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The Accuracy and Precision of Saccades to Small and Large Targets

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Subjects made saccades to point and spatially-extended targets located at a randomly-selected eccentricity (3.8–4.2 deg) under conditions designed to promote best possible accuracy based only on the visual information present in a single trial. Saccadic errors to point targets were small. The average difference between mean saccade size and target eccentricity was about 1% of eccentricity. Precision was excellent (SD = 5–6% of eccentricity), rivaling the precision of relative perceptual localization. This level of performance was maintained for targets up to 3 deg in diameter. Corrective saccades were infrequent and limited almost exclusively to the point targets. We conclude that the saccadic system has access to a precise representation of a central reference position within spatially-extended targets and that, when explicitly required to do so, the saccadic system is capable of demonstrating remarkably accurate and precise performance.

Saccadic eye movement Saccades Localization

Saccadic eye movements bring the line of sight to details of interest in the visual scene. Most of us have the subjective impression that we can use our saccades to shift the line of sight accurately, yet the oculomotor literature suggests otherwise. Saccades are usually reported to be inaccurate, undershooting the target by about 5–10% of the target's eccentricity, and requiring one or more "catch-up" saccades to correct these errors (Aitsebaomo & Bedell, 1992; Becker, 1972; Becker & Fuchs, 1969; Henson, 1978, 1979; Lennie & Sidwell, 1978; Prablanc, Masse & Echallier, 1978; Pelisson & Prablanc, 1988). In this paper we asked whether such errors represent best possible saccadic performance. We studied saccades to single-point targets because this is the traditional laboratory stimulus, but we also studied spatially-extended targets. This is the more interesting case because these targets, not points, are the targets present in natural environments.

Prior research using point targets has shown that saccadic undershoots may be reduced if special procedures are used, but there is little consensus about which procedures are most important and why they work. For example, Lemij and Collewijn (1989) found that undershoots of 10–15% of target eccentricity, observed while tracking a target stepping back and forth, were reduced to only 3–6% of eccentricity when the moving target was replaced by two stationary points fixated alternately in response to a metronome (see also Collewijn, Erkelens & Steinman, 1988). But whether targets are stationary or moving has not always been important. Zingale and Kowler (1987) found undershoots while scanning stationary targets, while Van Opstal and Van Gisbergen (1989) showed that target steps were followed by highly accurate and precise saccades when the same displacement (5 deg) was tested repeatedly within a block of trials.

Kapoula (1985) and Kapoula and Robinson (1986) succeeded in eliminating undershoots for 5 deg target steps by including larger target steps (up to 20 deg) on randomly-selected trials in the same experimental session. When the larger steps were included, saccades to the smallest target steps (5 deg) tended to be too large while saccades to the largest steps were too small (the "range effect"). The range effect thus represents the influence of the past history (e.g. learning and expectations) on performance. Kapoula and Robinson (1986) also studied saccades to 5 deg target steps presented alone, and found that saccades undershot the target by about 8% (a result that conflicts with that of Van Opstal and Van Gisbergen), leading Kapoula and Robinson (1986) to conclude that, without the contribution of the range effect, undershooting was the "normal" operation of the saccadic system.

Aitsebaomo and Bedell (1992) and Lemij and Collewijn (1989) took a different view and suggested that undershooting was not necessarily normal, and occurred only when insufficient time was taken to program the saccade. The importance of programming time was supported by the results of Abrams, Meyer and Kornblum (1989). They found that when subjects tried to

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be as accurate as possible, prolonging latency if necessary, saccades were accurate for small target steps (3–4.5 deg) tested in the context of larger steps (up to 9 deg), with only modest undershoots (5%) for the larger steps. But the variability of saccade size for the smaller steps was unusually large (SD = 15–20% eccentricity). Thus, although their data do not show systematic undershoots, individual saccades were rarely accurate.

The diversity of observations and views described above illustrates that oculomotorists still disagree about a very basic property of saccades, namely, how accurate and precise the movements can be. We set out to determine the best possible accuracy and precision of saccades by asking subjects to track target steps of random size as accurately as possible. Our goal was to determine the accuracy and precision that can be achieved solely on the basis of the *visual* information present in a single trial. For this reason we used randomly-selected target displacements and tried to avoid experimental procedures that might improve or impair performance due to the influence of extraneous behavioral factors. In addition, we tested saccadic performance both with single-point targets, typically used in laboratory research, as well as with target forms, the naturally-occuring stimulus for saccades. Forms are different from points because the saccadic endpoint is not explicitly designated, and must, therefore, be computed based on pooling or integration of the spatial information within the target. Any losses in either accuracy or precision with increasing target size would have implications for how well such pooling can be carried out and the size of the retinal regions over which effective spatial pooling can occur. [See He and Kowler (1989, 1991) for discussions of spatial pooling and saccades; and Hirsch and Mjolsness (1992), Morgan, Hole and Glennerster (1990), Morgan and Glennerster (1991), and Vos, Bocheva, Yakimoff and Helsper (1993) for experiments on the role of spatial pooling in perceptual localization.]

The methods we used proved to be successful in that we obtained highly accurate and precise saccadic landing positions with single-point targets, a result which then allowed a valid estimate of the loss in accuracy and precision resulting from increases in target size. Such losses proved to be surprisingly small.

METHOD

General approach

We attempted to obtain best possible saccadic accuracy and precision, while at the same time minimizing the influence of extraneous behavioral factors that might artificially improve or impair performance, in the following way.

(1) The size of the target displacement was chosen at random to avoid the improvements in accuracy that might come into play when subjects know target location in advance of the trial, or make saccades to the same target location over and over again in successive trials (Lemij & Collewijn, 1989; Van Opstal & Van Gisbergen, 1989; Collewijn *et al.*, 1988).

(2) The target displacements differed from each other by very small amounts. Specifically, the displacements tested were 228, 234, 240, 246, and 252 min arc. The difference between two successive values (6 min arc or 2.5% of the average eccentricity) was somewhat less than the threshold for the perceptual discrimination of target location (White, Levi & Aitsebaomo, 1992). We hoped to accomplish two things by using target displacements that were so close in size to one another. One was procedural: we wanted to discourage a strategy of quickly recognizing which target displacement had been presented and selecting the appropriate response from a pre-programmed set. Such a strategy might be less attractive if the targets were hard to discriminate from one another. The second was analytic: we wanted to assess saccadic accuracy and precision by finding out whether very small changes in target position would produce comparable changes in saccadic landing position.

(3) Subjects were instructed to increase latency as much as necessary to achieve the best accuracy possible.

(4) Subjects were instructed to reach the target with a single saccade. Allowing a subject to adopt the alternative strategy of hopping toward the target with two or more saccades (an option available in prior saccadic experiments) would produce misleading estimates of saccadic accuracy because the first saccade would not necessarily represent the subject's best attempt to reach the target. To emphasize the importance of making a single saccade, subjects were told to avoid making subsequent corrective saccades even if they felt that the first saccade had missed the target.

Subjects

The authors served as subjects. EK is a highly experienced eye movement subject. BE's prior experience was limited to a few sessions in a different study of saccades. BE requires no spectacle correction. EK is myopic and a spectacle correction was incorporated into the optics of the display (see below).

Eye movement recording

Two-dimensional movements of the right eye were recorded by a Generation IV SRI Double Purkinje Image Tracker (Crane & Steele, 1978). The subject's left eye was covered and the head was stabilized on a dental biteboard.

