Vision Res. Vol. 25, No. 8, pp. 1077–1082, 1985
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0042-6989/85 $3.00 + 0.00

ACCURACY OF SPATIAL LOCALIZATIONS NEAR THE TIME OF SACCADIC EYE MOVEMENTS*

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(*Received* 12 *March* 1984; *in revised form* 18 *March* 1985)

Abstract—Two-dimensional eye movements were recorded while subjects used a hammer to strike targets that were flashed-on briefly before, during or up to 750 msec after a horizontal saccade. Mean position of hammer blows was 20 min arc (SD = 67 min arc) from the target when the only cue to target location was eye position. Position of responses varied slightly with time of target exposure relative to the saccade. These results show that observers can closely monitor small changes in eye position during and near the time of saccadic eye movements.

Saccades Visual localization Eye position signal

INTRODUCTION

Information about both the position of an object's image on the retina and the position of the eyes is required to accurately localize objects seen with the moving eye (Helmholtz, 1963). Eye position information is needed for localization because the relation between retinal image position and object location relative to the head is not fixed, but changes as a result of eye movements. Consequently, subjects must take eye position into account when they localize objects. Models of localization in which neural analogues of object position on the retina and eye position in the head are added to determine object location have been proposed by Sperry (1950), von Holst (1954) and von Holst and Mittelstaedt (1950). These models postulate that information about eye position is obtained from nonretinal sources, such as efference copies of motor commands sent to the extraocular muscles.

Several investigators have attempted to assess the quality of nonretinal eye position information under dynamic conditions by asking subjects to report the location of targets flashed briefly before, during or after a saccade made in the dark. These studies showed that subjects mislocalized targets flashed-on during or near the time of a saccade in a way suggesting that there was poor temporal correspondence between changes in the nonretinal eye position signal and actual eye position during the saccade (Matin, 1972, 1976; Matin and Pearce, 1965; Matin *et al.*, 1969; Matin *et al.*, 1970; Pola, 1976).

These experimental results are surprising because they make it difficult to understand the accuracy of visuo-motor localizations under normal conditions. If the eye position signal is as sluggish as the psychophysical results imply, and it is used in localizations, stationary objects in the visual field should appear to move constantly during normal periods of looking around with saccadic eye movements (Skavenski and Hansen, 1978). This is a direct consequence of the sluggish growth of the eye position signal. Since observers do not report such apparent movement of stationary objects either under normal or impoverished viewing conditions, it has been suggested that some other mechanism must account for the eye movements. For example, Matin and Matin (1972) and Campbell and Wurtz (1978) proposed that spatial–visual interactions, such as metacontrast, are used to suppress perception when there are large discrepancies between nonretinal eye position information and eye position following a saccade. More recently, it has been suggested that localization is based solely on information contained within the retinal image in normal lighted environments [the "visual capture" of Matin *et al.* (1982)]. However, the results of the passive eye displacement experiments (Helmholtz, 1963) suggest that these visual factors alone cannot explain the perceived stability of visual space. To illustrate, observers report that objects seem to change position when the eye is passively moved, and the image of the entire visual field sweeps across the retina. In this case, information about changes in eye position was not obtained from visual sources.

This failure of visual mechanisms to provide information about changes in eye position encouraged us to re-examine the role of nonretinal eye position information in visual localization during saccadic eye movements using a motor task. This response was selected because other studies had shown that it was sensitive to small changes in eye position during

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*This research was supported by National Science Foundation Grant BMS 75-18181 and National Eye Institute Grant EY 2409 to A. A. Skavenski and National Eye Institute Grant EY 05325 to A. B. Fulton.

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fixation (Hansen and Skavenski, 1977) and smooth pursuit (Hansen, 1979). In the following experiment, we found that subjects could accurately localize a target that was flashed-on briefly before, during, or up to 750 msec following a saccade made in the dark when they attempted to hit it with a hammer.

METHODS

Eye movements were recorded using a modified version of the magnetic-field scleral search-coil technique developed by Robinson (1963). Two magnetic fields alternating at 5.5 kHz in spatial and temporal quadrature were produced by passing sinusoidal currents through coils of wire mounted along the edges of a 2 m wooden cube. These large coils, about three times the size of those used by Robinson (1963), were designed to prevent subjects from touching the coils when they pointed to stimuli, and to make the system relatively insensitive to head translations. For example, a head translation of 5 cm produced an artifact equivalent to less than 10 min arc of eye rotation. Consequently, it was not necessary to restrain the subject's head during these experiments. Electric potentials induced in a search coil mounted on a tight-fitting molded scleral contact lens permitted simultaneous recording of horizontal and vertical eye position relative to the head. Twenty to thirty-five mm Hg suction was used to minimize contact lens slippage. The left eye was closed and covered. Potentials from the search coil were resolved into horizontal and vertical components with a lock-in amplifier, scaled and recorded on magnetic tape for later analysis. In the final measurements, eye position could be resolved to within 5 min arc. Overall system bandwidth was 160 Hz.

