Eye-position signals in successive saccades

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Accuracy of the eye-position signal (EPS) in successive-saccade conditions was examined by analyzing the subject's performance in tracking his gaze by pointing with his unobservable hand in the dark. The size of constant error in manual pointing was found to increase with the number of the component saccades and to be inversely proportional to the size of the largest component saccade. The results are interpreted as showing that, in successive-saccade conditions, subjects are not able to use the sum of EPSs from each component saccade, but rather use only the EPS from the largest component saccade.

Many studies have been done on the accuracy of eye-position signals¹ (EPSs), that is, signals concerning eye position within the orbit, produced by saccades or smooth pursuit eye movements. Some of these studies have shown that, as suggested by Rashbass (1961), a saccade provides a more accurate EPS than smooth pursuit eye movements (Festinger & Canon, 1965); others have shown that pursuit eye movements provide an accurate EPS when a specific response mode (ballistic aiming) is used as an index of EPS (Hansen, 1979; Hansen & Skavenski, 1977).

In most of these studies, the accuracy of a saccade's EPS was examined in only single-saccade conditions. Skavenski and Steinman's (1970) subjects, however, were able to return their gazes to the original target position after making 30 large saccades in the direction specified by the experimenter. Hallett and Lightstone (1976) showed that subjects made corrective saccades to targets flashed before, during, or after saccade, indicating that in multiple-saccade conditions accurate EPSs were available more or less continuously. In Honda's (1984) recent study, in which the accuracy of EPS was examined by analyzing the subject's tracking of his gaze by manually pointing in the dark, pointing after two or three saccades was as accurate as that after one saccade. These studies all suggested that subjects were able to know the position of the eye after the completion of successive saccades.

The present study was designed to systematically investigate the characteristics of EPS provided by successive saccades. We examined the effects on EPS of the number and size (magnitude) of the component saccades in successive-saccade conditions by analyzing the subject's performance in pointing with

his unseen hand to a just-extinguished visual target in various conditions of eye movement to the target.

METHOD

Subjects

Three right-handed male subjects participated in the experiment. One was the author (H.H.) and the remaining two were university students (A.K. and T.K.).

Apparatus and Procedure

A subject was seated in total darkness facing the apparatus and asked to tightly fix his head to the head- and chinrest. Figure 1 shows the apparatus used in this study. A He-Ne laser beam (JLH-R20S, Nihon Lasers), projected on a black screen through a galvanic mirror, produced the visual stimuli in the saccade and pursuit-eye-movement conditions. A half mirror was set before the subject's eye, and the subject looked at the optical image of the light spot (2 mm in diameter) of the laser beam projected in front of him. A stimulus projected at the center of the visual field was used as a fixation point, and the experimenter was able to move it horizontally at various speeds by driving the galvanic mirror. In the pursuit-eye-movement conditions, the visual stimuli moved from the fixation point toward the right at a velocity of 3 deg/sec. In the saccade conditions, the visual stimulus jumped from the fixation point to one of nine stimulus positions that were arranged linearly along the path of the moving stimulus. Figure 1b shows the relative locations of the visual stimuli. The distance between each stimulus position was 2 deg, and the distance between the subject's eye and the fixation point was about 48 cm.

On each trial, a warning signal (2 sec in duration), generated by a buzzer, was given, and then the fixation point was presented for 2 sec. The subject was asked to keep watching the fixation point, and to place the index finger of his right hand on a movable fingerrest that was placed at the position of the projected fixation point. After offset of the fixation point, visual stimuli for eye movement were given in the following six presentation conditions. (1) Condition 1-S: Ten milliseconds after the offset of the fixation point, a target stimulus was presented for 2 sec. The subject was asked to move his eyes to the target position by a saccade. (2) Condition 2-S: Ten milliseconds after the offset of the fixation point, two stimuli were successively presented from the left to the right. The first stimulus was presented for 850 msec, and the second for 2 sec. The subject was asked to successively direct his eyes to these stimuli by saccades. (3) Condition 3-S and (4) Condition 4-S: Three or four stimuli were presented successively from the left to the right. Only the last stimulus was presented for 2 sec; the remaining stimuli were presented for 850 msec each. As in Condition 2-S, the subject successively directed his eyes to these stimuli by saccades. In these successive-saccade conditions, the time interval between each visual stimulus was 10 msec. (5) Condition P

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Figure 1. (A) Schematic illustration of the apparatus. (B) Relative locations of the fixation point and the visual stimuli for saccades. The fixation point was placed at the center of the visual field.