The voltage output of the Tracker was fed on-line through a low-pass 50 Hz filter to a 12-bit analog-to-digital converter (ADC). The ADC, under control of a computer (LSI 11/24) sampled eye position every 10 msec. The digitized voltages were stored for later analysis.

Tracker noise level was measured with an artificial eye after the tracker had been adjusted so as to have the same first and fourth image reflections as the average subject's eye. Filtering and sampling rate were the same as those used in the experiment. Noise level, expressed as a SD of position samples, was 0.4 min arc for horizontal and 0.7 min arc for vertical position.

Recordings were made with the tracker's automatically movable optical stage (auto-stage) and focus-servo disabled. These procedures are necessary with Generation IV Trackers because motion of either the auto-stage or the focus-servo introduces large artifactual deviations of Tracker output. The focus-servo was used, as needed, only during intertrial intervals to maintain subject alignment. This can be done without introducing artifacts into the recordings or changing the eye position/voltage analog calibration. The auto-stage was permanently disabled because its operation, even during intertrial intervals, changed the eye position/voltage analog calibration.

Stimulus

Stimuli were generated on a display monitor (Tektronix 608, P4 phosphor) located directly in front of the subject's right eye. The luminous directional-energy of the point was 12 cd-μsec per point (Sperling, 1971). Displays were refreshed every 20 msec, a rate high enough to prevent visible flicker in these display.

The stimuli were seen against a dim (3.7 cd/m^2), homogenous background produced by a raster on a second display monitor located perpendicular to the first. The views of the two displays were combined by a pellicle beam splitter. The combined displays were viewed in a dark room through a collimating lens which placed them at optical infinity.

The background field subtended 20 deg horizontally $\times$ 18 deg vertically for one of the subjects (BE) and 9.5 deg horizontally $\times$ 7.6 deg vertically for the other subject (EK). The difference in field size was due to the negative lens, placed between the eye and collimating lens, which EK requires to compensate for her myopia and keep the stimuli in sharp focus.

Saccadic target

There were nine different types of targets. One was a single-point and the remaining eight were forms. The forms were either an outline drawing of a circle or four points configured as a diamond (i.e. a square with the long axis vertical). The diameter of either type of form target (circle or four points) was set to one of four values (60, 120, 180, or 240 min arc). The targets were presented to the left or to the right of fixation at an eccentricity of either 228, 234, 240, 246, or 252 min arc, where eccentricity was defined as the distance between the center of the target and a small (5 $\times$ 5 min arc) fixation crosshair.

The fixation crosshair was displaced from the center of the display by 120 min arc to the right when leftward eccentricities were tested, and 120 min arc to the left when rightward eccentricities were tested. This was done so that eye movements would be recorded within the central 5 deg of the visual field, where separate eye calibration sessions showed that tracker output is linear. In these calibration sessions, subjects were allowed 5 sec to reach the target, which was a single-point located at one of the 10 eccentricities tested in the experiment. Average eye position at the end of the 5 sec was within 1% of the true target position (SD < 4% eccentricity).

Procedure

The fixation crosshair was displayed before the start of the trial on to either the right or the left of the center of the display (see above). The subject pressed a button to start the trial when ready. After 100 msec the target point appeared at one of the five eccentricities on the right (when the fixation crosshair was on the left), or one of the five eccentricities on the left (when the fixation crosshair was on the right). The position of the fixation crosshair (right or left) and the eccentricity were chosen randomly on each trial. The fixation crosshair and target remained visible throughout the trial, which ended 900 msec after the saccadic target appeared.

Instructions

The subject was instructed to reach the target with a single saccade and to prolong latency as much as necessary to achieve the best accuracy possible. When targets were forms, we added the instruction to "look at the form as a whole", rather than to aim toward a specific place within the form (He & Kowler, 1991). This instruction was used to make it more likely that the observed landing positions would depend on the pooling of spatial information over the target form, rather than on voluntary choice about what the landing position should be. No feedback was given about performance with one exception: subject BE was told from time to time that the number of trials containing more than one saccade was tending to increase and that he should try to make only one saccade to the target. No trial-by-trial feedback about the number of saccades was given because we did not want such messages to reveal to BE any possible relationship between the number of saccades/trial and the stimulus conditions employed.

Catch trials were included (10%) to discourage programming saccades before the target appeared. EK made a saccade on 9% and BE on 34% of the catch trials.

Experimental sessions

Experimental sessions contained 100 trials and subjects were tested in 1–4 sessions/day.

Target type (nine possibilities), direction (right or left), and eccentricity (five possible values/direction) were selected randomly and independently on each trial, with the subject knowing only the direction in advance (this revealed by the location of the fixation crosshair; see above). There were, then, a total of 90 stimulus conditions (9 targets $\times$ 2 directions $\times$ 5 eccentricities/direction), which had the consequence of limiting the total number of trials/condition/day to about 4.

Analysis of eye movement data

The beginning and end positions of saccades were detected by means of a computer algorithm employing an acceleration criterion. Specifically, we calculated eye velocity for two overlapping 20-msec intervals. The onset time of the second interval was 10 msec later than the onset time of the first. The criterion for detecting the beginning of a saccade was a velocity difference between the samples of 300 min arc/sec or more. The criterion for saccade termination was more stringent in that two consecutive velocity differences had to be < 300 min arc/sec. This more stringent criterion was used to ensure that the overshoot at the end of the saccade would be bypassed. The value of the criterion (300 min arc/sec) was determined empirically by examining a large sample of analog records of eye position. Saccades as small as the microsaccades that may be observed during maintained fixation (Steinman, Haddad, Skavenski & Wyman, 1973) could be reliably detected by the algorithm.

In this experiment we defined the size of each saccade as the distance between the position of the eye at the start of the trial and the position of the eye at the end of the saccade. By using eye position at the start of the trial, rather than eye position at the onset of the detected saccade, our estimate of saccade size also incorporated any anticipatory drifts (Kowler & Steinman, 1979) that occurred during the brief (200–400 msec) latency interval. The data reported are based on the first saccade of each trial, regardless of whether subsequent saccades occurred.

Number of trials tested and excluded

EK was tested in a total of 2693 trials and BE in 2500 trials (excluding catch trials). A few trials were excluded from analyses. The rare trials with latencies < 100 msec (0.3% trials for EK and 1.2% for BE) were excluded because with such short latencies it was unlikely that the stimulus played a significant role in the saccadic program. Trials in which the error of the first saccade was > 100 min arc (0.1% trials for EK and 2.7% for BE) were also excluded because we felt that with such large errors (nearly 50% of the eccentricity) the first saccade was not a genuine attempt to reach the target. In addition, trials in which eye tracker lock was lost (0.6% of EK's trials and 0.3% of BE's trials) were excluded. The data reported are based on the remaining 2664 trials for EK and 2394 trials for BE.

RESULTS

The size of saccades to single-point targets

The sizes of saccades to single-point targets nearly matched the target eccentricity. Mean sizes, shown in Fig. 1, departed from actual target eccentricity by, on average, 3 min arc. This value is only 1.25% of the average target eccentricity of 240 min arc. The largest departure was 10 min arc, observed for EK's leftward saccades to targets at an eccentricity of 228 min arc.