Two subjects, R.H. and A.S., participated in this experiment. Both subjects were emmetropic with the contact lens in place, and both had participated in other eye movement experiments.

Targets were pieces of white paper with a black line drawn through the center, and placed on a movable anvil 1 m from the subject's right eye. The anvil consisted of a heavy, light-tight wooden box covered by a piece of clear lucite. A xenon-arc strobe tube mounted inside the anvil produced a brief (< 2 msec) flash that illuminated a 3 × 4 deg arc elliptical area centered on the black line drawn on each paper target (luminance = 6.4 cd/m^2). The light output of the strobe was monitored by a high-speed phototransistor (MRD-3050-7535) mounted in the anvil. Pulses produced by the phototransistor were recorded on magnetic tape along with eye position. The anvil was placed on a track that allowed it to be positioned at randomly chosen points along a 25 deg arc to the right of straight ahead. Eight target positions were employed.

Subjects adapted to a 270 cd/m^2 Ganzfeld for 30 sec before each 5 sec trial to ensure that they were light adapted and, therefore, less sensitive to stray light. The subject began a trial immediately after being placed in the dark. Three seconds after the beginning of a trial, a brief tone (100 msec) signalled the subject to make a large horizontal saccade to the right (average amplitude = 8 deg arc; range: 2–20 deg arc). Horizontal eye position was differentiated by an analog circuit, and the resulting signal compared to a reference potential difference. When horizontal eye velocity exceeded 125 deg arc/sec, a digital logic system presented a flashed target after a delay of 0–750 msec. In addition, on some trials, the target flash occurred during the latency period prior to saccade onset. This was accomplished by using the signal that triggered the tone to initiate a delay of 0–200 msec before the target flash. About 500 msec after the flash, the subject attempted to strike the black line on the target with the rounded end of a ball peen hammer. This response was selected because it is precise (Howarth, Beggs and Bowden, 1971), and sensitive to small changes in target position during fixation (Hansen and Skavenski, 1977) and smooth pursuit (Hansen, 1979). After the response, the Ganzfeld was repositioned and illuminated. The paper target, bearing a small impression where the hammer struck, was removed for measurement, and the anvil moved to a new position. A total of 45 pointing responses were collected for each time of target exposure. Data were collected for saccades directed to the right for both R.H. and A.S.; R.H. later repeated the experiment with saccades directed to the left.

During trials, subjects could not see any part of their bodies, the hammer, or any other visual feature in the room except the target when it was flashed-on.

Subjects were not allowed to practice localization of these targets when visual cues to target location were available, and never received feedback about the accuracy of their responses. This strategy was adopted to ensure that subjects could not learn target position or correct systematic errors they may have made by deliberately introducing a bias in their responding. In addition, the subject did not know when the flash would occur, or which target would be presented on a given trial. Possible auditory cues to target location were masked with white noise (80 dB).

Under these conditions, localizations depended critically on the position of the eye in the head, because no visual cues to target location were available. In addition, since the target was flashed briefly, it was unlikely that information about retinal image motion provided any useful information about target location.

RESULTS

To assess performance, error (the signed angular distance between position of the hammer blow and target position) was measured for every trial. No systematic improvement in the accuracy of target localization was observed during these experiments.

