Saccades to partially occluded objects: Perceptual completion mediates oculomotor control

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Oculomotor behavior typically consists of directing gaze to objects in complex scenes for the purpose of extracting detailed perceptual information. Here, we probed the nature of the visual representations over which saccades to objects are computed. We contrasted an image-based oculomotor control hypothesis, holding that saccades are computed solely over information explicit in the retinal image, and an object-based oculomotor control hypothesis, holding that saccades are computed over object representations reflecting the three-dimensional structure of the scene. We recorded saccade landing positions to partially occluded objects in a naturalistic search task. In Experiment 1, saccade landing positions were biased toward the center of the perceptually completed object. Experiment 2 demonstrated that the bias held even when it would have been strategically advantageous to avoid it. Experiment 3 demonstrated that the bias was not due to image-level differences generated by the presence of occluders. The results indicate that saccade motor programs are computed, at least in part, over object-level representations reflecting the completion of occluded surfaces.

Introduction

High-resolution visual information is acquired from only a small region of the visual field, corresponding to the fovea. This necessitates movements of the eyes to orient the fovea to relevant parts of the environment, leading humans to make more than 100,000 saccadic eye movements each day. The selection of saccade target objects within a scene tends to reflect higher-level task goals (e.g. Navalpakkam & Itti, 2005; Torralba, Oliva, Castelhano, & Henderson, 2006; Malcolm & Henderson, 2010). One might, for example, look toward a desk in a room, rather than toward a window, when searching for a pen. In this case, the general goal is in terms of an object in the world: the top surface of the desk. The saccade itself, however, is defined in terms of retinal space: a two-dimensional motor vector specifying the required change in retinal projection. This raises the question of the nature of the representation over which oculomotor planning is based. We tested two hypotheses. The first is that individual saccade target locations are computed based entirely on information that is explicit in the retinal image, such as contrast regions and edges within the two-dimensional space of the visual field (image-based oculomotor control hypothesis). The second is that individual saccade target locations are computed based on representations that have been abstracted from image-level information to reflect the three-dimensional structure of the scene and objects within it (object-based oculomotor control hypothesis). We begin with a discussion of reasons to consider these alternative hypotheses and then discuss the competing predictions they generate.

The image-based oculomotor control hypothesis holds that saccades are programmed and executed based on image-level information, without regard to the structure of the scene or the objects within it. Under this hypothesis, a higher-level goal of where to move one's eyes could be in terms of an object within the scene (e.g. the top of the desk), but the computation of the specific saccade vector would operate over explicit image-level information. A reason why this might be the case is given by the nature of the neurophysiology underlying saccadic execution. The superior colliculus, for example, which sends motor commands directly to the brainstem to initiate saccades, integrates information within neural maps of the visual field, whereby localized activity triggers

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two-dimensional vector shifts of the eye (e.g., Marino, Trappenberg, Dorris, & Munoz, 2012). The neural maps are of the visual field and do not incorporate scene structure. Therefore, the proximal target of the saccade may have to be image based. Consistent with this possibility, psychophysical studies of saccades to spatially extended objects have revealed that at least under some conditions, the landing positions of saccades appear to be biased toward the centers of image-level contrast regions, rather than toward the centers of objects within the scene (Vishwanath, Kowler, & Feldman, 2000; see also Vishwanath & Kowler, 2004).

The object-based oculomotor control hypothesis holds that saccades are programmed and executed based on representations that include information about the three-dimensional structure of the scene and objects within it. This representation is abstracted from the information that is explicit in the image through perceptual organization processes, such as the assignment of border ownership, the labeling of relative depth, and the completion of occluded surfaces. One reason for entertaining the object-based oculomotor control hypothesis draws from research on covert attention. Covert attention and saccades are tightly associated, such that saccades are typically preceded by a shift of covert attention to the saccade target location (Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Zhao, Gersch, Schnitzer, Dosher, & Kowler, 2012). In addition, the control of covert attention is often object-based (see Chen, 2012, for review), with selection of perceptual objects rather than image regions. Thus, given the likely role of covert attention in saccade planning, it is reasonable to hypothesize that saccade planning is sensitive to object structure.

Here, we discriminated between image-based and object-based oculomotor control by measuring the landing positions of saccades to spatially extended targets as a function of implied object structure. The foundation of the logic was a series of studies by Kowler and colleagues showing that when making single, unspeeded saccades to spatially extended targets, the landing position tends to be near the center of area (COA) of the targets. For example, Melcher and Kowler (1999) compared the spatial properties of saccade landing positions and the spatial properties of the stimulus. Using different target shapes, including circles, ellipses, and cardioid shapes, participants' saccade landing positions were biased consistently toward the COA defined by the external contour of the target.

