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LETTER TO THE EDITORS

THE OCULOMOTOR ERROR SIGNAL IN THE FOVEA

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FIXATION stability remains much the same when the fixation target generates a visual error signal anywhere on the foveal floor. To illustrate, STEINMAN (1965) asked subjects to fixate at the center of concentric homogeneous disks of white light that varied in dia. from 1·9 to 87·2′ arc and found that fixation stability was good and almost uniform over the entire region studied, i.e. standard deviations of eye position remained less than 4 min arc even when the error signal was generated by the edges of disks that fell at increasing distance from the preferred fixation locus. RATTLE (1969) confirmed and extended this finding (1) by showing that fixation stability (root-mean-square angular deviation of the eye from its mean position) "increases by less than a factor of two" when subjects fixate at the center of disks whose diameters varied from 19′ to as much as 240′ arc, and (2) that the greater circumference of large targets was not responsible for this effect because similar results were obtained when subjects fixated at the center of 2 small dots separated either vertically or horizontally 230′ arc.

These findings are puzzling because they suggest that the oculomotor error signal is generated by different physiological arrangements than those which determine characteristics of visual acuity, known to deteriorate markedly as tests are made at increasing distances from the preferred fixation position (LE GRAND, 1967). This puzzle may arise from the technique Steinman and Rattle used to estimate the way the oculomotor error signal varies within the fovea. Both measured fixation stability during maintained fixation of stationary targets stimulating different foveal regions. Fixation stability measures may, however, reflect the operation of two inputs: a visual error signal generated by the position of the target on the retina and a proprioceptive signal recently shown to flow in from the eye muscles (SKAVENSKI, 1972). The visual and proprioceptive inputs, working together, might generate the relatively flat error functions reported by Steinman and Rattle. When subjects fixate targets small enough to be confined within the foveal bouquet, fixation stability may depend almost exclusively on visual errors signaled by deviations of the target image from the preferred fixation position. Proprioceptive signals are not needed and not attended. However, as the significant features of the target (edges of disks or separated points) fall on more peripheral portions of the foveal floor, the subject may attend more to the *proprioceptive* inflow signal and use it to keep his eye stable since *visual* error signals may well be less precise when the target stimulates remote portions of the fovea. This suggested change in the relative importance of visual and proprioceptive error signals gains some support from the finding that saccades become infrequent when the visual error signal is generated in peripheral parts of the fovea without adverse effects on fixation stability (STEINMAN, 1965).

We measured the *first* saccadic response to target steps of various sizes in order to examine the way the visual error signal varies across the fovea free from variations in the proprioceptive inflow signal. Characteristics of this first saccadic response depend, primarily, on visual error signals generated when the target steps to some more or less remote part of the fovea. With such stimulation, the proprioceptive inflow signal will be the same when different visual error signals are generated because a new inflow message will only arise after the saccade has placed the eye in a new orientation.

METHOD

A contact lens optical lever was used to record horizontal eye movements on 35 mm infra-red film moving at 2·5 cm/sec in a modified Grass Kymograph camera. The technique, described elsewhere (STEINMAN, 1965), records small rotations of the eye free from contamination by translations of the head. Eye position was measured to about 3 sec arc with the projection film reader employed.

The fixation target was a sharply focussed luminous point in an otherwise dark room. The point (1·00 log unit above absolute foveal threshold) was provided by a Tektronix (Model 503) oscilloscope with a very short persistence phosphor (P-20) located 1·0 m from the right eye. Two experienced *S*s (*AS* and *RS*) served in the experiment. Each 10 sec record began with an initial period of 2·5 sec during which the target remained centered followed by a step displacement of the target to the right or left by some randomly determined distance where it remained for 5 sec and then returned to the center for the final 2·5 sec of the trial. The direction as well as target step size was determined randomly. Step displacements of the target (marked on the film by an infrared strobe flash) ranged from 5 to 180′ arc in 7 steps (5′, 10′, 24′, 42′, 60′, 120′ 180′ arc). Head orientation, relative to the stimulus display, was varied for each experimental block of 10 trials so that features of the saccadic response, which were due to the target step itself (the visual error signal), could be separated from features that were due to changes in the position of the eye in the orbit (muscular determinants of oculomotor output). The target was presented with either the dental acrylic bite board centered, in which case the centered target appeared straight ahead, or with the bite board rotated 18° arc to the right or left. Each record consisted of 2 trials. In the first half of each record, *S* did not know the magnitude or direction of the target displacement (unpredictable trial). In the second half, the direction and approximate size were known because the target returned to its original centered position (predictable trial) where it had been seen only 5 sec earlier.

