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Saccadic localization of occluded targets

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Abstract

Saccadic eye movements are able to localize spatially-extended targets, including patterns of random dots and simple shapes, with a high degree of precision [McGowan, Kowler, Sharma & Chubb (1998). *Vision Research*, *38*, 895–909; Melcher & Kowler (1999). *Vision Research*, *39*, 2929–2946]. This paper investigates the representations of object shape that guide saccades. We studied saccadic localization of partially-occluded triangles (two or three vertices removed) to find out whether saccades have access to a representation of the full shape, despite the missing portions. Targets were configured so that they could be seen either as triangles, which were partially occluded by polygons, or as fragments in front of the same polygons. Subjects tried to saccade to the inferred full triangle and a discrimination paradigm was used to evaluate their success. Occlusion cues were ineffective in that saccades directed to the occluded triangles landed near the center of the visible fragment, even when it was configured as a triangle behind occluders. Removing the occluders and leaving only three segments of the triangle (vertices removed) helped somewhat, but performance never resembled that achieved with either a full triangle or a 3-dot configuration. We conclude that the saccadic system is insensitive to at least some cues that can be used to infer the shape of objects. For occluded targets, the representation used by saccades may be closer to the configuration of the retinal image. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Saccadic eye movements are used to inspect visual scenes, creating a succession of high-resolution views of the most important spatial regions. People can use saccades to look where they wish. The choices are dictated typically by the demands of the visual, motor or cognitive task (for recent examples see Viviani, 1990; Epelboim, Steinman, Kowler, Edwards, Pizlo, Erkelens et al., 1995; Ballard, Hayhoe, Pook & Rao, 1997).

Choice of targets is just the first step. Bringing the line of sight to the appropriate place depends on attentional and visual processes that determine the oculomotor commands. For example, since targets are typically surrounded by irrelevant material, selective attentional filters are needed to ensure that saccades are aimed toward the target and are not deviated in the direction of visual backgrounds (Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher & Blaser, 1995; Deubel & Schneider, 1996). Also, since selected targets are typically objects of some spatial extent, specialized visual mechanisms are needed to determine the precise location of the saccadic endpoint within the chosen object. This paper is about the nature of the visual mechanisms that determine the endpoint of the saccade.

The present work is an outgrowth of prior studies showing that saccades to large targets land near the center with a high degree of precision, implying that a spatial pooling mechanism averages information across the selected target object and determines the exact landing position (He & Kowler, 1991; Guez, Marchal, Le Gargasson, Grall & O'Regan, 1994; Kowler & Blaser, 1995; McGowan, Kowler, Sharma & Chubb, 1998; Melcher & Kowler, 1999). (For discussions of spatial pooling in different situations, namely, small targets, in unpredictable locations, surrounded by distractors, see Findlay, 1982; Ottes, Van Gisbergen & Eggermont, 1985; Coëffe & O'Regan, 1987; He & Kowler, 1989.)

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Pooling across the selected target is crucial for the effective use of saccades, yet little is known about how it works. For example, does pooling operate on a visual representation that resembles the spatial configuration of the objects we perceive, or on a representation that is closer to the configuration of the raw retinal image? The finding that saccades directed to a cluster of random dots land near the average dot location (McGowan et al., 1998) might seem to suggest that averaging operates at a very early level, even before the component elements of a form are integrated into a shape. But elements turn out not to be decisive. When elements are arranged into a well-defined shape, saccades land near the center of the shape, regardless of the distribution of elements. Similar results apply to perceptual localization, which also relies on spatial pooling (Whitaker & Walker, 1988; Morgan, Hole & Glennerster, 1990; Hirsch & Mjolness, 1992; Burbeck & Hadden 1993), and is, like saccadic localization, independent of the internal luminance distribution (Proffitt, Thomas & O'Brien, 1983; but see Whitaker, McGraw, Pacey & Barrett, 1996; Akutsu & Levi, 1998). The independence from elements implies that the visual representation used to guide saccades, and perhaps perceptual localization as well, includes transformations at least up through the level of the construction of shape.

Shape construction in these prior experiments, described above, was a matter of integrating nearby elements into a contour and distinguishing elements on the contour from those inside the shape. These operations are performed relatively early in the visual processing stream (Zucker, Dobbins & Iverson, 1989; Field, Hayes & Hess, 1993; Kovacs, 1996; Feldman, 1997). Visual processing in later stages is more complex. For example, changes in viewpoint or the presence of occluders can drastically alter the retinal image without producing the impression that the shape of the object has changed.

In the present paper we sought to find out whether operations at later stages of visual processing are included in the representation that guides saccades. Specifically, we tested occluded targets to find out whether landing position is determined by the completed shape or by the visible fragment present on the retina. Perceiving objects as continuing behind occluders is crucial for maintaining the impression of an unchanging visual world, but there is no a priori reason to assume that the oculomotor system should be sensitive to visual information not physically available on the retina. Thus, the study of occlusion can be useful in either extending or establishing limits on the availability of high-level visual representations to the oculomotor system.

1.1. Rationale of the approach

Targets were triangles with two of the vertices removed (Fig. 1). The subject's task was to direct the saccade to the inferred full triangle, using any available shape and occlusion cues to complete the triangle. Two types of targets were tested: (1) triangles partly occluded by two polygons (shape and occlusion cues); and (2) fragments of triangles appearing in front of the same polygons (shape cues only). The shape of the fragment in the second type of target matched the visible portion of the occluded triangle in the first type of target.

Triangles with occluded vertices were used because, unlike squares or circles, the center of a fully-completed shape cannot be estimated by a strategy of isolating a local landmark, such as the midpoint between selected locations on the visible boundary. Instead, two segments of the visible contour have to be extrapolated in order to find a vertex. Extrapolating contours to complete an occluded vertex is more difficult than completing a straight or curved contour that is partially occluded (Kellman & Shipley, 1991). We felt that beginning with such a challenging task was the appropriate experimental strategy because the outcome would indicate either that a high-level representation of shape could control saccades, or that there was a clear limit on the sorts of visual representations available to saccades.

The ability to saccade to the completed triangle was evaluated by examining the differences in saccadic landing positions obtained for a set of five triangles with different centers-of-area (COA). COA, defined as the average horizontal and vertical location of the uniformly filled shape (see also Melcher & Kowler, 1999), was varied by changing the length of the base of each completed triangle (see Fig. 1). The important aspect of this measure was that the differences among the COAs of the five completed triangles were greater than the differences among the COAs of the corresponding visible fragments. Thus, finding large differences among landing position, comparable to the differences among the full triangle COAs, implies that a representation of the full triangle was available; small differences implies that saccades were programmed on the basis of the visible fragment.

Studying landing position differences, rather than absolute landing position relative to landmarks on any particular form, was necessary for two reasons. First, subjects could try to deliberately increase or decrease the sizes of saccades in an attempt to reach the occluded portion of the triangle without actually using a representation of the completed shape. Testing discrimination reduces the likelihood of erroneously inferring that a full representation of an occluded shape is available when subjects were merely choosing to bias saccades to one or another portion of the target. Second, although mean landing position within triangles and other shapes is typically close to the center-of-area, there are, nevertheless, consistent under- or overshoots with respect to the center of area that are independent of the type of shape presented (Kowler & Blaser, 1995; McGowan et al., 1998; Melcher & Kowler, 1999). Studying discrimination, rather than absolute landing position, allows us to ignore these under- and overshoots (or at least analyze them separately) and use differences among landing position as the main performance measure. (See Kowler & McKee, 1987, for an application of an oculomotor discrimination measure to the study of smooth pursuit.)