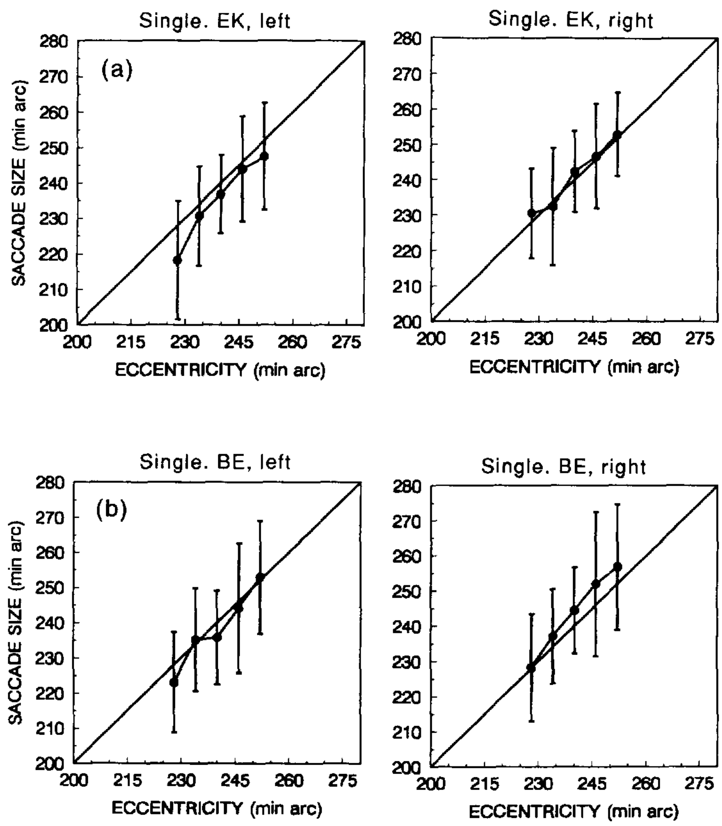

FIGURE 1. Saccade size as a function of target eccentricity for EK (a) and BE (b) for targets on the left and right, under instructions to reach the target as accurately as possible with a single saccade. Saccade size was based on the distance between the eye position at the end of the saccade and eye position at the start of the trial. The diagonal line indicates perfect performance. Error bars represent ±1 SD. Each datum point is a mean of approx. 25–30 observations.

There was no consistent tendency either to undershoot or to overshoot target location. EK tended to undershoot slightly when making saccades to the left while BE tended to overshoot slightly when making saccades to the right. In both of these cases (EK's leftward and BE's rightward saccades), the small differences between saccade size and target eccentricity were statistically reliable (see the Appendix for a description of the statistical test). In the remaining cases (EK's rightward and BE's leftward saccades), the saccades were virtually on target and differences between saccade size and eccentricity were not statistically reliable.

There was also no tendency to overshoot the targets at the smallest eccentricities and to undershoot those at the largest eccentricities, i.e. no range effect was observed.

The variability of saccade size around the mean was small. Standard deviations, shown by the error bars in Fig. 1, were on average 14 min arc for EK and 16 min arc for BE, about 6% of target eccentricity. Average saccadic error, determined by averaging the absolute value of the difference between the size of each saccade and target eccentricity, was only 13 min arc (5% eccentricity) for both subjects.

Average saccade sizes with target forms

Mean horizontal sizes of saccades to the target forms are shown in Fig. 2 for EK and Fig. 3 for BE. Data obtained from single-point targets, described above, is also shown for comparison.

These figures show that for all targets, except the largest four-point configuration, the average saccade size shifted approximately in proportion to the eccentricity of the target, which means that the subjects adopted a consistent average landing position with respect to the contour of the form.

This consistent average landing position did not always coincide with the center of the form. Average saccade size depended on the subject and the visual field. EK's saccades fell short of the center of the form when she looked at targets on the left and exceeded the center when she looked at targets on the right, with the distance between the saccadic endpoint and the center increasing with target diameter. BE, on the other hand, landed near the center when targets were on the right, but showed a peculiar pattern of saccadic endpoints when targets were on the left. He fell short of center for the smallest diameters (60 and 120 min arc), with saccade size gradually coming closer to, and then exceeding, target eccentricity as the diameter increased. These departures from center amounted to no more than about 10% of the diameter of the target for each subject.

The scatter of landing positions

The reliability of the saccadic landing positions was excellent. Standard deviations of horizontal saccade sizes, averaged over the five eccentricities for each target diameter, remained quite low—between 12 and 16 min arc (5–6% of target eccentricity)—as target diameter increased to 120 min arc (for BE) and

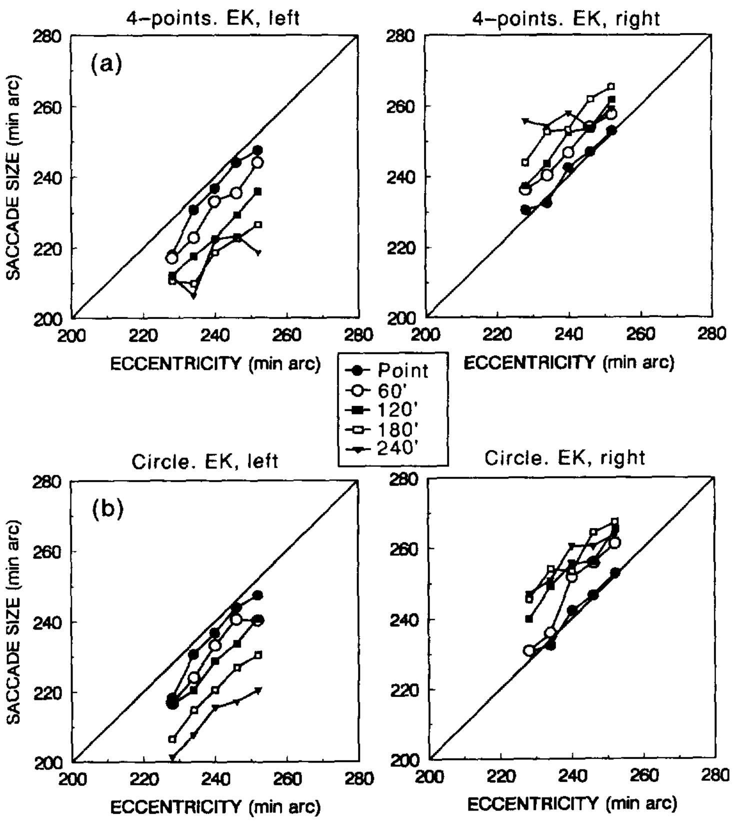

FIGURE 2. Average saccade size (horizontal component) as a function of eccentricity for subject EK. Data are shown for the four-point (a) and circle targets (b) of different diameters located to the left or to the right of the fixation crosshair. The diagonal line indicates sizes of saccades directed to the center of the target. Each datum point is a mean of approx. 25–40 observations.