(pursuit eye movement): After a warning signal, the fixation point was presented for 2 sec, and then moved toward the right at a velocity of 3 deg/sec and stopped at a given position. The visual stimulus was presented for 2 sec at the final position. (6) Condition C (control): Ten milliseconds after the offset of the fixation point, a target stimulus was presented for 7 sec. This condition was introduced to examine pointing accuracy when subjects pointed to a visible target with the unseen hand.

In all stimulus presentation conditions, three target positions were employed for manual pointing: 14, 16, and 18 deg to the right of the fixation point. In Conditions 1-S, P, and C, the target stimulus appeared at one of the three target positions. In the successive-saccade conditions, that is, in Conditions 2-S, 3-S, and 4-S, the last visual stimulus appeared at one of the three target positions. The positions of visual stimuli for intervening saccades were selected from among the positions between the fixation point and the target of each trial. The selection of the visual stimuli for intervening saccades was done by taking into account the size and position of the largest component saccade in each successive saccade trial. As a result, in Condition 2-S, the size of the largest component saccade ranged from 50% to 89% of the target distance. For example, when the target was at 18 deg and the combination of component saccades was 2 and 16 deg, the size of the largest component saccade was 89%. Similarly, the size of the largest component saccade ranged from 33% to 79% in Condition 3-S and from 25% to 67% in Condition 4-S. The largest component saccade was placed at either the first or the last of the series of the component saccades. In the former case, the saccade size decreased as its position neared the end of the series; in the later case, it increased as it neared the end of the series. This was

not so when the component saccades were all the same size. In all, there were 20 different series of component saccades in each successive-saccade condition. The visual stimuli were timed and the galvanic mirror was driven by a microcomputer (μ PD-8085A).

In all conditions except Condition C, the subjects were allowed to point after the target stimulus had disappeared. They moved the tip of the index finger of the unseen right hand to where the target had been. While pointing, the subjects were required to keep watching the target position. Only in Condition C, in which the target was presented for a longer time (7 sec) than in the remaining conditions, did the subjects point, with the unseen hand, to a target that was visible. The subjects were allowed to point at any speed they wished but were encouraged to keep the speed as constant as possible throughout the experiment. The tip of the index finger of the pointing hand was set in a small hole (1.5 cm in diameter) at the center of the movable fingerrest, and when the subject pointed to the target, the fingerrest moved with the finger. A needle attached to the fingerrest was used as an indicator of the finger position. The position of the index finger was measured by recording the position of the needle using a video-camera system. The distance between the target position and the tip of the index finger was measured to within 2 mm. After pointing, the subject was asked to return the finger to the original starting position, that is, to the position of the fixation point. A small metal tack was attached at the starting position so that the subject could locate the position by touching the tack with the tip of the index finger.

Each subject was given 2 trials on each series of component saccades and 4 trials on each of three kinds of target positions of Conditions 1-S and P, a total of 144 trials in random sequence, divided into four blocks of 36 trials each. In addition, each subject was given three blocks of Condition C with 3 trials for each target position being given in random sequence. The experimental conditions were used in Blocks 1, 3, 5, and 7, and the control condition (Condition C) was used in Blocks 2, 4, and 6. The time interval between trials was about 10 sec. There was a rest period of about 5 min between blocks.

The subject's horizontal eye movements were monitored by a photoelectric apparatus, which recorded the movement of the subject's left eye with an accuracy to at least 0.5 deg for a 20-deg rotation of the eye to the right of central gaze. Calibration trials were inserted at the start, middle, and end of each experimental block, in which visual stimuli were successively presented at the nine stimulus positions. The subject was asked to try to be as accurate as possible in making each saccade to a stimulus.