2. Experiment 1

2.1. Method

2.1.1. Subjects

Two subjects were tested. BS had prior experience as a naive eye movement subject in saccadic experiments employing spatially-extended targets, but had no knowledge of the purpose of this experiment. BS has normal vision and needed no spectacle correction. EK (one of the authors) is myopic and used a corrective lens in order to maintain the stimulus in sharp focus.

2.1.2. 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, controlled by a PC, sampled eye position every 10 ms. 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 standard deviation of position samples, was 0.4′ for horizontal and 0.7′ 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 Genera-

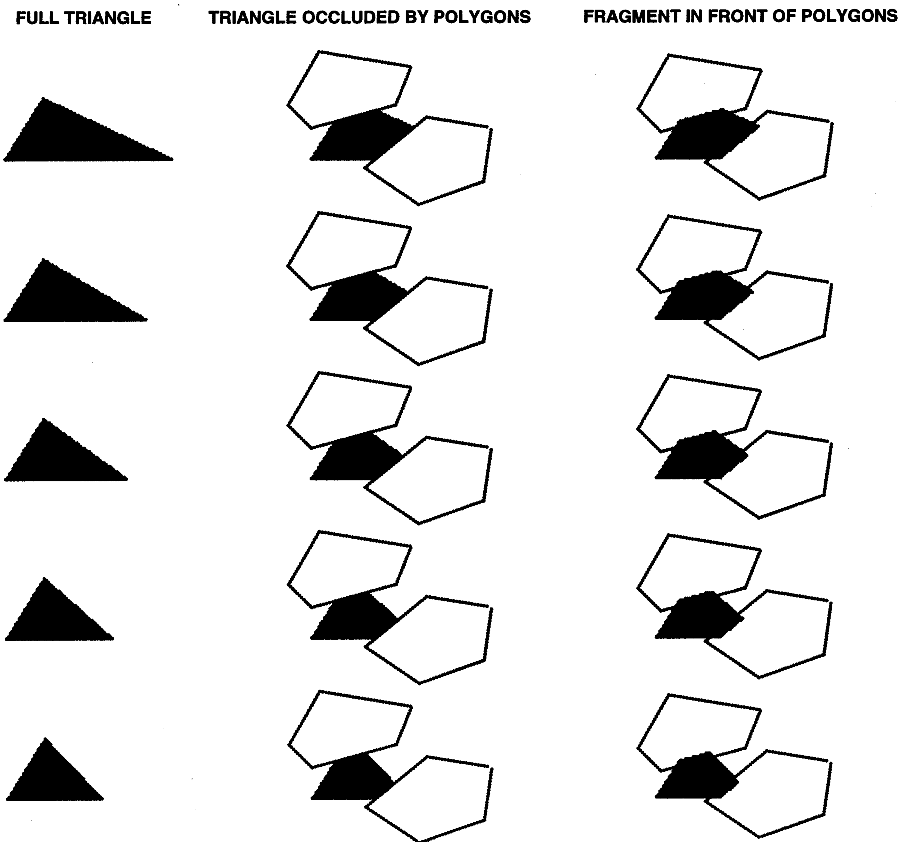

Fig. 1. The two stimulus conditions tested in Experiment 1 (triangle behind occluder and fragment in front of occluder) based on five scalene triangles (shown in the left-hand column) of varying base-length (124–218 min arc). Lefthand base angle and location of top vertex are the same for all triangles.

tion IV Trackers because motion of either the auto-stage or the focus-servo introduces large artifactual deviations into 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.

2.1.3. Stimulus

The stimulus was generated by digital-to-analog converters and shown on a display monitor (Tektronix 608, P4 phosphor) located directly in front of the subject's right eye. The display was refreshed every 20 ms, a rate that was high enough to prevent visible flicker. The luminance of the display, measured by a UDT photometer (model 61) from a 2.2 × 2.2 cm region containing 1600 points refreshed every 20 ms, was 17 cd/m^2.

The stimuli were seen against a dim (1.8 cd/m^2), perceptually homogenous background produced by a high frequency raster generated 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° horizontally by 18° vertically for subject BS and 9.5° horizontally by 7.6° vertically for EK. The difference in background 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. The retinal size of the saccadic targets, described below, was the same for both subjects.

2.1.4. Saccadic targets

Targets were based on a set of five scalene triangles of constant height (80′), one constant base angle (65°) and five different base sizes ranging from 126 to 218′, as shown in the left-hand column of Fig. 1. At these sizes the targets fit well within the spatial region over which visual information can be pooled and precise saccadic landing positions (SD < 10% eccentricity) achieved (Kowler & Blaser, 1995; McGowan et al., 1998). At these sizes targets were also large enough so that the horizontal centers-of-area of the different triangles in the set would be spread far enough apart to allow reliable differences in saccadic landing position to be detected (Kowler & Blaser, 1995).

Targets were made up of single points separated by 4′. The occluders were outline shapes and the triangles were filled-in with a uniform array of dots. The entire stimulus (including occluders) subtended on average 330′ horizontally and 210′ vertically. The exact shape and size of the occluders was varied randomly from trial to trial, although the visible portion of the each of the five occluded triangles was not varied. The size of the visible portion of the five occluded triangles varied between 106 and 132′ horizontally, and 58 and 62′ vertically. Targets were configured either as triangles partially occluded by polygons or as fragments in front of the same polygons (see Fig. 1, middle and right-hand column).

The horizontal and vertical center-of-area (COA) of each target was calculated in two ways: (1) as the average horizontal and vertical locations of the fully-completed, filled-in versions of each triangle (the fully-completed triangle was not actually displayed); (2) as the average horizontal and vertical locations of the displayed portions of each triangle. Targets were displayed either to the left or to the right of a 5 × 5′ fixation cross. In the presentation of the results the eccentricity of the target will be expressed as the distance between the fixation cross and the center of area (COA) of the *fully-completed* triangle. Targets were positioned such that the top vertices of the five triangles would be aligned if the targets were superimposed. With such an alignment the horizontal eccentricities of the five fully-completed triangles ranged between 212 and 242′. Eccentricities of the corresponding visible fragments covered a much smaller range, 237–247′. The range of vertical COAs of the five triangles in the set was quite small (< 10′) and for this reason analyses were restricted to the landing position of saccades with respect to the horizontal component of the COA.

To avoid strict coupling between the type of triangle and its eccentricity, eccentricity was subjected to a random jitter of ± 12′ on the horizontal meridian and ± 30′ on the vertical meridian, with horizontal and vertical values selected independently.

The displayed portion of each triangle was shown with occlusion cues (Fig. 1, middle column) or without occlusion cues (Fig. 1, right-hand column). The first condition will be referred to as the occluded triangle condition, the second as the fragment condition. In either case, the shape of the displayed portion could be used to complete the triangle.

The fixation cross was located 120′ to the left or right of the center of the display (for testing rightward and leftward saccades, respectively), which restricted testing to the central 5° of the visual field, where eye tracker output is linear.

All the stimulus variations described above, namely, the direction of the target with respect to fixation, the size of the triangle, the condition (occluded triangle or fragment), and the jitter of horizontal and vertical eccentricities, were selected randomly on each trial. The subject knew the choice of direction in advance because it was disclosed by the location of the fixation cross. All other choices were not revealed until the target appeared.