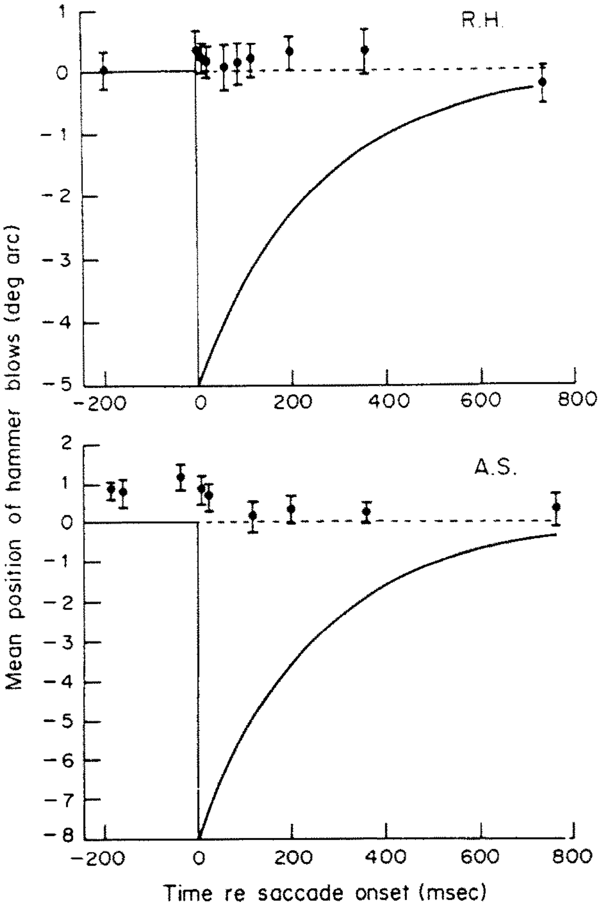

Fig. 1. Summary of the results of a localization experiment in which subjects struck small targets flashed-on at various times before, during or after saccadic eye movements. *Mean position of hammer blows* for subjects R.H. and A.S. is plotted as a function of *time with respect to saccade onset* when saccades were directed to the right. Zero corresponds to hammer blows directly on target, and to the time of saccade onset. Positive numbers represent hammer blows to the right of the target, and to times after saccade onset. Data points are the mean of 45 responses; error bars show ±2 SEM. The solid lines indicate the expected mean position of hammer blows predicted with a sluggish eye position signal.

Also, the size of these errors did not vary with saccade size. Consequently, a mean error was calculated for each target position and time of target presentation with respect to saccade onset. Analysis of variance revealed that performance did not vary with target position ($F = 0.51$; d.f.: 7,450; NS for right saccades, and $F = 0.56$; d.f.: 7,450; NS for left saccades for subject R.H. and $F = 0.57$; d.f.: 7,320; NS for subject A.S.). Hence a mean error was calculated for each time of target presentation. Figure 1 shows mean error and its standard error as a function of time of target presentation. Although performance varied with time ($F = 2.1$; d.f.: 9,400; $P < 0.05$) for R.H. when he made saccades to the right, the mean position of hammer blows was always close to actual target position. Mean errors for A.S. were larger because a response bias caused him to consistently strike hammer blows to the right of the target. This tendency can be seen in the mean position of hammer blows 200 msec before and 750 msec after the saccade. Again, for A.S. analysis of variance showed that performance varied systematically with time ($F = 2.1$; d.f.: 7,320; $P < 0.05$). Performance did not vary with direction of the eye movement (Fig. 2); errors were comparable when R.H. directed saccades to the left ($F = 5.3$; d.f.: 9,400; $P < 0.05$).

DISCUSSION

The present results have shown that subjects can strike hammer blows to within minutes of arc of targets flashed-on during or near the time of a saccadic eye movement; assuming that head position was known, the only cue to target location was eye position. Furthermore, although accuracy of localization varied systematically with time, responses usually fell near the actual target position. These results suggest that eye position was monitored closely, and that there was excellent temporal correspondence between changes in eye position and the eye position signal during the saccade. This can be seen by comparing the mean position of the hammer blows with the solid continuous line which indicates the expected mean position of hammer

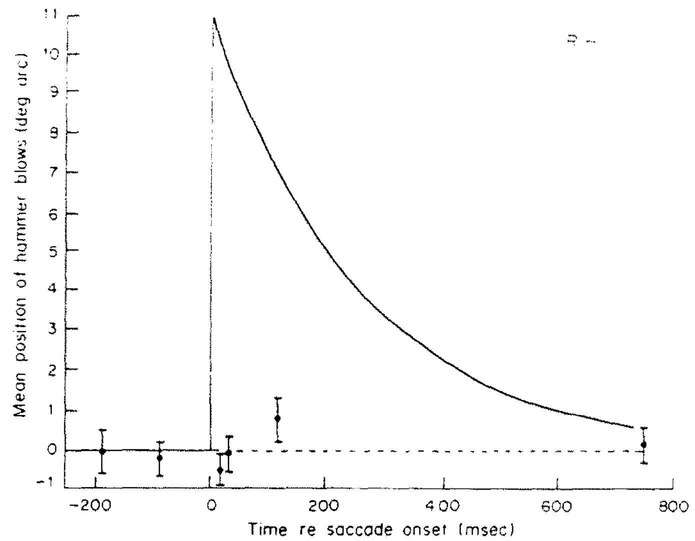

Fig. 2. *Mean position of hammer blows* for subject R.H. is plotted as a function of *time with respect to saccade onset* when saccades were directed to the left. All other features are similar to those in Fig. 1.