RESULTS

Eye Movements

The subjects' horizontal eye movements were drawn on the recording chart by a large-amplitude rectifier (RJG-4024, Nihon Kohden) at a speed of 10 mm/sec and analyzed by visual inspection. As expected, the subjects often showed small corrective saccades in the saccade conditions. The corrective saccades occurred in 54.7%, 35.2%, and 71.1% of all saccade trials for Subjects A.K., H.H., and T.K., respectively. Further analysis showed that corrective saccades occurred more frequently as the saccade size increased. Although the subjects gazed at the expected position in almost all saccade trials, two subjects showed pursuit eye movements in some saccade trials (5 and 12 trials for Subjects A.K. and T.K., respectively). These trials were regarded as failures and were excluded from the data analysis of pointing performance.

In the pursuit-eye-movement conditions, two subjects sometimes showed a drift (four and three trials for Subjects A.K. and T.K., respectively). Except for one trial with a large drift, however, the size of the drifts was rather small (usually less than 1 deg), so these trials with small drift were included in the data analysis of pointing. Subject H.H. showed large saccades in three trials of Condition P. These trials were considered failures of pursuit eye movement and were excluded from the data analysis of pointing.

Pointing Performance

To examine pointing accuracy, the distance between the position of the projected target and that of the tip of the pointing finger was measured on each trial, and the mean of the constant error (CE) and the variable error (VE), that is, the SD of the CEs, were calculated for each subject. Figure 2 shows the mean CEs in each eye-movement condition separately for each subject. In Condition C, in which the subjects pointed to a visible target with unseen hand, Subject T.K. largely undershot the target, whereas Subject H.H. slightly overshot the target. This suggests that each subject had an indigenous directional bias in visually directed pointing of the hand, and that the direction and the size of the bias were different among the subjects. This kind of error in visually directed pointing has been reported by Foley (1975) and Honda (1984). Similar directional bias has been shown in prism adaptation, too (Hardt, Held, & Steinman, 1975). The constant directional bias shown in the present experiment seems to be mainly due to factors in the motor control system of the hand, inasmuch as in my previous study (Honda, 1984) a large

between-hand difference in the direction and size of bias was shown by each subject.

As shown in Figure 2, the subjects tended to undershoot the target more in the successive-saccade conditions than in Conditions 1-S and C. In addition, for each subject the size of undershooting increased with the number of component saccades. In Condition P, the subjects showed the largest undershooting. According to an ANOVA, all subjects showed significant differences in CEs among the six eye-movement conditions [Subject A.K.: $F(5,160)=90.73$, $p < .01$; Subject H.H.: $F(5,165)=20.35$, $p < .01$; Subject T.K.: $F(5,153)=26.66$, $p < .01$].

The vertical bars in Figure 2 show the VEs. The VEs among the eye-movement conditions were not significantly different [Bartlett test, $\chi^2(5) \leq 3.83$, $p > .05$, for all subjects].

Next, we analyzed the effect of component saccade size on pointing performance. We calculated the mean CEs for each condition of the component saccade series, and then transformed them into percentages by dividing the CE by the distance of the target. Figure 3 shows the proportion of the CEs as a function of the size of the largest component saccade. In three successive-saccade conditions, that is, in Conditions 2-S, 3-S, and 4-S, all subjects tended to undershoot the target, and this tendency decreased with the size of the largest component saccade.

Solid lines in Figure 3 are best fitting regression lines for the data from four saccade conditions (Conditions 1-S, 2-S, 3-S, and 4-S). The slopes of the regression lines were +0.45, +0.38, and +0.30 for Subjects A.T., H.H., and T.K., respectively. The slopes were all significantly different from 0 [$F(1,31)=159.64$, $F(1,31)=85.89$, and $F(1,31)=43.53$ for Subjects A.T., H.H., and T.K., respectively, $p < .01$ in all cases]. This means that for all subjects the percentage of CEs consistently increased about 3.0% to 4.5% in the negative direction, that is, in the direction of undershooting, as the size of the largest component saccade decreased by 10%. Thus, it is suggested that the main determinant of the size of the CEs in the successive-saccade conditions was the size of the largest component saccade.