2.1.5. Procedure

The fixation cross was displayed before the start of each trial. The subject started the trial, when ready, by means of a button press. After a delay of 100 ms, the fixation cross disappeared and the saccadic target was displayed. The stimulus remained on for 1900 ms, at which time the trial was over. Target type (i.e. which one of the five triangles would be tested), whether it was a partially occluded triangle or a fragment, target direction (right or left of fixation), and the random jitter of eccentricity relative to fixation were chosen at random before each trial.

2.1.6. Instructions

In the first set of sessions, subjects were instructed to look at the full triangle as a whole. This meant they were to do their best to use all available shape and occlusion cues to generate an impression of the full triangle, and to then shift the line of sight to that triangle. After testing was completed, a new set of sessions was run in which subjects were instructed to look at the visible fragment alone, and not to attempt to infer the triangle.

As in prior work, where the instruction to look at the form as a whole was used (Kowler & Blaser, 1995; Melcher & Kowler, 1999), the instructions emphasized saccadic accuracy in order to allow assessment of the best spatial performance of saccades and to minimize extraneous sources of error that could impair accuracy. To that end subjects were asked to use a single saccade to reach the target and avoid secondary, corrective saccades even if the first seemed to miss the intended goal. The instruction to avoid corrective saccades was used in an attempt to encourage best possible accuracy of the first saccade and discourage a strategy of reaching the target with a sequence of two or more eye movements. The subjects were instructed to adopt saccadic latencies sufficiently long to avoid compromising accuracy, the only constraint being to try to complete the saccade before the end of the trial.

2.1.7. Detection and measurement of saccades

The beginning and end positions of saccades were detected by means of a computer algorithm employing an acceleration criterion. Specifically, eye velocity was calculated for two overlapping 20-ms intervals. The onset time of the second interval was 10 ms 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′/s or more. The criterion for saccade termination was more stringent in that two consecutive velocity differences had to be less than 300′/s. 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′/s) 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.

The landing position of the saccade on each trial relative to initial fixation was calculated by finding the distance between the position of the eye at the start of the trial (average of first 50 ms) 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 saccadic landing position also incorporated any drift (Kowler & Steinman, 1979) that might occur during the latency interval. The data reported are based on the first saccade of each trial, regardless of whether subsequent saccades occurred. Analyses will be confined to the horizontal components of saccades. Vertical components were small ($<$ about 30′), as expected, given that targets were positioned close to the horizontal midline of the visual display.

2.1.8. Number of trials tested and excluded

EK was tested in a total of 23 and BS in 26 sessions. Trials were eliminated as follows: trials with latencies less than 100 ms (EK, 0.4% of trials; BS, 0.3%), since with such short latencies it was unlikely that the stimulus played a significant role in determining the landing position of the saccade; trials with saccade errors of more than 100′ with respect to the center-of-gravity (EK, 1.4%; BS, 2.7%) because with such large errors the first saccade was not a genuine attempt to reach the target; trials in which no saccade was made (EK, 1.0%; BS, 2.9%) or in which the onset of the first saccade occurred in the last 100 ms (too late to be sure of accurate measurement of saccade offset position) (EK, 2.0%; BS, 0.6%). Analyses were based on 2746 trials for EK (95%) and 2921 trials (93%) for BS. Mean saccadic landing positions shown in the following graphs were calculated based on between 40 to 80 trials/datum point.

2.2. Results

In accordance with the instructions to emphasize high accuracy, average saccadic latencies were long (450–700 ms for EK; 1100–1400 ms for BS) and the majority of trials (78% for EK and 93% for BS) contained only a single saccade. For both subjects, saccadic precision was excellent, with standard deviations of landing position equal to 6–10% of eccentricity for all conditions.

Fig. 2 shows the mean landing positions for the occluded triangle and the fragment conditions as a function of the eccentricity of the COA of the triangles in the target set. The figure also shows the landing positions that would be predicted if saccades were

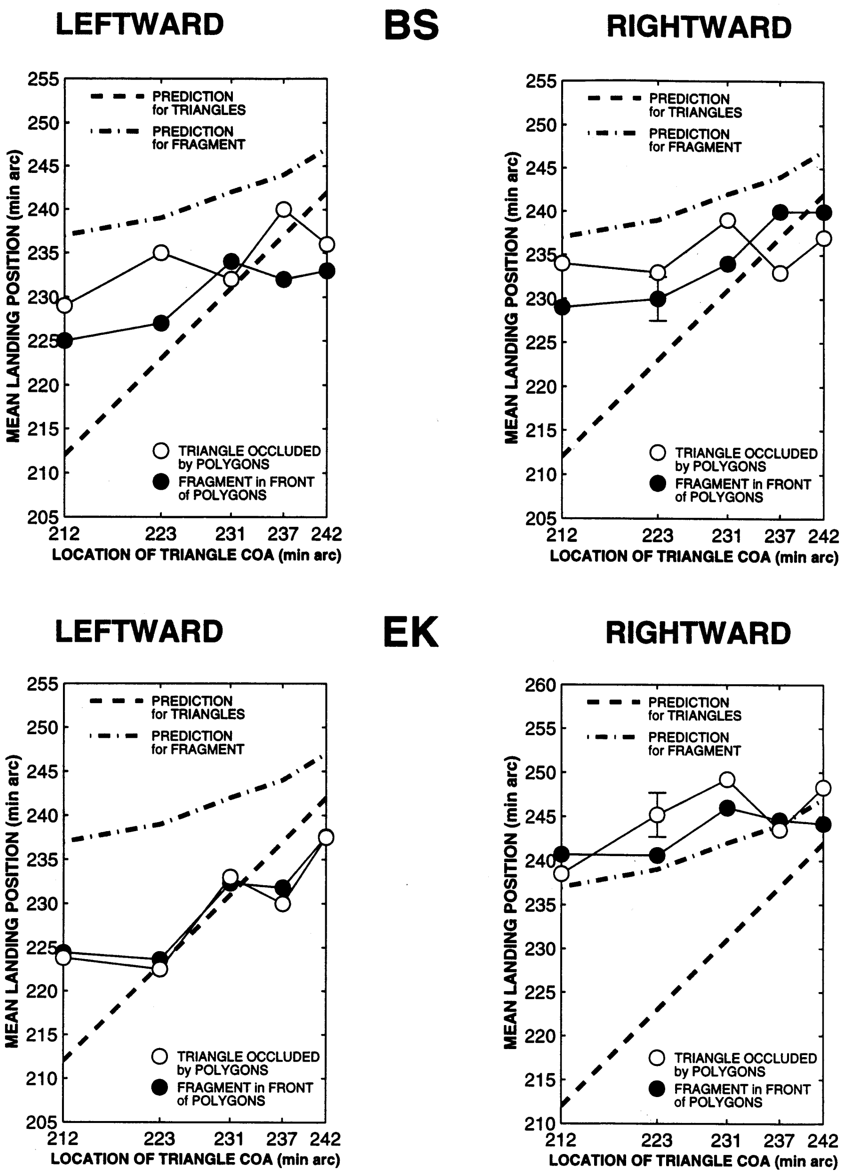

Fig. 2. Mean horizontal saccadic landing positions in the occluded triangle and fragment conditions as a function of location of the COA of the full triangle for subjects BS and EK under instructions to generate and look at the full triangle. Error bars indicate largest standard error for each subject. Lower dashed lines represent predicted landing position if saccades landed at the COA of the full triangle; upper dashed lines the COA of the visible fragment. $N = 50$–80 observations/datum point.

directed to the COA of the completed triangle and to the COA of the fragment. Slopes were quite close to the fragment prediction despite the attempts of subjects to direct saccades to the inferred full triangle. The presence of the occluders did not help. The results are much the same as those obtained when saccades were deliberately directed to the fragment (Fig. 3). The similarity of results across these two very different instructions applies not only to the slopes, but also to the net offset of the functions from the predictions. Thus, if subjects were trying to deliberately shorten saccades in an attempt to land closer to the estimated COA of the full triangle, the attempts did not succeed.