blows predicted with a sluggish eye position signal. This prediction was obtained by adding retinal image position to an eye position signal that followed the actual change in eye position with a 250 msec time constant during an 8 deg arc saccade for A.S. and a 5 deg arc saccade for R.H. Clearly, hammer blows were much closer to the target than the prediction during and just after the saccade. For both subjects, the mean position of the hammer blows during and just after the saccade was moderately displaced to the left of the mean position just before the saccade. The modest displacement suggests that the eye position signal was good but not perfect in following the actual change in eye position during the saccade.

We estimated the dynamic characteristics of the eye position signal using a model adapted from the one proposed by von Holst (1954) and others, and shown in Fig. 3. According to this model, signals proportional to retinal image position ($\theta_{T/E}$) and eye position ("$\theta_{E/H}$") are added to reconstruct target position ("$\theta_{T/H}$"). The model in Figure 3 has been modified by adding an element that causes the eye position signal to grow exponentially with time constant $1/a$. This modification provided a close description of Matin's (1972, 1976) results when a long time constant (250 msec) was used to estimate changes in the eye position signal (Hansen and Skavenski, 1977; Skavenski and Hansen, 1978).

Using data from the present experiment, the position of the target image on the retina was determined by subtracting measured eye position relative to the head from the position of the target with respect to the head. Position of the target image on the retina was then subtracted from the position of the hammer blow to estimate the value of the eye position signal on that trial. To account for differences in saccade

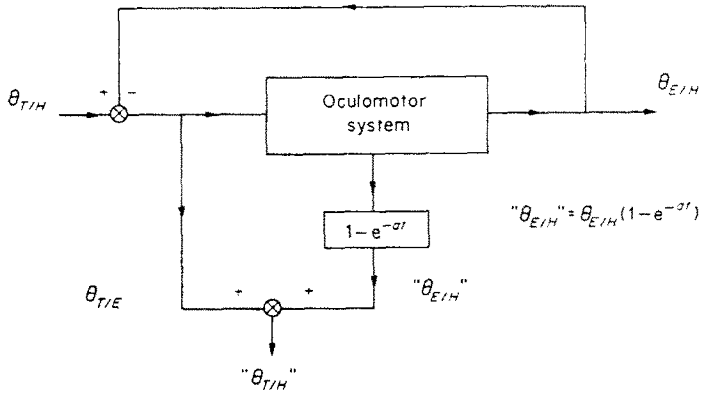

Fig. 3. Schematic diagram of a model of localization. The model postulates that neural signals representing the position of a target's image on the retina ($\theta_{T/E}$) and the position of the eye in the head ("$\theta_{E/H}$") are added to determine the position of the target with respect to the head ("$\theta_{T/H}$"). Information about eye position, called the eye position signal ("$\theta_{E/H}$"), is thought to arise from nonretinal sources, such as motor commands sent to the extraocular muscles. Objective target position is shown as $\theta_{T/H}$; $\theta_{E/H}$ is measured eye position. This model includes an element that causes "$\theta_{E/H}$" to follow eye position ($\theta_{E/H}$) exponentially with time constant $1/a$.

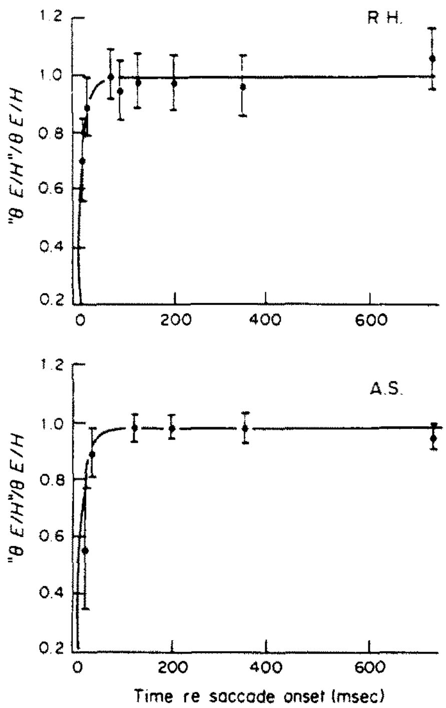

Fig. 4. Fraction of the change in eye position registered by the eye position signal ("$\theta_{E/H}$"/$\theta_{E/H}$) as a function of *time* in msec for subjects R.H. and A.S. Each point is the mean of 45 fractions; error bars represent ±2 SEM. Best fittings exponentials are shown as solid lines. (See text for computational details).

