detectability of flashes during saccades and nystagmus, using the same axes as Fig. 1. At $P = 0.5$ (arrow) the thresholds for fixation (solid circle) and for vs and vn (open circles) are shown. The crosses show probability of detecting flashes whose intensities were 0.3, 0.4 and 0.7 log units above threshold. At 0.9 log units above threshold the flash was always seen (indicated by triangle).

the oscillopsia, some apparent movement of the stabilized afterimage would have been observed.

GENERAL DISCUSSION

These results show that saccadic suppression is similar in magnitude during voluntary nystagmus and during voluntary saccades of the same magnitude, and that the operation of an extraretinal signal during voluntary nystagmus cannot account for the results. We can conclude that saccadic suppression is not adequate by itself to prevent the subjective appearance of movement of the visual world during saccades, for our results have shown voluntary nystagmus to be clear counter-example.

Our results also test the conclusion of Stark *et al.* (1977) and Shults *et al.* (1977) that voluntary nystagmus is saccadic, for saccades of all other types are known to produce saccadic suppression (Zuber and Stark, 1966), and the finding of saccadic suppression for voluntary nystagmus strongly suggests that it should be included with voluntary versional saccades, microsaccades, and optokinetic and vestibular nystagmus saccades as products of the saccadic control system.

The results also show that saccadic suppression is related to the mechanism of saccade generation itself, and not to the process of retargeting the eye, for the intersaccadic latency of about 25 msec during voluntary nystagmus is much shorter than the minimum interval of about 200 msec for the generation of a versional saccade. Saccadic suppression is undiminished under conditions where retargeting cannot take place; presumably, retargeting mediates stabilization.

Many mechanisms, peripheral and central, have been proposed to account for saccadic suppression—masking, smear of the image, mechanical shear of retinal elements during eye rotation, overload of visual information processing, non-specific central inhibition, and most recently positional uncertainty (Cohn and Lasley, 1974; Matin, 1974; Greenhouse, Cohn and Stark, 1977). Uncertainty would in principal be greater during saccades of voluntary nystagmus accompanied by oscillopsia than in same sized normal voluntary saccades. Our finding of similar saccadic suppression under the two conditions contradicts this prediction of the uncertainty hypothesis.

Another possible interpretation of our result is that the increase in threshold resulted from a shift in criterion for flash detection rather than from a true decrease in sensitivity. Although it is possible that the subject's criterion may rise during and just before the saccade, resulting in an increase in apparent thresholds even though the sensitivity remained unchanged, we consider this to be unlikely since Pearce and Porter (1970) have shown that saccadic suppression of flashes cannot be accounted for by criterion shifts; the effect remains when a criterion-free, two-alternative forced-choice method is used. More recently, Bridgeman and Stark (1979) have shown that saccadic suppression for target displacements can be obtained with a two-alternative forced-choice procedure.

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