Thus, this paper describes high velocity oculomotor responses (saccades) to both predictable and unpredictable target steps of various sizes with the eye in different orientations. We will consider only the characteristics of the first saccade made just after the target step because errors signalled after this may differ in unknown ways from errors signalled by the sudden change of the position of the target itself, e.g. either the overshoot of the first saccade (ROBINSON, 1964) or the steady state error immediately following the overshoot might signal the next high velocity movement.

The following sets of measures were made for each trial: (a) the mean position of the eye prior to the target step was calculated from 5 eye position samples (4, randomly sampled, within successive 0·5 sec intervals of the 2 sec period immediately preceding the target step and the position of the eye at the onset of the first saccade following the target step); (b) the size of each first saccade was calculated by subtracting the saccade onset position from the steady state eye position measured after the first saccade. In all, 420 trials were recorded for each *S*, 60 for each of the 7 target step sizes, one-third at each of the 3 head positions. Half of these were predictable and half were not.

RESULTS

1. *Saccade direction*

The proportions of first saccades that went in the same direction as target steps are summarized in Table 1a. Both subjects fairly consistently (> 75 per cent) made their first saccade with all but the smallest step (5′ arc) in the direction of the target. Even with the smallest step, there was a statistically reliable tendency for the first saccade to follow the target (*AS*: $\chi^2 = 11{\cdot}27$, $df = 1$, $p < 0{\cdot}01$; *RS*: $\chi^2 = 4{\cdot}27$, $df = 1$, $p < 0{\cdot}05$). If a saccade latency of 150 msec is allowed on the assumption that saccades made sooner than this after the target step may be "spontaneous" (not elicited by the target displacement), then a larger proportion of first saccades went in the correct direction for all target steps (Table 1b). Further analyses will be restricted to those trials on which responses met this latency criterion in order to reduce the likelihood of including such "spontaneous" fixation microsaccades.

TABLE 1a. PROPORTION OF FIRST SACCADES IN THE DIRECTION OF THE TARGET STEP FOR SUBJECTS *AS* AND *RS* (N = 60/step size)

Step size (min arc)	*AS* *Prop.*	*RS* *Prop.*
5	0·71	0·63
10	0·83	0·82
24	0·88	0·88
42	0·93	0·82
60	0·83	0·77
120	0·98	0·85
180	0·95	0·85

TABLE 1b. PROPORTION OF FIRST SACCADES IN THE DIRECTION OF THE TARGET STEP FOR THOSE SACCADES MADE 150 OR MORE MSEC AFTER THE TARGET MOVED. THE NUMBER (N) OF SACCADES THAT EXCEEDED THIS LATENCY CRITERION IS ALSO GIVEN

Step size (min arc)	*AS*		*RS*	
	N	*Prop.*	*N*	*Prop.*
5	46	0·76	49	0·65
10	48	0·92	46	0·87
24	50	0·98	47	0·98
42	50	1·00	46	0·96
60	45	0·98	42	0·90
120	59	1·00	43	0·98
180	58	0·98	38	0·95

Neither the predictability of direction, nor the head orientation had a marked or systematic effect on the proportions of first saccades that went in the correct direction. These variables also had little or no effect on other saccade characteristics and will, therefore, not be reported separately (see Table 2).

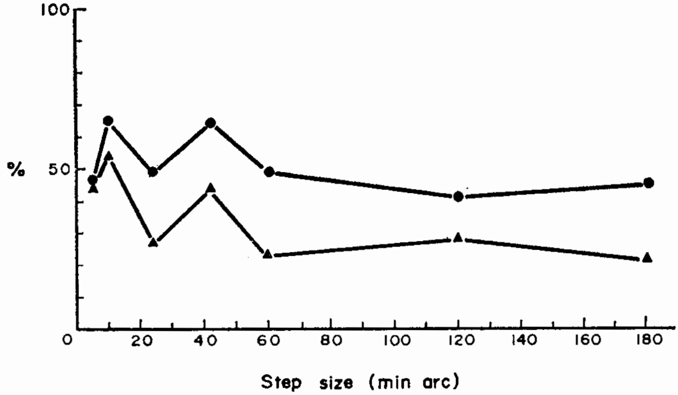

FIG. 1. Per cent error remaining after the first saccade made in the direction of target steps of various sizes. Subject *AS* is shown by circles; *RS* by triangles.

TABLE 2a. MEAN FIRST SACCADE OFFSET ERROR (MIN ARC) AS A FUNCTION OF PREDICTABILITY OF DIRECTION AND HEAD ORIENTATION FOR SUBJECTS *AS* AND *RS*

	AS	*RS*
Predictable	30·9 (2·33)	15·8 (1·27)
Unpredictable	29·5 (2·18)	17·9 (1·45)
Head left	27·4 (2·64)	13·9 (1·24)
Head center	28·3 (2·76)	16·8 (2·04)
Head right	34·8 (2·80)	19·3 (2·14)

Standard errors are given in parentheses.