size from trial to trial, the estimated value of the eye position signal was divided by the actual change in eye position to obtain "$\theta_{E/H}$"/$\theta_{E/H}$, the fraction of the change in eye position registered by the eye position signal. Mean values of "$\theta_{E/H}$"/$\theta_{E/H}$ and its standard error are plotted in Fig. 4 to show the temporal growth of the eye position signal. Best fitting exponential functions were found using a least squares criterion. These functions had time constants of 9 msec for R.H. and 12 msec for A.S. Such short time constants support our conclusion that the eye position signal very closely followed the change in eye position during saccades in our localization task.

Previous investigators have shown that subjects can use nonretinal eye position information to guide the trajectory of saccades to positions defined by previously seen fixation targets (Becker and Fuchs, 1969; Becker and Jürgens, 1976; Becker and Klein, 1973; Gresty and Leech, 1976; Hallett and Lightstone, 1976a,b; Hansen and Skavenski, 1977; Levy-Schoen and Blanc-Garin, 1974; Ono and Nakamizo, 1977; Skavenski and Steinman, 1970) suggesting that reliable eye position information was available to the oculomotor system. However, these investigators reported that the average final eye position was 1–6 deg arc from the goal. These relatively large errors seem to indicate that nonretinal eye position information provided only a crude indication of eye position during the saccade. A localization mechanism based solely on an eye position signal with these characteristics would be ineffective because large localization errors would be made after every saccade. However, the eye position signal may not be as sloppy as these results indicate. In studies of control in the dark, the subject looked back to the remembered target position some time after the target was removed from view. The errors may have been due, in part, to poor spatial memory for target location. That is, the localization mechanism may have had access to accurate non-retinal eye position information but poor spatial memory may have interfered with an accurate response. It is unlikely that this factor contaminated the present results because of the very short interval between target presentation and the response (500 msec).

The discrepancy between the present results and those obtained in prior psychophysical studies of perceived visual direction cannot be explained easily. In the present study, subjects localized targets more accurately than previously reported in studies of perceived visual direction. For example, Matin (1972) reported that subjects made errors of about 1 deg arc when they verbally reported the location of a target flashed-on near the end of a 2 deg arc saccade. In the present study, we found that the mean position of hammer blows was 22 min arc away from targets flashed-on near the end of an 8 deg arc saccade. Bridgeman *et al.* (1975) have noted a similar discrepancy; they found that subjects accurately pointed to targets that were displaced during saccadic eye movements even though they verbally reported that the target had not changed position. It is possible to explain these results by assuming that the different tasks employ different localization mechanisms. Pointing may tap a basic motor control system that relies heavily on information about eye position. The verbal report, on the other hand, may employ a mechanism based on information about retinal image motion, and not have access to the same eye position information used to guide the motor response. This type of localization mechanism could account for retinal image motion resulting from eye movements by analysis of that retinal image motion. That is, the mechanism would determine that an eye movement occurred when the images of all objects in the visual field shifted by an equal amount. However, the passive eye displacement experiment seems to rule this type of mechanism out because when the eye is pressed, the subject reports that the visual field has shifted. In this case, the perceived displacement is the same as it would be following an eye movement (Skavenski *et al.*, 1972).

A second, more likely explanation is that these two tasks employ different frames of reference. Prior psychophysical experiments required that subjects report the location of one target with respect to a previously seen fixation light. Consequently, the subjects may have ignored changes in eye position, and based their responses primarily on the relative position of the retinal images of the target and fixation light. Pointing an eye or a limb, on the other hand requires that the subject take eye position into account so that the target can be localized in space.

In summary, the present results have shown that accurate nonretinal eye position information is available for localization before, during, and after saccades, and that there is excellent temporal correspondence between changes in eye position and the eye position signal during the eye movement. This information could be employed in a localization mechanism like the one proposed by von Holst (1954) and others, and thus play an important role in visual localization.

Acknowledgements—We thank Janet Conway, Susan Harris, Christopher Leonard and Rose Marie White for their valuable technical assistance. These results were reported to the AVRO meeting of May, 1977 at Sarasota, Florida.

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