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RESEARCH NOTE

SACCADIC SUPPRESSION OF IMAGE DISPLACEMENT[1]

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INTRODUCTION

Helmholtz (1867) suggested that the retinal image displacement vector, the afferent signal, is compared with the expected saccadic displacement vector, the efferent copy (Holst and Mittelstaedt, 1950) carried by the corollary discharge (Sperry, 1950) and this process may be called the "vectorial Helmholtzian comparator for the frame of reference". The results presented in this report show that collinear and orthogonal image displacements undergo quantitatively similar raising of thresholds with saccades; thus, saccadic suppression of displacement is a quantitative but non-vectorial effect following the vectorial Helmholtzian comparator.

The relationship between saccadic suppression and the Helmholtzian frame-of-reference computation was first suggested by Stark, Michael and Zuber (1969) and also discussed by Bridgeman, Hendry and Stark (1975). It is known from the work of Bischof and Kramer (1968), Matin, Matin and Pola (1970), and Matin (1974) that this computation is not simultaneous with the time course of the saccadic trajectory; indeed, objects of attention and foveal images are computed before other parts of the retinal image (Bischof and Kramer, 1968). Thus, saccadic suppression of image displacement appears to have functional correlates, in contrast to such various other phenomena as have been established to be suppressed during a saccade—light flash detection (Latour, 1962; Zuber and Stark, 1966; Volkmann, Schick and Riggs, 1968; Matin *et al.*, 1970), pattern recognition (Stark, 1971), pupillary response (Stark *et al.*, 1969), visual-evoked responses (Stark *et al.*, 1969), and auditory-evoked responses (Ebersole and Galambos, 1969).

Our results speak to the issue of relating a functional role for non-vectorial saccadic suppression to dynamic or static mismatches in the vectorial Helmholtzian comparison. They support the saccadic suppression of image displacement which was first quantitatively presented by Bridgeman *et al.* (1975), and in turn extend earlier results (Ditchburn, 1955; Wallach and Lewis, 1965; Sperling and Speelman, 1966; Gross, Vaughan and Valenstein, 1967; Beeler, 1967; Mack, 1970; Chase and Kalil, 1972).

METHODS

The subject's head was stabilized by a bite bar at the center of a semi-cylindrical screen of radius 0.85 m which formed a "one-dimensional ganzfeld" (0 log ft-L) (Bridgeman *et al.*, 1975). The stimulus, consisting of a 10° square containing numerous dots in a random pattern (1.8 log ft-L), was projected onto the ganzfeld by a mirror mounted on a galvanometer (the target velocity of 900° $\sec^{-1}$ was the fastest stable speed obtainable with our apparatus). Thus, the time and size of the target displacement could be varied. The stimulus was slightly defocused, making the target borders less defined, and consequently, less effective as displacement cues; this defocusing decreased the rate of change of luminance with time without changing the density of random dots. Background auditory noise effectively masked any stimulus displacement-related sounds.

The subject viewed the target binocularly and was instructed to perform horizontal saccadic eye movements from one vertical border of the stimulus target to the other border. The stimulus was displaced at unpredictable times to the left or right in the first set of experiments (collinear) and up or down in the second set (orthogonal). Collinear and orthogonal thus relate direction of stimulus displacement to direction of eye movement. The subject's task was to signal the occurrence of any stimulus movement by depressing a switch. By avoiding a division of the task into discrete trials, we reduced the "false alarm" rate nearly to zero.

Eye movements were monitored by the use of i.r.-sensitive photocells (Bahill, Clark and Stark, 1975; Stark, Vossius and Young, 1962) positioned so close to the eye that focused contours from the monitoring apparatus were not present.

Experiments were performed until the subject reported fatigue or until the dynamics of the eye movements appeared irregular (Bahill and Stark, 1975a), usually 10–15 min per session. The three subjects usually performed saccades at approximate rates of from 0.5 to 2 $\sec^{-1}$, interacting with random target displacements averaging 1 $\sec^{-1}$. All of the eye movements which occurred within 100 msec of a target displacement were used (about one-fourth of 20,000 total eye movements); thus, 20–40 movements contributed to each point of the graphs in Fig. 1. For each experimental session, the particular displacement size and its orientation were constant and thus known to the subject; the direction of displacements and the timing with

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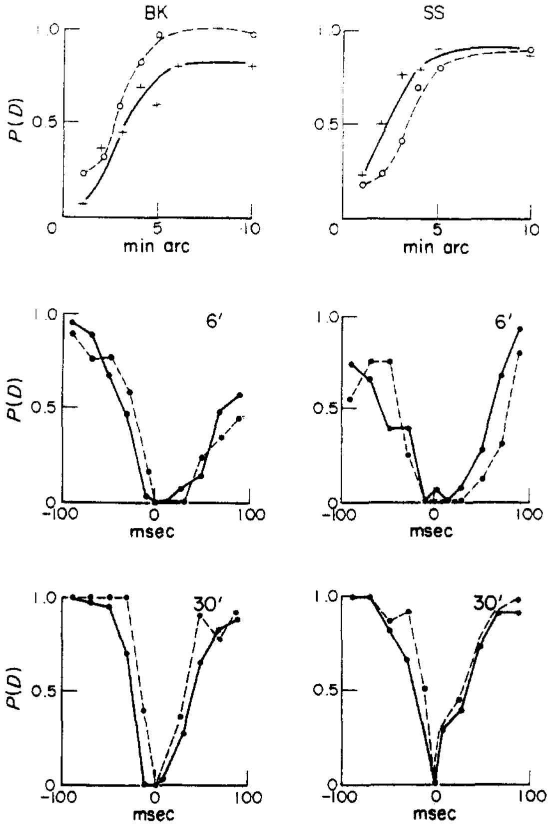