Fig. 4 summarizes the slopes obtained from straight lines fit to all functions in Figs. 2 and 3. Slopes were all quite close to those predicted by the COA of the fragment alone (lower dashed line of the graph) and far from the slope of 1 that would be obtained if saccades were programmed on the basis of the full triangle.

Perhaps the shallow slopes indicate that saccades ignored the target entirely and landed instead at some arbitrary location. This proved not to be the case. We examined landing position as a function of the $\pm 12'$ random variation in horizontal eccentricities (see Section 2.1). Despite the small difference in eccentricity, saccadic landing positions discriminated among the targets accurately (He & Kowler, 1991). Landing positions were separated on average by 11 and 10′ for EK's leftward and rightward saccades, respectively, and by 12 and 10′ for BS's leftward and rightward saccades.

2.3. Discussion

Saccades were sensitive to the location of the visible portion of the triangle and not to visual information that had to be inferred from shape or occlusion cues. Thus, either completion of the triangle was not possible with the available shape and occlusion cues, or this information was not useful for saccadic localization.

Despite the failure of saccades to reach the competed triangle, saccadic precision (as assessed by SD's of landing position) remained quite good. This result, along with the high sensitivity to small changes in eccentricity, suggests that saccades were guided in a consistent way by the visible features in the form and were insensitive to higher-order extrapolated or inferred features, even in the presence of perceptual cues (i.e. occluders) that encouraged the percept of the whole form.

Guidance by visible features suggests that accurate discrimination of the five triangles would be possible with only the vertices since their average location is the

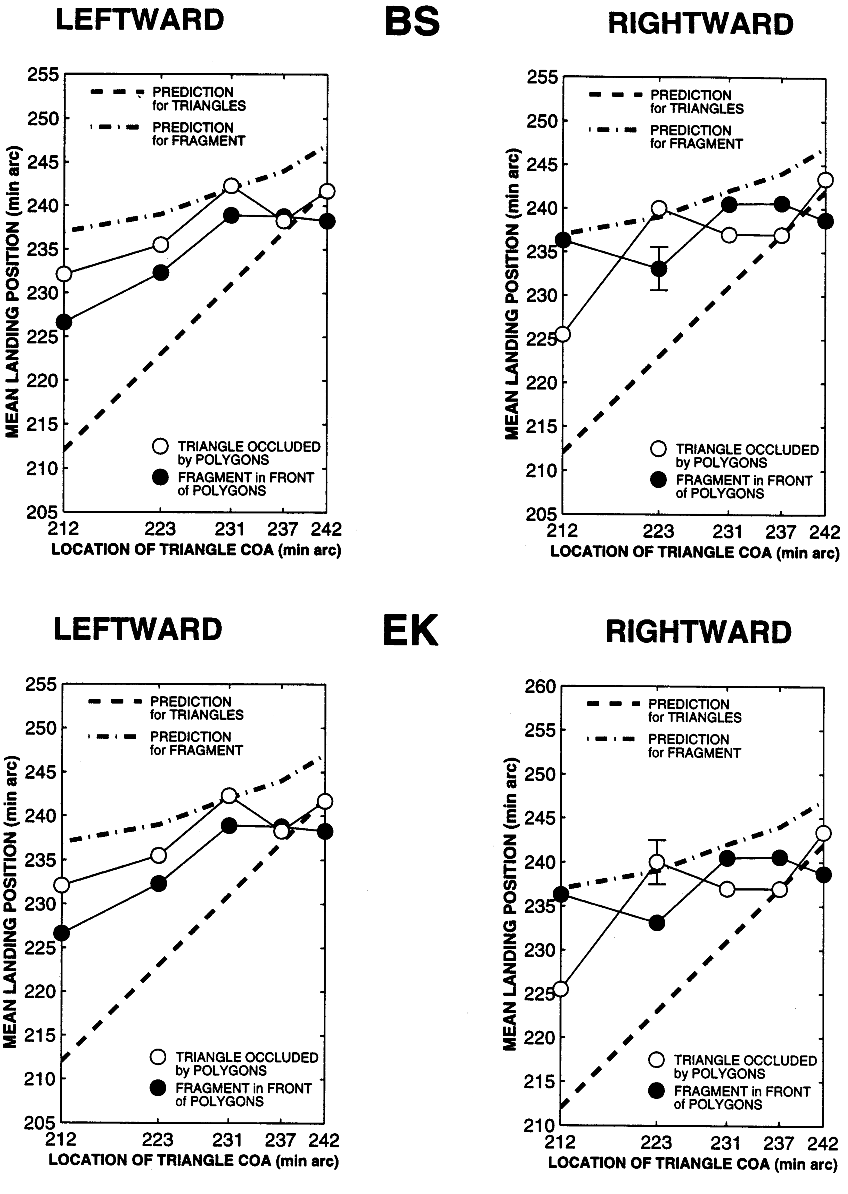

Fig. 3. Mean horizontal saccadic landing positions in the occluded triangle and fragment conditions as a function of location of the COA of the full triangle for subjects BS and EK under instructions to look at the visible fragment. Error bars indicates largest standard error for each subject. Lower dashed lines represent predicted landing position if saccades landed at the COA of the full triangle; upper dashed lines the COA of the visible fragment. $N = 40$–60 observations/datum point.