TABLE 2b. PROPORTIONS OF FIRST SACCADES IN THE CORRECT DIRECTION AS A FUNCTION OF PREDICTABILITY OF DIRECTION AND HEAD ORIENTATION FOR SUBJECTS *AS* AND *RS*

Predictable	0·94 (168)	0·72 (150)
Unpredictable	0·94 (170)	0·83 (128)
Head left	0·89 (117)	0·84 (102)
Head center	0·83 (106)	0·69 (81)
Head right	0·88 (115)	0·80 (95)

The number of saccades is given in parentheses.

2. *Saccade accuracy*

Both subjects' first saccades fell short of the displaced target. Ratios of mean saccade offset error (distance between the steady state offset position of the eye after the first saccade and the displaced target position) to the total error introduced by the target step are shown as percentages in Fig. 1. For *AS* approximately 50 per cent of the error introduced by each of the target steps remained after the first saccade. *RS*'s first saccades were slightly more effective, i.e. only 35 per cent of the error introduced by each of the target steps remained after his first saccade.

3. *Saccade reliability*

Standard deviations of saccade offset errors increased markedly across the range of target step sizes studied (*AS*'s standard deviations increased by a factor of 15·6, *RS*'s by a factor of 10·2).[1] Changes across the fovea were not uniform, however. For both subjects, variability was 3·6 times as large at the edge of the foveal floor (42′ arc) as it was very near the "optimal" fixation locus (5′ arc). Whereas, the increase in variability from just outside the foveal floor (60′ arc) towards the periphery (180′ arc) was not as marked (*AS*'s increased by a factor of 2·0, *RS*'s by a factor of 1·8). These results are summarized in Table 3.

[1] Our use of the variability of saccade offset error to estimate input characteristics rests on the assumption that muscular characteristics do not contribute much to output characteristics. We believe that this assumption is reasonable in the present experiment because both subjects' variability of saccade offset error was similar for 3 very different eye orientations. Our use of the variability of saccade offset error to describe the way in which the visual error signal is generated in different retinal regions also assumes that the accuracy of saccades (mean saccade offset error) will be similar in different retinal regions. Both subjects, although they corrected only about half of the error introduced by the target step, performed similarly and reasonably consistently across the various target step sizes.

TABLE 3. STANDARD DEVIATIONS (S.D.) OF SACCADE OFFSET ERROR FOR SACCADES MADE IN RESPONSE TO TARGET STEPS OF VARIOUS SIZES BY SUBJECTS *AS* AND *RS*. THE NUMBER (*N*) OF SACCADES IS ALSO GIVEN

Step size (min arc)	*AS* *N*	*AS* S.D. (min arc)	*RS* *N*	*RS* S.D. (min arc)
5	35	1·4	32	2·0
10	44	2·3	38	2·6
24	49	4·1	46	5·5
42	50	5·1	44	7·2
60	44	10·7	38	11·8
120	59	13·7	42	18·3
180	57	21·9	36	20·5

IMPLICATIONS

These results have 3 implications: (1) The oculomotor "dead zone" is surely smaller than 10′ arc and may even be less than 5′ arc—smaller than the 0·25–0·5° "dead zone" reported by RASHBASS (1961) with similar stimulus conditions. Given sufficient time (more than 150 msec), our subjects consistently (more than 87 per cent of the time) and correctly responded to target steps ranging from 180′ arc down to 10′ arc. Response patterns across this range were quite similar both in terms of the proportion of first saccades in the correct direction and in the percentage of error remaining after the first saccade. Further, our subjects' response patterns for the 5′ arc step did not differ markedly from those for the larger target steps.[2]

(2) The oculomotor visual error signal may be served by the same receptive field organizations that determine visual acuity. If the standard deviation of first saccade offset error is used to estimate retinal variations in the size of the receptive fields, the reliability of the first saccades was found to vary in a manner similar to variations in visual acuity across the same regions (LE GRAND, 1967, p. 136). If anything the slope within the foveal floor is steeper than found for visual acuity in the same region.

(3) Since the reliability of the visual oculomotor error signal falls off sharply within the fovea, the proprioceptive signal must become increasingly important because we know that fixation stability remains relatively uniform across this region (STEINMAN, 1965; RATTLE, 1969).

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Department of Psychology,
University of Maryland,
College Park,
Md. 20742.

GEORGE T. TIMBERLAKE[3]
DIANE WYMAN
ALEXANDER A. SKAVENSKI[4]
ROBERT M. STEINMAN

[2] In a subsequent experiment, WYMAN and STEINMAN (1971) have found that *RS* and an inexperienced subject consistently and accurately correct for target step displacements of 3·4′ arc. Such small corrections were frequently found to require more than one tiny saccade.

[3] Now at the Department of Psychology, Northeastern University.

[4] Now at the Division of Biomedical Engineering, Johns Hopkins Medical School.

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