Fig. 1. Upper: Vertical and horizontal target displacement detection sensitivity for subjects BK (left column) and SS (right column) during steady fixation. Dashed lines, vertical target displacement; solid lines, horizontal displacement. Probability of target displacement detection, *P*(*D*), is plotted on the ordinate, and amplitude of displacement is represented on the abscissa in min of arc. Middle: Detection of collinear and orthogonal target displacements of 6' of arc with 10° horizontal saccades. Dashed lines, orthogonal displacement; solid lines, collinear displacement. Probability of target displacement detection is plotted on the ordinate and time, in msec, with respect to the initiation of eye movement on the abscissa. Negative time refers to time before the eye movement begins. Lower: As above for a second experimental session with target displacements of 30' of arc.

respect to the saccade were unpredictable. Eye position, stimulus position, and subject response were recorded simultaneously on strip chart paper for later analysis.

RESULTS

Typical ogive-shaped detection sensitivity curves exhibited by two subjects for both vertical and horizontal displacements during steady fixation are shown in Fig. 1 (upper). A 0.5 probability of detection rate (threshold) was attained for target displacements between 2' and 3' of arc in size. Target displacements of 6' of arc or greater were detected at much higher frequencies.

Saccadic suppression of detection of target displacement during saccadic eye movements was similar for displacements either collinear or orthogonal to the orientation of the saccade. Probability of detection for a 6' displacement vs time with respect to the beginning of a saccade for both orthogonal and collinear displacements is shown in Fig. 1 (middle). Partial suppression began less than 100 msec before the initiation of a saccade. Nearly 100% suppression of detection was reached up to 20 msec prior to the saccade and persisted for 40–50 msec. The suppression subsequently fell off between 50 and 100 msec after initiation of the saccade.

Suppression of detection of a 30' displacement was also similar for collinear and orthogonal directions as shown in Fig. 1 (lower). For both displacement orientations, the extent of the suppression was diminished compared to the 6' target displacement. The probability of detection was higher at all times and the duration of the suppression effect was also noticeably reduced. Thus the effect of the increased target displacement is to counteract saccadic suppression.

DISCUSSION

Saccadic suppression of target displacement is greater for larger saccades and for smaller target displacements. From quantitative studies Bridgeman *et al.* (1975) concluded that saccadic suppression of displacement "is complete if eye movement is more than about three times larger than target displacement"; this quantitatively explains why we do not see our own saccadic eye movements in a mirror—the ratio of target displacement to eye movements is too low. Contrariwise, if the ratio is increased by looking at the eye in a strongly magnifying mirror, the eye movement can be seen.

The significant finding that collinear and orthogonal displacement equally suffer saccadic suppression strongly argues against the vector arguments relating saccadic suppression to the frame-of-reference computation in a direct manner; further support is obtained when the Bridgeman *et al.* (1975) data are seen to have had no sign effect; that is, target displacements in either direction with respect to saccadic direction were equally suppressed in a quantitative fashion. Recently, Bahill and Stark (1975b) have shown that most horizontal eye movements have small vertical components; thus, the possibility exists that obliquity of our subject's eye movements not recorded with our horizontal eye movement devices might have provided enough vertical movement to provide the orthogonal displacement effect. The strength of our orthogonal effect, however, suggests this is not the case. Suppression of orthogonal displacement is as large as suppression of collinear displacement and both are similarly functions of target displacement. The vertical components of the eye movements would have had to be nearly as large as the horizontal components if obliquity of eye movements were to explain our results. This conclusion is strengthened by Mack's (1970) finding that vertical displacements during saccades were about as strongly suppressed as horizontal displacements, although Mack did not vary the interval between eye movement onset and target movement.

Thresholds of angular displacement reported here are important relative to one another, but should not be taken as generally applicable values; changes in stimulus brightness, sharpness and configuration, and in instructions to subjects, may influence threshold values. Bell and Lappin (1973) found a psychophysical interaction between detectability of direction of a displacement and the density of a displaced random dot pattern, such that displacement detectability is lower for high-density patterns than for low-density patterns. The results of Bridgeman *et al.* (1975) extrapolated to the saccade size used here show similar thresholds, however, despite differences in target stimuli.

The overload hypothesis for saccadic suppression put forward by Stark *et al.* (1969) remains viable, and indeed our results can be used as additional evidence for this non-vectorial effect.

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