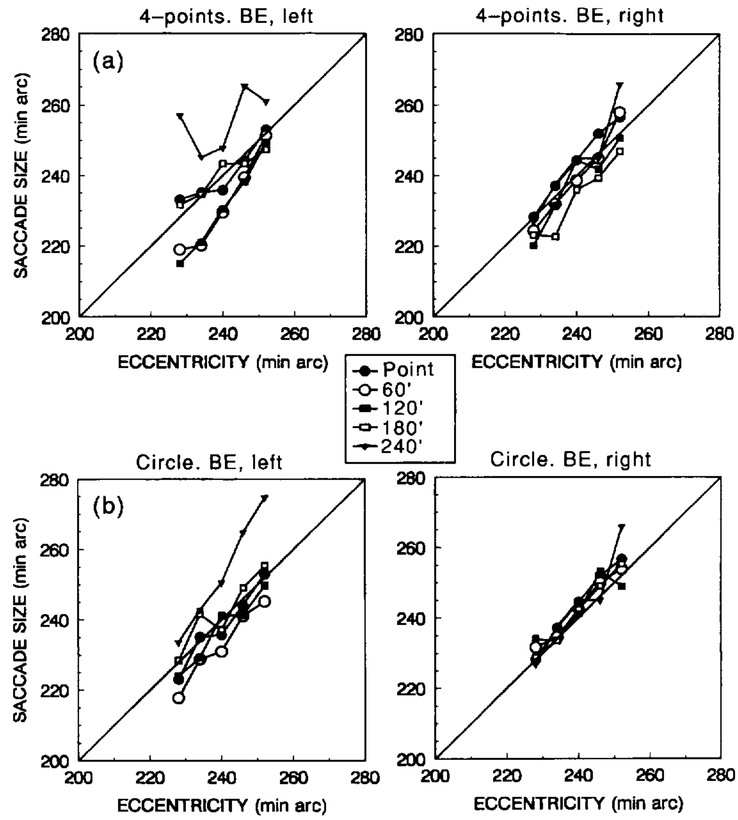

FIGURE 3. Average saccade size (horizontal component) as a function of eccentricity for subject BE. Data are shown for the four-point (a) and circle targets (b) of different diameters located to the left or to the right of the fixation crosshair. The diagonal line indicates sizes of saccades directed to the center of the target. Each datum point is a mean of approx. 20–40 observations.

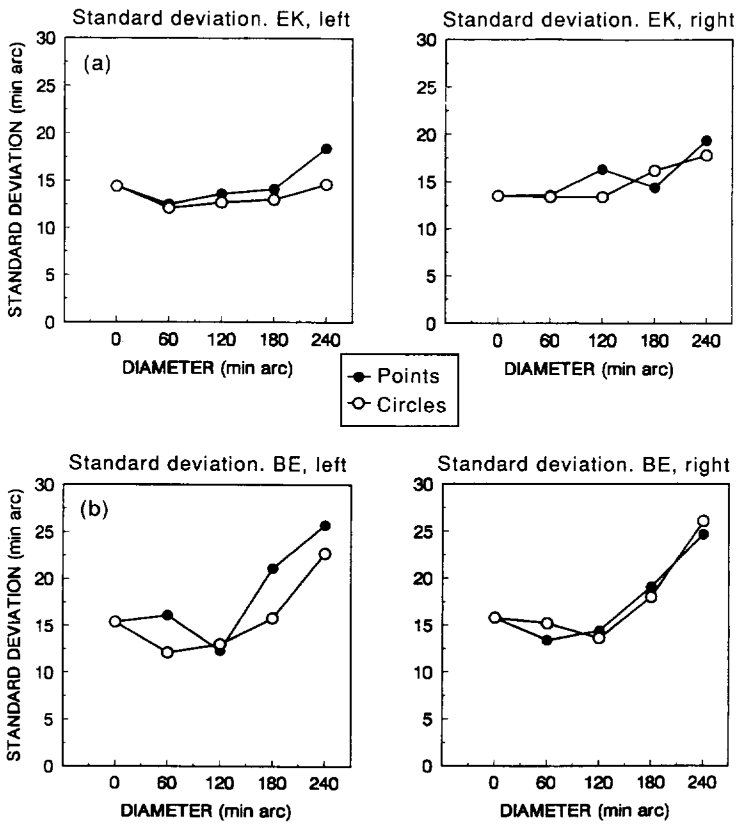

FIGURE 4. Mean SDs of saccade size for four-point and circle targets of different diameters located to the left or to the right of the fixation crosshair. Mean SDs were determined by averaging the SD obtained for each of the five target eccentricities.

180 min arc (for EK) (see Fig. 4). Standard deviations increased for the largest targets, more so for BE than for EK, but the largest values were only about 10% of target eccentricity. Standard deviations were similar for circles and four-point targets.

The vertical component

Analysis of the vertical component of the saccades shows that saccades landed near, but not precisely at, the center of the form. BE's vertical error was about 10% of the target diameter with SDs of about 5–10 min arc. EK's vertical errors and SDs were about the same as BE's when the target was on the left. When the target was on the right, her vertical error was smaller (about 5 min arc) and independent of target diameter. The vertical component of saccades was about the same for the form and the point targets for both subjects.

Learning

We examined saccades made to the single-point targets to find out whether the highly accurate performance could have been due to practice. Effects of practice seemed unlikely because the number of stimulus conditions was so large (9 targets × 2 directions × 5 eccentricities/direction) that each stimulus condition was tested only about four times in a single day. The 90 different stimulus conditions not only provided a wide variety of visual error signals but also different average saccade sizes as well (Figs 2 and 3).

Figures 5 and 6 show the sizes of saccades made over trials. Keep in mind that the successive trials shown on the abscissa of each graph do not represent consecutive trials within an experimental session because target type and stimulus eccentricity were randomly intermixed during each session. The graphs in Figs 5 and 6 show performance after the trials were sorted into groups depending on the stimulus condition.

The data in Figs 5 and 6 verify that there was no improvement with practice. The slopes of the best fit lines (shown on the graphs) show that EK tended to decrease and BE to increase saccade size over trials. But there was no relationship between the slope and the eccentricity of the target, showing that these tendencies, whatever their origin, neither improved nor impaired performance.*

Latency

Subjects did not achieve accurate and precise saccadic landing positions with target forms by prolonging latency. Figure 7 shows that latency did not increase with target diameter. Latency did depend on the type of target for EK, whose latencies were shorter for the circles than for the four-point targets. BE's latencies were 50–100 msec longer and more variable than EK's.

These results show that adding the requirement to find a saccadic landing position within a form took no additional time. If anything, latencies were longer with the single-point targets than with the forms.

Trials with more than one saccade

In the vast majority of trials subjects made one, and only one, saccade, as instructed. Second saccades did, however, occur from time to time. These second saccades, unlike the first saccades, were "reflex-like" in that neither subject tried to make them, neither knew they had occurred, and, what is most surprising, neither knew that second saccades were confined almost exclusively to trials with the smallest targets. Figure 8 shows the proportion of trials with more than one saccade as a function of target diameter.

Analysis of trials with the single-point targets, where second saccades were most numerous, sheds some light on their origin. Second saccades were almost always (>90%) in a corrective direction, with half correcting for undershoots and half for overshoots of the first saccades. Second saccades reduced by 2–3 times the error left behind by first saccades: the average of the absolute (unsigned) error of the first saccade on trials with more than one was 23 min arc (SD = 11, $n = 22$) for EK, and 19 min arc (SD = 13, $n = 104$) for BE. Second saccades reduced this average error to 8 min arc for EK (SD = 6) and 9 min arc (SD = 7) for BE. This was similar to the average error on trials with only one saccade (for EK, mean error = 12 min arc, SD = 9, $N = 272$; for BE, mean = 10 min arc, SD = 8, $N = 185$). These results show that second saccades had the highest likelihood of occurring when the error left behind by the first saccade was relatively large, and that second saccades were quite effective in abolishing the error and bringing the target into the acceptable fixation region for each subject.