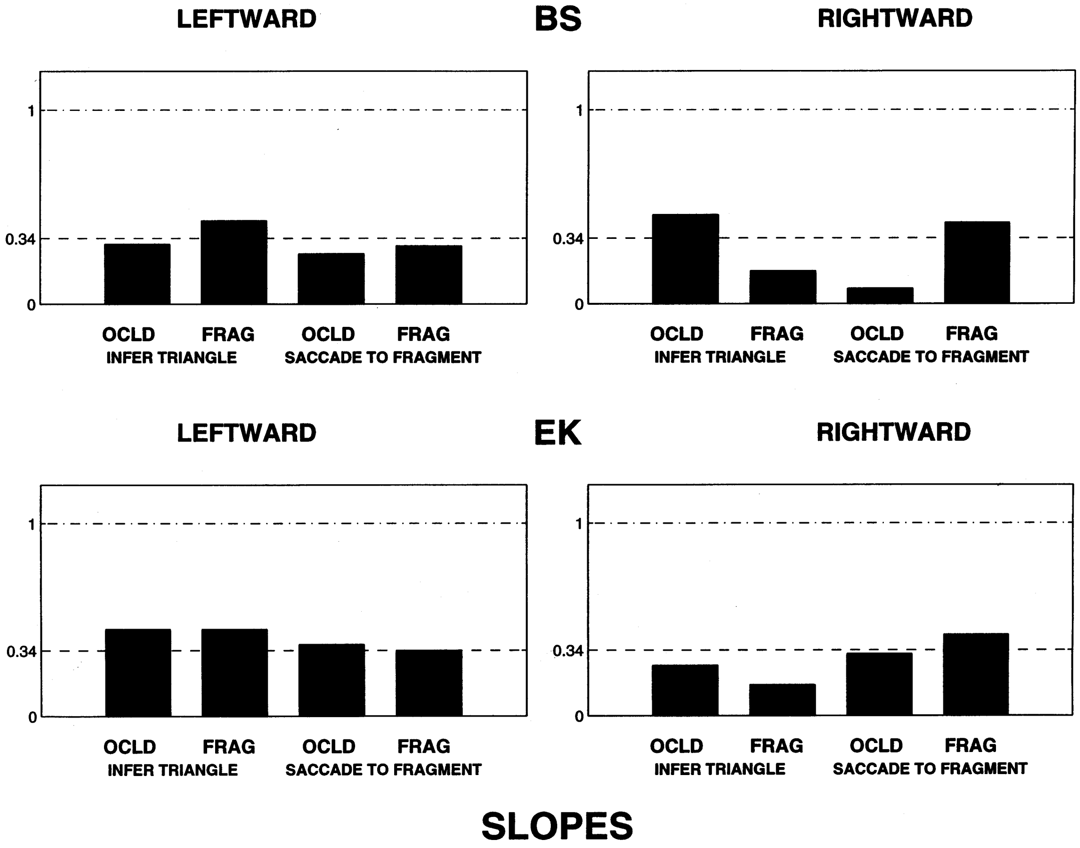

Fig. 4. Slopes of the landing position functions in Figs. 2 and 3. Upper dashed line indicates predicted slope if saccades landed at the COA of the full triangle. Lower dashed line indicates predicted slope if saccades landed at the COA of the visible fragment.

same as the COA of the fully completed triangle. The visible-features hypothesis also suggests that the occluders themselves may have gotten in the way and contour extrapolation might be facilitated if the line segments by themselves (no occluders) were shown.

Experiment 2 was run to further test the role of visible features vs. shape-completion cues. The targets covered a greater range of variation in the perceptual cues to completion, ranging from full triangles to polygonal fragments with no occluders or backgrounds. Targets containing the three vertices only and targets containing three line segments only (vertices removed) were also tested, along with the partially-occluded triangles, in order to find out whether vertices are sufficient and whether occluders interfere with completion because of the dominance of the visible features of the target.

3. Experiment 2

The types of targets, all based on triangles, are shown in Fig. 5. Vertices were present in two conditions: the full triangle and the configuration of three dots (i.e., vertices-only). Vertices were removed in the rest: seg-

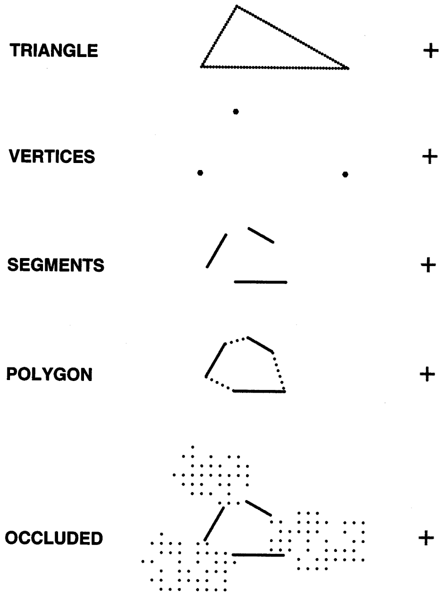

Fig. 5. The five different stimulus conditions for Experiment 2. Actual stimuli were constructed from a set of five scalene triangles of constant height and varying base size as in Experiment 1.

ments, polygon and partially occluded triangle. As in Experiment 1, five triangles of different sizes and with different centers-of-area were tested within each of the conditions so that discriminability of triangle COA, reflected in larger differences among the landing positions for the set of five triangles, was the principal measure of performance.

If saccades were constrained to respond to the visible features of the form, with no influence of the inferred vertices, then discrimination should be better with the full-triangle and vertices-only conditions than in the other three conditions in which vertices were removed.

Predictions can also be made about relative performance in the three conditions with vertices removed. If saccades are sensitive to perceptual cues encouraging the generation of the full triangle, then performance should be better (i.e. closer to that obtained with the full triangle) with the occluded triangle than with either the segments or the polygon. The polygon might be a particularly difficult target since the added line segments could work against attempts to generate the full triangle (Bregman, 1981). If perceptual cues are unimportant, and saccades are influenced by any visible features present in the attended region, then the presence of occluders might actually impair performance. In that case, the segments condition might produce better performance than either the occluded triangle or the polygon.

Experiment 2 also included trials in which the target was an outline drawing of a circle. This was done to allow estimation of any tendencies on the part of the individual subjects to over- or undershoot the COA; such tendencies are independent of the particular target shape (see Melcher & Kowler, 1999). Correction of mean landing position for such tendencies may give a better estimate of where the saccades land with respect to the contour. Since the same correction was applied to all saccades of a particular direction, regardless of the small differences in target eccentricities, this correction affects only the offset, and not the slopes, of the functions relating saccadic landing position to COA.

3.1. Method

3.1.1. Subjects

In addition to BS and EK (the subjects tested in Experiment 1) subject DM was also tested. He does not require spectacle correction. DM had prior experience in eye movement experiments and was aware of the purpose of this experiment.

3.1.2. Saccadic targets

The target conditions are shown in Fig. 5. Targets in each were (as was the case for Experiment 1) based on a set of five scalene triangles of constant height (80′), one constant base angle (60°) and five different base sizes ranging from 130 to 210′. Stimuli were made up of single points separated by a spacing of 4′. Triangles were outline shapes, while the occluders were made up of a sparse distribution of random dots.

Stimuli were again positioned with respect to the fixation cross such that the triangles were aligned on their top vertex (264′ from fixation). The horizontal eccentricities (distance between the fixation cross and COA) again ranged from 212 to 242′, depending on which of the five triangles was presented. In addition, eccentricity was randomly varied about these values both horizontally (-12, 0, 12′) and vertically (-30, 0, 30′).

Procedure and instructions were the same as in the prior experiment. Subjects were once again asked to use all available shape completion cues to direct a single saccade to the triangle as a whole.

3.1.3. Experimental sessions

Sessions contained 60 trials, each testing one of the five conditions shown in Fig. 5. The full triangle condition was tested last to reduce the contribution of memory for the shape. The other four conditions (vertices-only, occluded triangle, segments, and polygon) were tested separately in blocks of four 60 trials sessions. The order of testing blocks was randomly selected within each replication of four blocks. All other conditions (triangle size, eccentricity and direction with respect to fixation) were chosen randomly before each trial.

Each 60-trial session also included 10 trials randomly interleaved, in which the stimulus was an outline drawing of a circle (diam 186′). These trials allowed any shape-independent under- and overshoots of the subjects to be estimated and subtracted from the landing positions obtained with the other shapes (Melcher & Kowler, 1999).

3.1.4. Number of trials tested and excluded

EK ran in 20 sessions of 60 trials each for a total of 1200 trials for each stimulus condition of which 200 were circle trials. BS ran in 19 sessions of 60 trials for a total of 1140 trials of which 190 were circle trials. DM ran in 10 sessions of 60 trials each for a total of 600 trials for each stimulus condition of which 100 were circle trials. The following trials were excluded: trials with a latency less than 100 ms ($<1\%$), saccadic errors greater than 100′ (1%), no detected saccade (BS and EK: 1%; DM 4%), or lost tracker lock ($<1\%$). EK's results were based on over 95 trials per mean landing position (98% of trials tested), BS's on 92 trials/mean (98% of trials tested) and DM's on 46 trials/mean (95% of trials tested). As in the previous experiment mean saccadic landing positions were computed by pooling over the random variations in horizontal and vertical eccentricities.