Note that in the present experiment, the mean size of the component saccades was the same within each of the three successive-saccade conditions. In Figure 3, the proportions of the CEs in these successive-saccade conditions are plotted with different symbols. The tendency for the CEs to decrease with the size of the largest component saccade was observed even within each successive-saccade condition. For Subject A.K., the slope of the regression line of each successive-saccade condition was significantly different from 0 in all successive-saccade conditions [Condition 4-S: $F(1,8)=9.15$, $p < .05$; Condition 3-S: $F(1,8)=71.09$, $p < .01$; and Condition 2-S: $F(1,8)=$

Figure 2. Mean constant errors (CEs) in six eye-movement (stimulus presentation) conditions. The small numbers attached to each point indicate the number of samples used for calculating the mean CE.

Figure 3. The dependence of the proportion of CE on the relative size of the largest component saccade. In principle, each point is the average of nine measurements in Condition C or of four measurements in Conditions 1-S, 2-S, 3-S, 4-S, and P. This is not the case when some measurements are excluded from data analysis because of a failure, on the part of subjects, to make the expected eye movements. Dotted lines show the range of ± 1 SD of estimation by the regression line.

10.29, $p < .05$]. For Subject H.H., there was a significant difference in Conditions 3-S and 2-S [$F(1,8) = 6.45$, $p < .05$, and $F(1,80) = 59.36$, $p < .01$, respectively]. Similarly, Subject T.K. showed a significant difference in Conditions 3-S and 2-S [$F(1,8) = 8.80$,

$p < .05$, and $F(1,8) = 13.40$, $p < .01$, respectively]. Thus, it is concluded that the mean size of the component saccades was not the critical determinant of the size of CEs in the successive-saccade conditions.

Next, we analyzed the effect of the position of the largest component saccade in the successive-saccade conditions. Table 1 shows the mean proportion of CEs for two different positions of the largest component saccade, that is, the first and the last, in each successive-saccade condition, separately for each subject. A two-factor ANOVA (2 positions of the largest component saccade $\times$ 3 successive-saccade conditions) was applied to the data for each subject. The main effect of saccade condition was significant for two subjects [$F(2,109) = 4.25$, $p < .05$, and $F(2,114) = 19.99$, $p < .01$, for Subjects A.K. and H.H., respectively], but the main effect of the position of the largest component saccade was not significant for any subjects. Thus, whether the largest component saccade was located at the first or the last position was not the critical determinant of the size of the CEs in the successive-saccade conditions.

DISCUSSION

The analysis of pointing performance showed that the CEs in the pursuit-eye-movement condition (Condition P) were significantly larger than those in the single-saccade condition (Condition 1-S). This was consistent with Festinger and Canon's (1965) findings.

Rashbass (1961) suggested that pursuit eye movement was stimulated by the direction of movement and the velocity of the target, whereas the saccade was stimulated independently by the position of the target. In addition, it is well known that proprioceptive signals from the extraocular muscles do not provide conscious perception of eye position (Brindley & Merton, 1960). From these suggestions, Festinger and Canon interpreted their results as showing that the oculomotor system that elicits a saccade has an efferent signal concerning the position of the target and, therefore, the position of the eye within the orbit, and that the efferent signal in the pursuit-eye-movement condition would be concerned with velocity matching and not with precise target location.

Table 1
Proportion (%) of CEs in Two Positions of the Largest Component Saccade in Each Successive-Saccade Condition

Subject	First Position			Last Position		
	2-S	3-S	4-S	2-S	3-S	4-S
A.K.	-11.2	-18.9	-24.9	-13.1	-23.1	-26.7
H.H.	-5.6	-7.8	-14.8	-2.3	-12.1	-16.4
T.K.	-36.6	-38.1	-45.5	-38.7	-42.1	-42.8

Note—The negative sign indicates undershooting of the target position.