The latency of the second saccades to point targets was 167 msec for both subjects. This value was long enough to have allowed these corrective saccades to have been programmed on the basis of visual error information, rather than as part of pre-programmed package along with the primary saccade [an idea that had been suggested from time to time (e.g. Becker & Fuchs, 1969; Lemij & Collewijn, 1989)].

Why were second saccades so rare with target forms? This outcome was puzzling because the accuracy of the first saccade was similar for point and form targets, at least for diameters up to 180 min arc (Figs 2–4). One possible explanation is that the minimum size of the error

*The systematic changes of saccade size over trials, shown in Figs 5 and 6, might complicate the estimate of saccadic precision because the influence of the visual, motor and behavioral sources of variability would be confounded with the influences of whatever process is responsible for the gradual changes in saccade size over trials. We removed that portion of the variance accounted for by the gradual changes in saccade sizes by multiplying each standard deviation by $\sqrt{(1-r)^2}$, where r is the coefficient of correlation between saccade size and trial number. The resulting change in saccadic standard deviations was negligible. BE's standard deviation decreased from 16 to 15 min arc and EK's from 14 to 13 min arc. We did not correct the mean saccade size for the changes over time, even though the slopes of the best fit lines for the different eccentricities were slightly different. Given that the trials for each eccentricity were scattered over all the experimental sessions, from the first to the last, we felt that the best estimate of mean size would be the size averaged over all the trials. Had we truncated the sample so that mean values for each eccentricity would be based on the same number of trials, we would be eliminating data from the final experimental sessions for some of the target eccentricities.

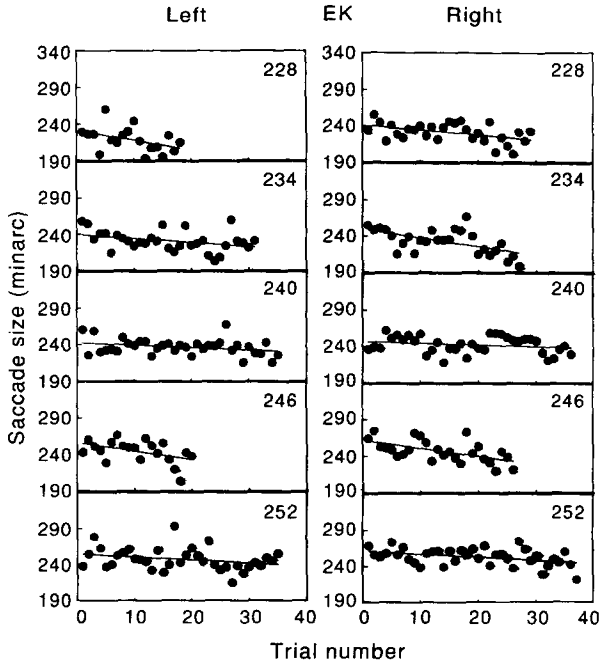

FIGURE 5. Saccade size as a function of trial number for subject EK for point targets on the left and right at the five eccentricities shown on the graph. Saccade size was based on the distance between the eye position at the end of the saccade and eye position at the start of the trial. The best fit lines were determined by a least squares criterion.

that elicited a corrective movement increased as targets become larger. To test this idea we examined the proportion of trials with more than one saccade as a function of the average error of the first saccade for targets of different diameters. Figure 9 shows that the larger the target, the larger the error had to be before

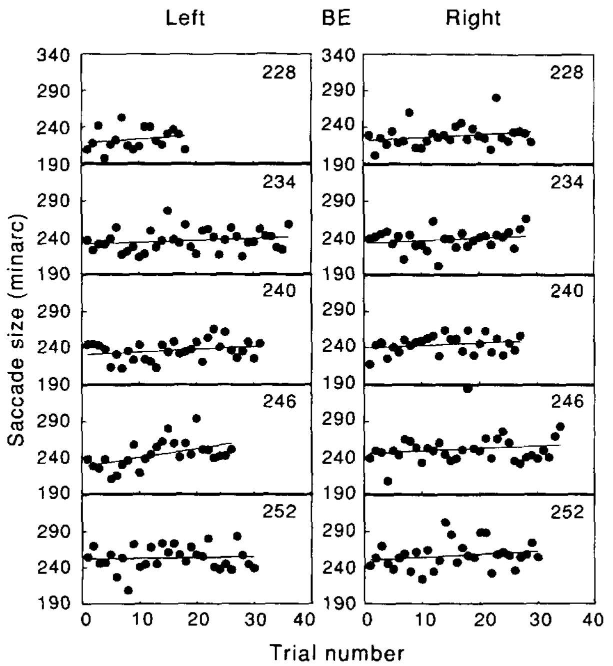

FIGURE 6. Saccade size as a function of trial number for subject BE for point targets on the left and right at the five target eccentricities shown on the graph. Saccade size was based on the distance between the eye position at the end of the saccade and eye position at the start of the trial. The best fit lines were determined by a least squares criterion.

second saccades appeared on an appreciable portion of the trials. With 60 min arc diameter circles, for example, BE was likely (proportion > 0.5) to make a second saccade only when the first saccade landed on or outside the boundary of the form, i.e. error > 30 min arc. With single-point targets, errors of only 20 min arc were followed by a high proportion of corrective saccades. Apparently, once the line of sight landed within the form, there was rarely an adequate "error signal" available to trigger the correction.

Is the presence of the fixation target important?

Lemij and Collewijn (1989) found that saccadic accuracy is better when subjects look back and forth between stationary targets than when they follow a target jumping back and forth. We had left the fixation target on when the eccentric point appeared. To find out whether this was important, we repeated the experiment, comparing saccades made when the fixation target remained on throughout the trial to saccades made when the fixation target was removed as soon as the saccadic target appeared (100 msec after trial onset). Thus, in the latter case the fixation target and saccadic target were never seen simultaneously. These conditions were tested in separate experimental sessions that contained single-point targets at the same eccentricities tested previously.

Performance was the same regardless of whether the fixation target was left on or turned off (see Figs 10 and 11). Performance in either condition was slightly poorer than performance observed in our main experiment in that the difference between the mean size of the saccade and the target eccentricity, averaged over the 10 target locations tested, increased from 3 to 6 min arc for EK and from 3 to 4 min arc for BE. Once again there was no tendency toward undershooting and no range effect.

This experiment shows that cues about relative visual location, provided when the fixation target remains on, did not contribute to the high degree of accuracy and precision we observed. This result stands in contrast to perceptual localization, which is impaired by sequential presentation of the targets to be compared (Westheimer & Hauske, 1975; White *et al.*, 1992).

Our results are not in conflict with the conclusion drawn by Lemij and Collewijn (1989). They suggested that saccades made between stationary points are more accurate than saccades made between jumping targets, not because stationary points provide cues to relative position, but because stationary points allow more time to process the target than jumping points. This idea implies that there should be no difference between leaving the fixation target on and turning it off when subjects take as much time as they need to program the saccade, which is exactly what we found.

DISCUSSION

There are four noteworthy results reported in this paper.