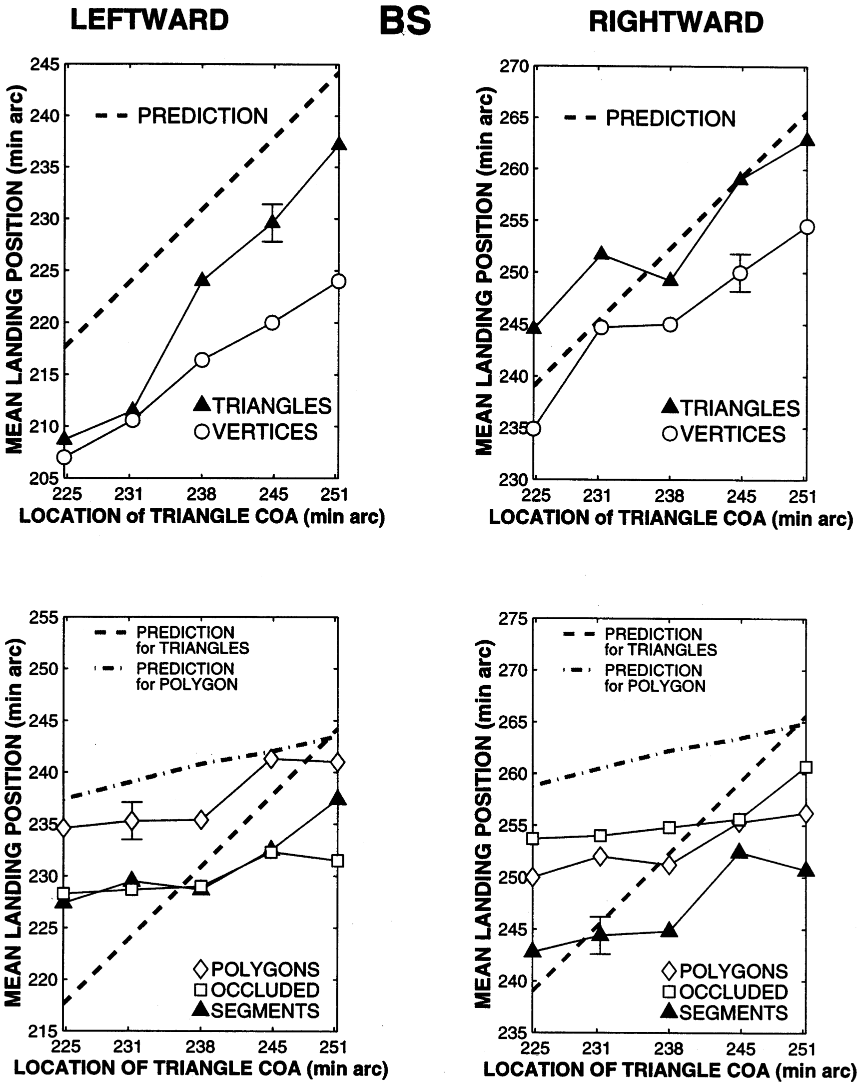

Fig. 6. Mean horizontal saccadic landing positions in the occluded triangle and fragment conditions as a function of location of the COA of the full triangle and vertices only condition (top) and for the three conditions with vertices removed (polygon; occluded triangle; segments) for subject BS under instructions to generate and look at the full triangle. Error bars indicates largest standard error. Lower dashed lines represent predicted landing position if saccades landed at the COA of the full triangle; upper dashed lines the COA of the visible fragment. $N = 80–95$ observations/datum point.

3.2. Results

Figs. 6–8 show mean saccadic landing positions as a function of COA for all three subjects. Saccadic precision was once again excellent, with standard deviations of about 6–10% of eccentricity. The dashed lines show the positions of the COA of the full triangle and the COA of the visible fragment. These predictions were shifted either upwards or downwards on the ordinate to account for the average under- or overshoot estimated from the circle trials for each subject and saccadic direction. (Average over- and undershoots were $< 15'$). Fig. 9 summarizes the slopes of the functions.

Differences among landing positions for the five triangles were much greater with the full triangle than with any of the three conditions in which vertices were removed, although slopes with the full triangle usually did not reach the predicted value of 1. Subjects BS and DM did about as well when only the vertices were present as they did with the full triangle. EK's performance was different in that she showed poor discrimination with vertices-only and even showed poor discrimination with the full triangle for her rightward saccades.

Discrimination of the five triangles in the conditions without visible vertices (occlusion, segments, polygon) was poor, and slopes of the landing position functions were close to that predicted by the COA of the visible portion. Among these three conditions without visible vertices, the best performance (i.e. greatest slopes) was achieved with the segments, in particular, for DM's leftward saccades. This implies that in both the occlusion and polygon conditions the extraneous information (lines, occluders) impaired discriminability. The occluded triangles, which should have shown the best performance of the three based on available perceptual cues, showed the poorest performance. The occluders were a hindrance, rather than a help.

As noted above, the inclusion of trials with circles as targets allowed us to correct mean landing position for net under- or overshoots and examine the corrected mean landing positions relative to the COA. BS (Fig. 6) tended to undershoot the COAs and DM was usually accurate. EK was accurate with the full triangle and vertices-only, but undershot the COA in the three conditions without vertices, landing closer to the COA of the full triangle. EK's undershoots could represent an attempt to deliberately direct saccades to the inferred triangle. If so, the attempt succeeded only in shifting all saccades in the same direction. It did not improve the ability of saccades to distinguish the five triangular shapes. Thus, an accurate representation of the full triangle was either not available, or, not useful to saccades.

3.3. Discussion

The results of Experiment 2, consistent with those obtained in Experiment 1, show that occlusion cues that contribute to perceptual shape completion were not effective in guiding saccades to the center of the perceptually inferred surface. Cues that impair completion (for example, the line segments completing the polygon) produced performance that was much the