However, in the saccade conditions of the present study, as well as in those of Festinger and Canon, the visual target was projected onto the extrafovea of the retina, whereas in the pursuit-eye-movement conditions, the visual targets remained within the fovea. Therefore, although at the time subjects started manual pointing there was no retinal image of the target, the prior extrafoveal projection of the target image in the saccade conditions might give subjects additional retinal information about the eye position, resulting in smaller CEs there than in the pursuit-eye-movement conditions. In this connection, however, it should be noted that, according to recent studies (Hallett & Lightstone, 1976; Mays & Sparks, 1980), the signal about target location received by the oculomotor system is coded in spatial, not on retinal, coordinates.

The present study showed that when subjects caught the visual target by successive saccades, CEs in pointing with the unseen hand to a just-extinguished visual target increased with the number of component saccades. Furthermore, it was indicated that the CE in the successive-saccade conditions was inversely proportional to the size of the largest component saccade. Thus, the increase of CEs with the number of component saccades (Figure 2) was due to the fact that the size of the largest component saccade decreased, on average, as the number of the component saccades increased.

As shown in Figure 3, the CEs in Condition 4-S reached the level of the CEs in Condition P. In addition, the CEs in the successive-saccade conditions were inversely proportional to the size of the largest component saccade. Then it was speculated that the CEs in Condition P corresponded to the value of CE when the size of the largest component saccade was made infinitely smaller. As shown in Figure 3, for each subject, one to three CEs in Condition P were within the range of ± 1 SD of the estimation by the regression line. However, note that in this study only one velocity of moving target (3 deg/sec) was employed, and that the size of CEs in the pursuit-eye-movement conditions may be largely dependent on the velocity of the moving target. Therefore, before we draw a final conclusion, it is necessary to examine the effect of target velocity on EPS in the pursuit-eye-movement conditions. In addition, as mentioned earlier, saccades and pursuit eye movements are thought to be elicited by different mechanisms. Thus, EPSs in the saccade and pursuit-eye-movement conditions are distinctively different in their nature. Therefore, the apparent fitting of CEs in Condition P to the estimated value of CE when the size of the largest component saccade was made infinitely smaller is not accepted as evidence for the continuity of EPSs in saccade and pursuit-eye-movement conditions.

The CEs in the successive-saccade conditions were all toward the fixation point. That is, in these condi-

tions, the subjects tended to undershoot the target. With regard to EPS, this means that subjects were given fewer EPSs in the successive-saccade conditions than in Condition 1-S. Why was EPS reduced in the successive-saccade conditions? At present, we have no clear answer to this question. But the present study showed that the size of CEs increased as the size of the largest component saccade decreased. This suggests that there may be some kind of comparator which picks out the largest saccade among many component saccades, and gives the subject the EPS from only the largest saccade. In other words, the EPS from the largest saccade seems to make ineffective the EPSs from the remaining component saccades. From the results of the present study, we can say, at least, that, in pointing, the subjects were not able to use the sum of the EPSs derived from each component saccade.

Thus, the results of the present study are incompatible with those of Skavenski and Steinman (1970), in which subjects were able to return their gazes to the original position, even after 30 large saccades. But the above-mentioned difference may be due to the following differences in the experimental methods of the two studies. First, in Skavenski and Steinman's study, an accuracy of eye movement itself was employed as an index of EPS, whereas in the present study EPS was estimated from the accuracy of the hand pointing to the target position. Manual pointing is an indirect index and, therefore, may be more influenced by perceptual factors. Second, in the present study, successive saccades were unidirectional, that is, all component saccades were made to the right. Thus, underestimation of saccade distance may be specific to unidirectional successive saccades.

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NOTE

1. In this paper, the term EPS includes both the retinal EPS, that is, information based on the location of the retinal image of

a target, and the extraretinal EPS, that is, the inflow or outflow signals about the eye position within the orbit. Extraretinal EPS is used only when there is no visible target prior to and during eye movements. When a subject is given a brief visual target prior to eye movement, the retinal eccentricity of the target may be a useful cue for estimating the amplitude of the eye movement. In this case, therefore, the term EPS was used.

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