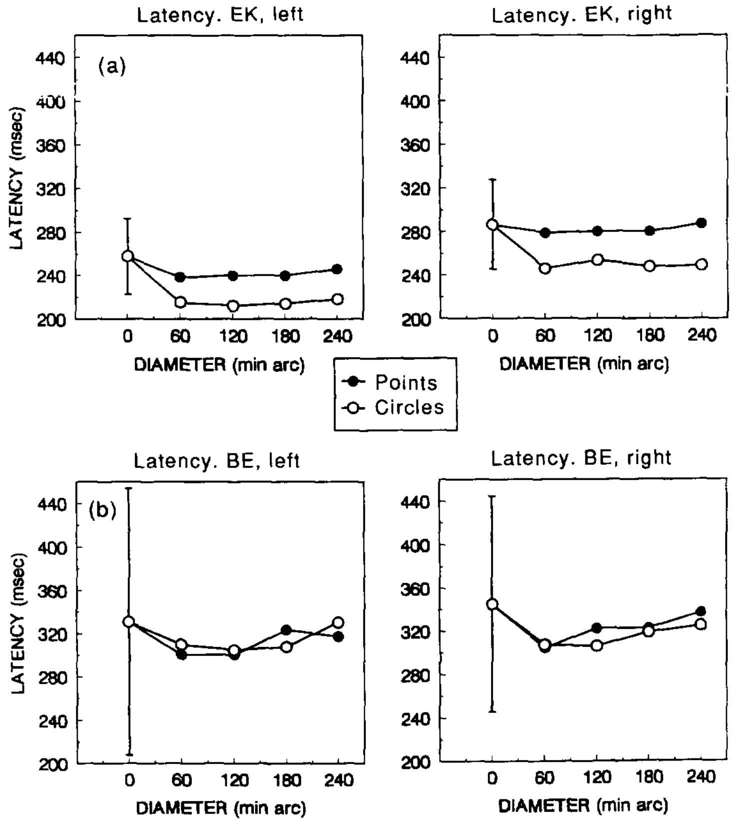

FIGURE 7. Mean latency of saccades to four-point and circle targets of different diameters located to the left or to the right of the fixation crosshair. Mean latencies were determined by averaging the mean latencies obtained for each of the five target eccentricities. The representative error bar shown for the latency of saccades to the single point target is the mean SD of saccadic latency averaged over the five eccentricities.

1. Saccades can be extremely accurate

Average saccadic landing positions missed the point target by only 3 min arc (1.25% eccentricity). There were no systematic undershoots. The absence of undershoots was not due to the range effect because we did not find the range effect in our data, i.e. there was no tendency to undershoot the largest and overshoot the smallest displacements of the target set. The high level of accuracy we observed was achieved with randomly-selected target displacements, without benefit of practice, and with no special stimuli or procedures other than the instruction to make a single saccade as accurately as possible.

Our results were obtained for target displacements ranging from 3.8 to 4.2 deg, sizes for which undershoots have been reported in the past and assumed to represent normal saccadic performance [e.g. Kapoula and Robinson (1986) found 8% undershoots for 5 deg displacements].

We do not know why the accuracy we reported was better than that reported in prior studies. The instructions may have been a critical factor. We asked subjects to try to be as accurate as possible, even if this requires a longer latency, and to avoid corrective saccades, even if it feels like the first saccade missed the target. Undershoots may be typical only in the absence of such instructions. It is also possible that sensory or sensorimotor factors may promote undershoots when latency is so short that the perceived location of the target is underestimated (Aitsebaomo & Bedell, 1992; O'Regan, 1984; Skavenski, 1990) or when saccades are made to targets at very large eccentricities with the head stabilized by a biteboard rather than free to move (Collewijn, Steinman, Erkelens, Pizlo, Kowler & Van der Steen, 1992). Since we were able to eliminate undershoots by simple instructions, drawing valid conclusions about such sensory or sensory–motor causes of undershoots will require testing performance when explicit instructions to strive for best possible accuracy with a single saccade are given and latency-accuracy trade-off functions are measured.

2. Saccades can be extremely precise

The precision of the saccades was excellent (SD about 6% of target eccentricity) and comparable to the precision of judging the separation between a foveal and eccentric target, where SDs of 3–6% of eccentricity have been found (White *et al.*, 1992). We confirmed this perceptual result with our own stimuli using 200 msec exposures and found SDs of about 4% of separation. This value was somewhat less than the SD of the saccades.

The similarity between saccades and perception was surprising and stands in contrast to what has been found for targets confined to the fovea. When targets steps are <30 min arc, the variability of saccades far exceeds that of perceptual judgments of step size (Westheimer, 1979; Timberlake, Wyman, Skavenski & Steinman, 1971; Kowler, 1990). The correspondence we found between

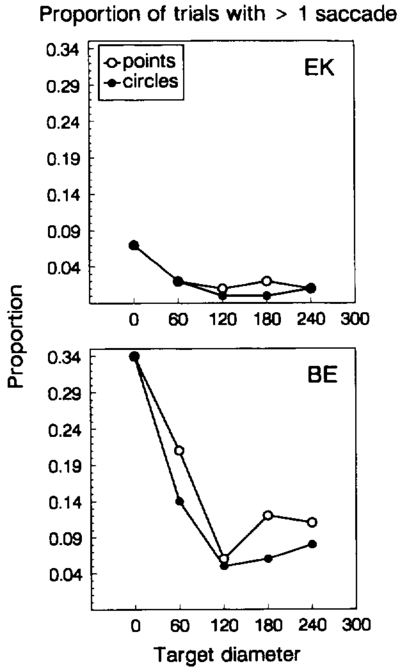

FIGURE 8. Proportion of trials with more than one saccade as a function of target diameter. Leftward and rightward saccades have been combined.

saccadic and perceptual localization for extra-foveal targets suggests either that each response—perceptual and saccadic—is limited primarily by a common source of variability, namely, the precision of coding the location of the eccentric target, or that the overall noise contributing to each response, albeit from different sources, turns out to be approximately the same.

3. Saccadic accuracy and precision do not diminish with increases in target size

Saccadic accuracy, precision and latency were all unimpaired by increases in target diameter up to 180 min arc, regardless of whether the target was an outline drawing of a circle or a diamond-shaped configuration of four points. The excellent performance with the target forms suggests that the saccadic system has access to an effective mechanism for computing a central reference location within an eccentric target, presumably by pooling visual information within selected spatial regions. Invoking the pooling mechanism did not increase saccadic variability nor did it require additional programming time: latencies were, if anything, shorter with target forms than with points.

Others have proposed that our ability to perceive the distance between two objects depends on a spatial-pooling mechanism that finds the center-of-gravity of objects (Hirsch & Mjolsness, 1992; Morgan *et al*., 1990; Morgan & Glennerster, 1991; Vos *et al*., 1993; Westheimer, 1979). Our results suggest that saccades use a pooling mechanism too, although the saccadic landing positions we found did not always coincide precisely with the center-of-gravity (Figs 2 and 3). We want to emphasize that the saccades were not automatically or reflexively drawn to a central landing position (He & Kowler, 1989). Subjects were instructed to "look at the form as a whole". The instruction is important because subjects can, if asked, look at different places within forms (He & Kowler, 1991).