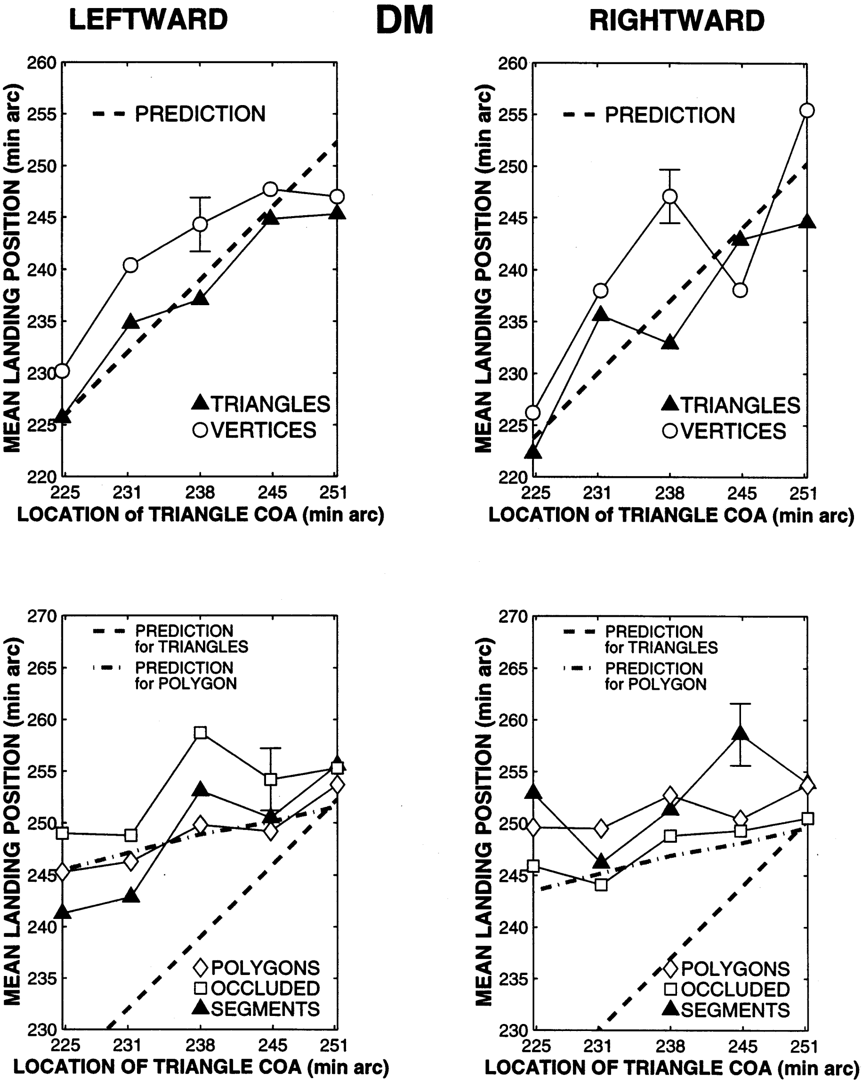

Fig. 7. Mean horizontal saccadic landing positions in the occluded triangle and fragment conditions as a function of location of the COA of the full triangle and vertices only condition (top) and for the three conditions with vertices removed (polygon; occluded triangle; segments) for subject DM under instructions to generate and look at the full triangle. Error bars indicates largest standard error. Lower dashed lines represent predicted landing position if saccades landed at the COA of the full triangle; upper dashed lines the COA of the visible fragment. $N = 40–50$ observations/datum point.

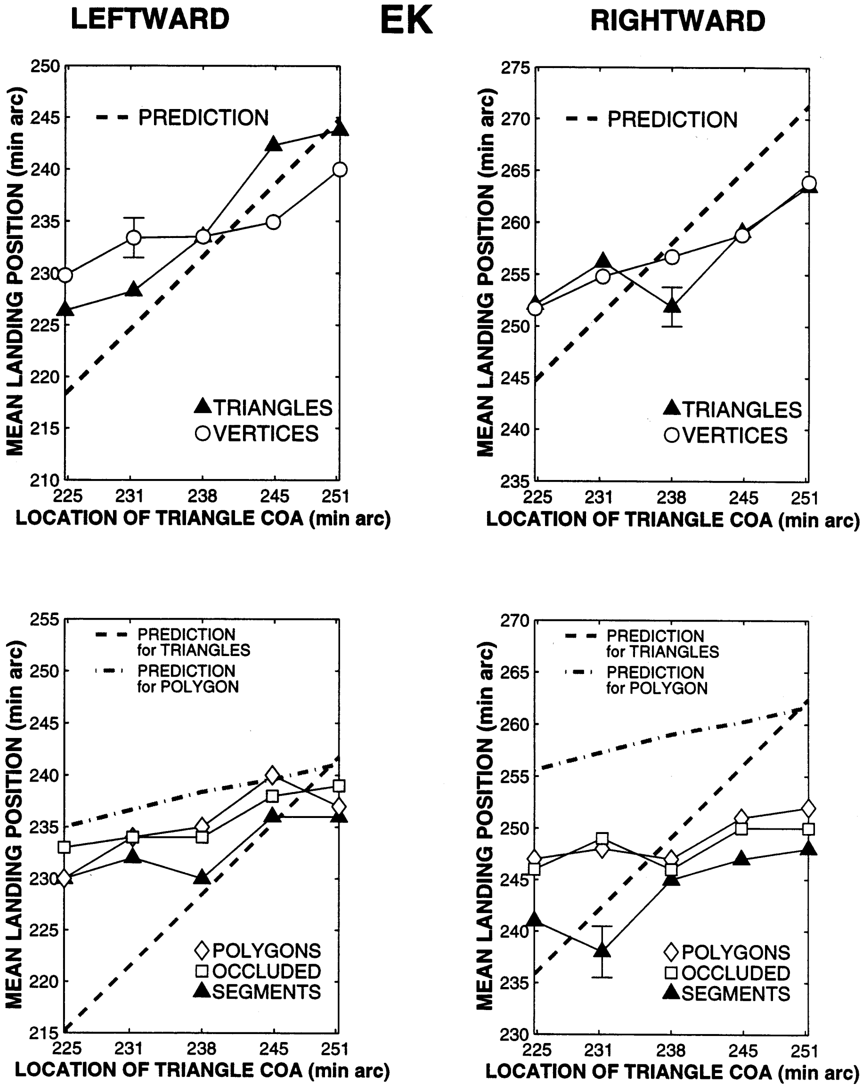

Fig. 8. Mean horizontal saccadic landing positions in the occluded triangle and fragment conditions as a function of location of the COA of the full triangle and vertices only condition (top) and for the three conditions with vertices removed (polygon; occluded triangle; segments) for subject EK under instructions to generate and look at the full triangle. Error bars indicates largest standard error. Lower dashed lines represent predicted landing position if saccades landed at the COA of the full triangle; upper dashed lines the COA of the visible fragment. $N = 95$–100 observations/datum point.

same as that found with occluders. The saccades responded on the basis of the visible features of the form.

4. General discussion

Saccades directed to spatially extended targets, such as random-dot clusters or simple shapes, have been shown to land at consistent locations near the center-of-area with a high degree of precision (He & Kowler, 1991; Kowler & Blaser, 1995; McGowan et al., 1998; Melcher & Kowler, 1999). Saccadic landing position is well predicted by the center-of-area of the target shape, and neither the distribution of elements making up the target's contour, nor the presence of internal or irrelevant distracter elements, affect landing position (Melcher & Kowler, 1999) (see Findlay, Brogan & Wenban-Smith, 1993, for a related point about the role of internal details).

The studies cited above support the idea that saccadic localization is based on a representation of shape, rather than on an averaging of the visible target elements. What is the nature of this representation of shape? The targets in the visual environment are usually complex solid objects, whose perceived shapes rarely coincide with the two-dimensional shape projected on to the retina. Perceived shape is also typically invariant over different lighting and viewing conditions. Finally, the location with respect to the fovea of what is visible (the 2D projection), and the projected location of what is perceived (the 3D object) is never guaranteed to be the same. It is, therefore, reasonable to ask whether the representation that determines the saccadic goal would be dependent on higher-order properties of the visual stimulus.

As a starting point to the investigation of higher order representations, we studied the effects of occlusion cues because of their powerful effects on the perceived structure of the stimulus, often resulting in large differences between the visible and the perceived shape of objects. The approach we took was to generate relatively simple stimuli which contained accessible cues to the shape with the goal of finding out how well these cues could be used to guide saccades. In two experiments using a discrimination paradigm, we found no evidence that shape completion or occlusion information was available to the saccadic system. Poor discrimination of target location showed that the saccadic landing positions were determined solely on the basis of the visible portion of the occluded target shape, even though cues were available that facilitated shape completion.

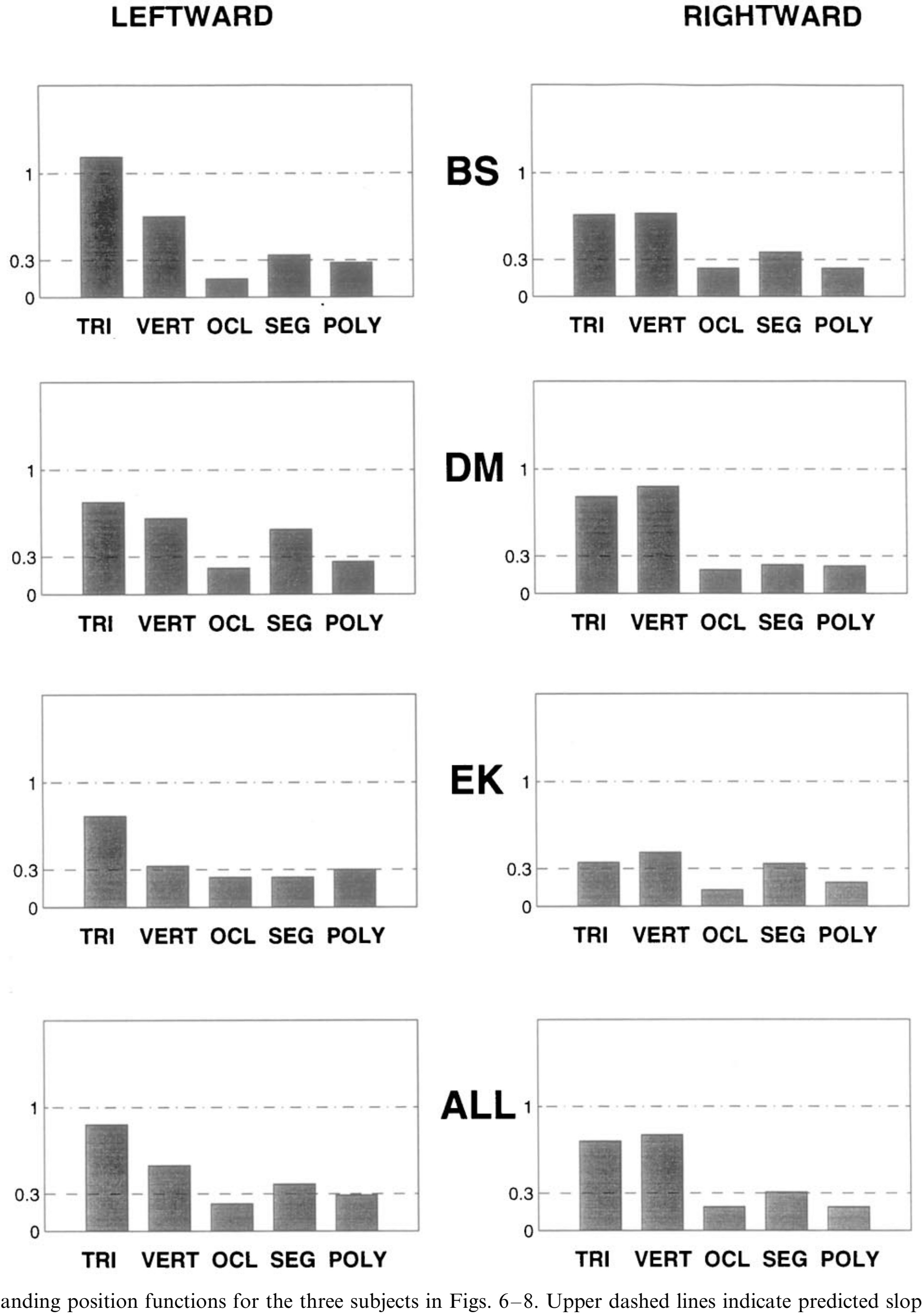

Fig. 9. Slopes of the landing position functions for the three subjects in Figs. 6–8. Upper dashed lines indicate predicted slope of saccades landed at the COA of the full triangle. Lower dashed lines indicate predicted slope if saccades landed at the COA of the visible polygon.

One interpretation of these results is that saccades are not affected by representations of shape beyond the level at which image elements are connected to form contours and closed two-dimensional shapes (Melcher & Kowler, 1999). Saccades may not have access to the higher-order representations of object shape that typically dominate perception. Perception and motor control have been often found to rely on different visual representations (Hansen, 1979; Wong & Mack, 1981; Kowler, van der Steen, Tamminga & Collewijn, 1984; Erkelens & Collewijn, 1985; Hansen & Skavenski, 1985; Goodale, 1995; for interesting exceptions see Steinbach, 1976; Enright, 1987; Ringach, Hawken & Shapley, 1996; Buetter & Stone, 1998). One way in which the representations of shape used by the perceptual and saccadic systems might differ is in their use of configurational cues. Global configurational cues to object shape may dominate percepts, but for saccades such cues may have weak effects, at best, with the retinal shape playing the stronger role. The distinction between saccades and perception is not necessarily surprising given that the perceptual analysis of a scene can proceed in parallel across large areas, while saccadic computation relies on the analysis of spatially local regions of the display. Thus, very different mechanisms may be involved.

It is possible that the failure to complete the shape in the present experiments using occluded triangles derived from the difficulty of corner completion. This has support from at least some prior perceptual studies, which have proposed that completion is weaker, and potentially ambiguous, when the percept of the whole shape depends on completing corners with angles less than 90° (Kellman & Shipley, 1991). Also, percepts of rigid motion of a square viewed through an aperture is not possible when the corners are occluded (Shiffrar & Pavel, 1991). However, other studies have shown that a completed representation of shape is perceptually available for shapes with occluded corners in tasks that involve visual search and visual priming (He & Nakayama, 1992; Sekuler & Palmer, 1994; Rensink & Enns, 1998; Joseph & Nakayama, 1999). Despite the controversies, using stimuli that require corner completion is crucial for studying effects of occlusion on saccadic localization. This is because unless completion of a significant portion of a shape is required, the difference between the location of the center of the visible portion of occluded targets and the center of the completed shape will be too small to be experimentally discriminable. Indeed, the capacity for saccades to use a representation of completed objects would be important only when there are large differences between the location of what is visible and what is perceived. In other cases, acceptable levels of saccadic accuracy with occluded shapes could be achieved by using visible cues or perhaps local features, such as selected points along the contours.

It is interesting that even though stimuli in the experiments contained accessible cues to aid completion of the shapes, and subjects were instructed to do their best to generate, attend, and look at the fully completed shapes, these conditions were all ineffective. In fact, if anything, the visual features that were added in an attempt to facilitate shape completion (namely, the occluders) had the opposite effect and impaired performance instead. Attention to the occluders may have enhanced the impression of the triangle to the perceptual system. From the point of view of the saccadic system, however, attention to the occluders resulted in their being incorporated into the pooled spatial information that determines saccadic landing position within spatially extended targets.

In conclusion, people rely on a rich representation of the objects in visual environment to generate plans and make decisions about where to direct saccades. Once such decisions are made, however, the saccadic system may analyze a very different sort of visual representation to control the landing position of saccades. Our results suggest that this representation contains information up to the level of integrating elements into contours, and is insensitive to at least one higher-order visual cue — occlusion — that is instrumental in creating impressions of true object shape. The representations used by saccades may be much closer to the literal configuration of the retinal image.

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