Morgan and Glennerster (1991) found results similar to ours, namely, little effect of target size, in a comparable perceptual localization task (estimating the distance

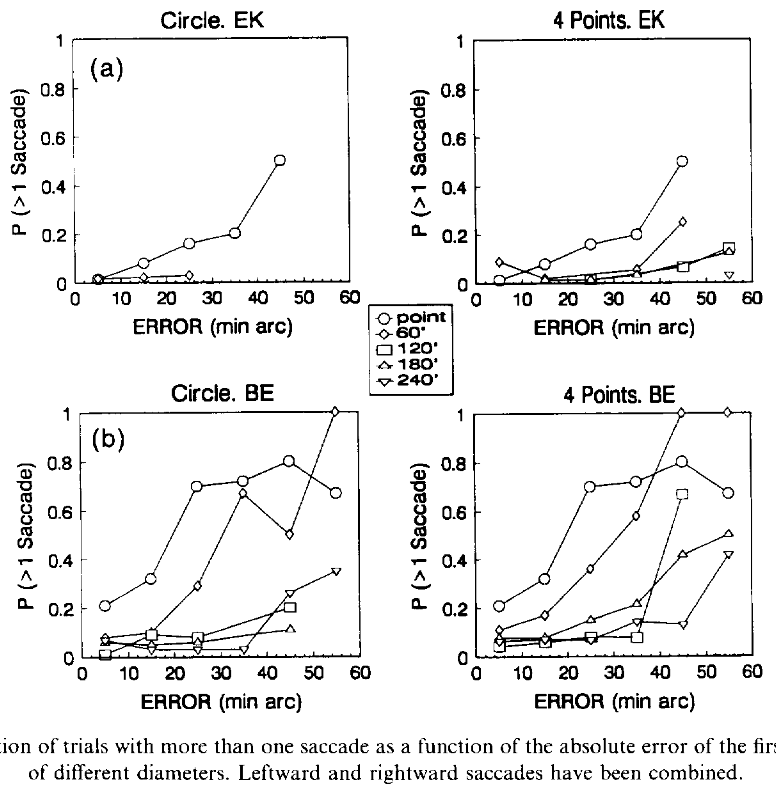

FIGURE 9. Proportion of trials with more than one saccade as a function of the absolute error of the first saccade for targets of different diameters. Leftward and rightward saccades have been combined.

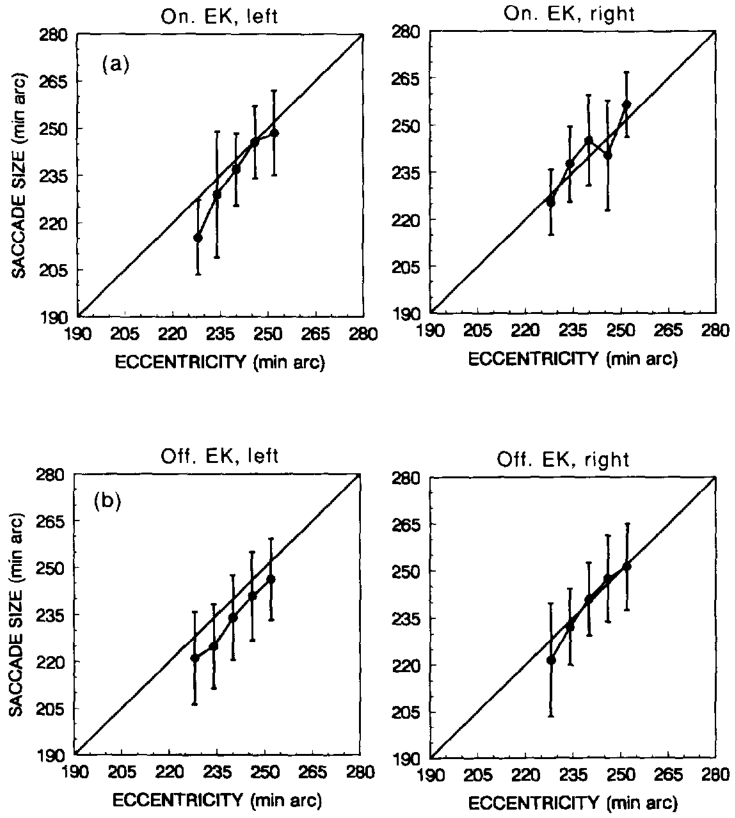

FIGURE 10. Saccade size as a function of target eccentricity for subject EK for targets on the left and right, under instructions to reach the target as accurately as possible with a single saccade while the central fixation crosshair remained on (a) or was turned off (b) when the target appeared. Saccade size was based on the distance between the eye position at the end of the saccade and eye position at the start of the trial. The diagonal line indicates perfect performance. Error bars represent ± 1 SD. Each datum point is a mean of approx. 25 observations.

between two circles). They explained the independence from circle size by proposing that the expected increase in the variability of estimating the center of the circle with increasing circle size is offset in part by the availability of more samples of position along the contour. Such a tradeoff may apply to perceptual localization, but it is not consistent with the equivalent precision we observed for the circle and four-point targets because increasing the size of the four-point targets did not provide additional position samples.

Independence from target size would be expected if the hypothesized spatial pooling mechanism estimates the central reference position within the form with a precision that is far better than the precision of coding the distance to the reference position. Specifically, if the SD of saccade size depends both on the precision of estimating the central reference position within the form (SD_c), and on the precision of directing a saccade to that central position (SD_p), and if these are independent, then the SD of saccades to the forms should be equal to:

$$\sqrt{[(SD_p)^2 + (SD_c)^2]}.$$

Setting SD_p to the SD of saccades to the point target (e.g. 14 min arc for EK) and assuming that the center of the target could be estimated with a SD of 5% of the diameter (i.e. the SD we found when we tried to judge the diameter of the eccentric target forms), then the SD of saccades to 180 min arc diameter target should increase to only 17 min arc. Thus, as long as the central reference position within the target can be estimated precisely, there will be little effect of increasing target size because the lion's share of the variability is coming from the estimate of the distance to the center.

We present this simple model in order to show that independence from target size implies that the saccadic system has access to a very precise representation of a central reference position within a target form. This representation may not, however, be available for very large targets. When targets were large with respect to eccentricity, we found a noticeable increase in saccadic variability, particularly for subject BE (Fig. 4). This finding is reminiscent of a perceptual result, namely, the precision of estimates of the separation of two spatial references depends on their separation, but only when the separation is smaller than the eccentricity (Levi & Klein, 1990; Burbeck & Yap, 1990). It remains to be determined whether or how the "separation dependent" mechanism, used for perceptual localization when separation is small with respect to eccentricity, relates to the spatial pooling process that guides saccades to target forms.

4. *Second saccades were rare with target forms*

Subjects followed instructions to reach the target with one and only one saccade. Second saccades were infrequent and limited almost entirely to the very smallest

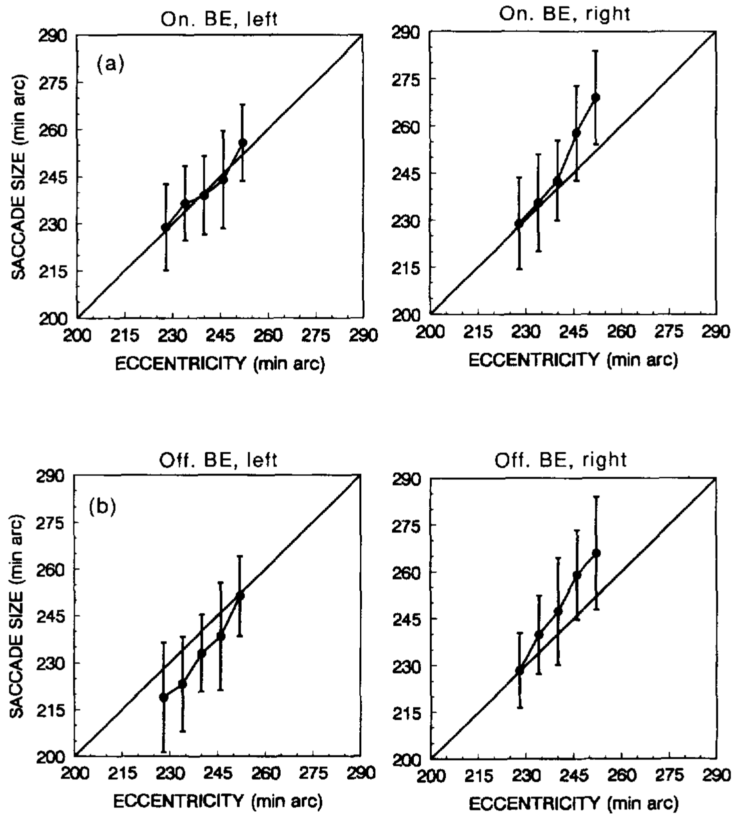

FIGURE 11. Saccade size as a function of target eccentricity for subject BE for targets on the left and right, under instructions to reach the target as accurately as possible with a single saccade while the central fixation crosshair remained on (a) or was turned off (b) when the target appeared. Saccade size was based on the distance between the eye position at the end of the saccade and eye position at the start of the trial. The diagonal line indicates perfect performance. Error bars represent ±1 SD. Each datum point is a mean of approx. 35 observations.

targets we studied. The second saccades were unusual in that subjects did not try to make them, did not know when they occurred, and did not realize they were limited to the small targets. They were corrective in that their direction brought the line of sight closer to the target point, or to the center of the target form, and in that the average saccadic error was reduced substantially after the second saccade.

Second saccades became far less frequent as targets became larger, as the size of the error needed to elicit an appreciable portion of corrections increased (Fig. 9). Apparently, the central reference position within the target forms, which we showed was quite effective in guiding *first* saccades, was no longer available to trigger corrective movements once the line of sight landed within the contour and the eccentricity of the form was reduced. This implies that the size of the region over which the spatial information is pooled to determine the central reference position depends on eccentricity, with pooling operating across a larger region as eccentricity increases.

We were surprised by the reflexive nature of the second saccades because so many prior attempts to demonstrate reflexive saccades have failed. For example, small fixation errors, produced either by motion of a target or by motion of the eye, can be ignored and need not be corrected with saccades (Steinman *et al*., 1973). Such results illustrate the inherently voluntary nature of saccades, even the very small ones. The reflexive character of the second saccades we observed, however, suggests that the volitional events required to launch a saccade, e.g. a shift of spatial attention to the target (Kowler, Anderson, Dosher & Blaser, 1995) or the issuing of a "go" signal (Kowler *et al*., 1995; Munoz & Wurtz, 1993) may remain in force even after a saccade is over if a detectable error remains.

In summary, saccades can be directed toward eccentric targets with excellent accuracy and precision. This high level of performance, demonstrated with single-point targets, can be maintained for large targets as well, showing that a precise representation of a central reference position within an eccentric target form is available to guide saccades. Now that we know that errors of saccades made to simple target forms can be extremely small, it becomes interesting to study a variety of different target types and configurations in order to understand how the central reference position is computed.

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APPENDIX

To find out whether the small differences between mean saccade size and target eccentricity, shown in Fig. 1, were statistically reliable, we tested the fit of the data to a model in which saccade size is assumed be distributed normally around the true target eccentricity. The statistical procedure used to test this model is described briefly below. For a more detailed description see Hoel, Port and Stone (1971). We compared two models, one constrained (C) and the other unconstrained (U). Both models stipulate that the sizes of saccades for each eccentricity e are normally distributed and both assume that the SD of saccade sizes (σ) around the target eccentricity e is independent of e. The constrained model has only one free parameter, σ. For any given value of σ, the likelihood of the constrained model is

$$L(\mathrm{C}|\sigma) = \prod_{\text{all trials } t} \frac{1}{\sqrt{2\pi}\sigma} \exp\left[\frac{-(x(t)-e(t)^2}{2\sigma^2}\right]$$

where $x(t)$ is the size of the saccade observed on trial t, and $e(t)$ is the eccentricity of the target on trial t. Thus, the constrained model requires the mean of the distribution of saccade sizes for each target eccentricity to be equal to eccentricity. We write $M(\mathrm{C})$ for the maximum likelihood of the constrained model C, i.e. the maximum value of $L(\mathrm{C}|\sigma)$ taken over all possible values of σ. The unconstrained model, unlike the constrained model, no longer requires mean saccade size to be equal to target eccentricity. For any target eccentricity e, we write μ_e for the mean size of saccades made to targets at eccentricity e. The free parameters in the

TABLE A1. Results of the likelihood ratio test for saccades to point targets for subjects EK and BE

	EK		BE	
	Left	Right	Left	Right
Slope	1	1	1	1
Intercept	0	0	0	0
χ^2	15.40*	2.82	4.61	9.60*
P value	<0.01	>0.50	>0.25	<0.05

Neither free (d.f. = 5).
*Rejection of hypothesis that data are fit by linear function with indicated slope and intercept.

unconstrained model are thus $\mu_{e_1}, \mu_{e_2}, \ldots, \mu_{e_5}$, for $e_1, e_2, \ldots, e_5$, the five target eccentricities used in the experiment; and σ, the SD of saccade size around target eccentricity. For any given values of these free parameters, the likelihood of the unconstrained model is

$$L(\mathrm{U}|\mu_{e_1},\mu_{e_2}, \ldots ,\mu_{e_n},\sigma) = \prod_{\text{all trials } t} \frac{1}{\sqrt{2\pi}\sigma} \exp\left[\frac{-(x_t - \mu_{e(t)})^2}{2\sigma^2}\right]$$

where, as in the constrained model, $x(t)$ is the size of the saccade observed on trial t, and $e(t)$ is the eccentricity of the target on trial t. Write $M(\mathrm{U})$ for the maximum likelihood of the constrained model U, i.e. the maximum value of $L(\mathrm{U}|\mu_{e_1}, \mu_{e_2}, \ldots, \mu_{e_5},\sigma)$ taken over all possible joint assignments of the free parameters $\mu_{e_1}, \mu_{e_2}, \ldots, \mu_{e_5}$, and σ. The statistical test used is based on a theorem of Wilks (see Hoel, Port & Stone, 1971) establishing that as sample size tends to infinity, the random variable

$$-2\ln\frac{M(\mathrm{C})}{M(\mathrm{U})}$$

tends to a χ^2 distribution with degrees of freedom equal to the difference between the number of free parameters in the unconstrained model and the number of free parameters in the constrained model. Table A1 shows that the constrained model could be rejected in two cases, namely, EK's leftward and BE's rightward saccades. Thus, in these two cases the depatures of saccade sizes from target eccentricity were large enough to allow us to reject the hypothesis that saccades are perfectly accurate.