The bias for saccades to land toward the COA of a spatially extended target can be used to discriminate between image-based and object-based oculomotor control. Consider the stimuli shown in Figures 1A–1C. At the image level, Figure 1A is a circular black contrast region with a white surround. At the object level, it is

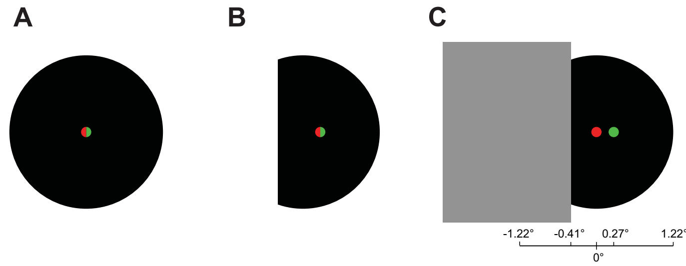

Figure 1. Examples of stimuli for which the image-based center of area (COA), marked in *green*, and the object-based COA, marked in *red*, are either the same (**A** and **B**) or different (**C**). Panel (**C**) shows the critical condition where the image-level representation is of a partial-circle region next to a gray contrast region, and the object-level representation is a full circle behind a gray occluder. Panel (**C**) also illustrates the key stimulus metrics used in the present experiments. The nearest contour of the occluding rectangle was 0.41 degrees from the center of the 1.22 degrees radius circular region. The object-based COA at the circle center (defined as 0 degrees) differed from the image-based COA of the partial-circle region (0.27 degrees).

a black circle in front of a white surface that extends behind it. For this stimulus, the COA of the image-level information is identical to the COA of the object-level information (represented by the half-red, half-green dot). Figure 1B is similar, but with an irregularly shaped contrast region with a white surround at the image level, and a black partial circle in front of an extended white surface at the object level. Again, the COA is identical at the two levels of representation. Figure 1C illustrates the critical condition. At the image-level, this is a black irregular contrast region that is identical to that of Figure 1B. At the object-level, however, it is a black circle, similar to that in Figure 1A, that happens to be occluded by a gray surface that is closer to the viewer than the circle. Given these representations, the corresponding COAs are also different. The COA for the image-level information is shown by the green dot, whereas the COA for the object-level information is shown by the red dot. Image-based oculomotor control then predicts that saccade landing positions will be biased toward the image-based COA for stimuli like that in Figure 1C, whereas object-based oculomotor control predicts that they will be biased toward the object-based COA.

Vishwanath et al. (2000) applied similar logic using triangles with two of their vertices occluded: image-level and object-level COAs were different. The landing positions of saccades directed to the objects were better predicted by the image-based COAs than by the object-based COAs. The results of Vishwanth et al. support the image-based oculomotor control hypothesis. In a subsequent study, Vishwanath and Kowler (2004) used rendered three-dimensional shapes with additional

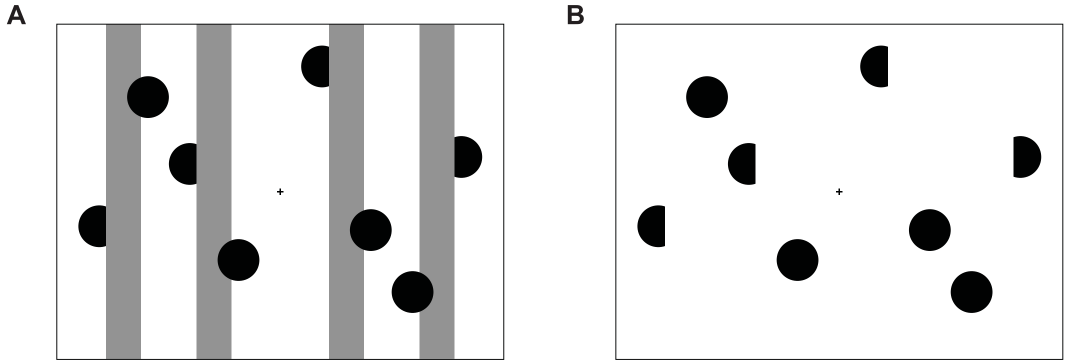

Figure 2. Illustration of sample search arrays, each containing four full-circle and four partial-circle regions. In the with-occluders display condition (**A**), the presence of vertical gray occluders supported perceptual completion of the partial circles. In the without-occluders display condition (**B**), the scene did not support perceptual completion of the partial circles.

cues to support the perception of object structure, such as shading and foreshortening, and found that, as in the triangles study, some participants appeared to use image-based oculomotor control. However, others appeared to use object-based oculomotor control, in that their saccade landing positions were biased toward the center of the three-dimensional shape, rather than the two-dimensional image region. In both studies, the goal was to examine saccade target computation under conditions where participants made a single, strategic, controlled saccade. Task instructions were explicit about using either object-based information or image-based information to direct one's gaze. Participants were also encouraged to take as much time as they needed to prepare the saccade and to make only a single movement (i.e. avoid corrective saccades). Finally, the goal of the task was the eye movement itself, rather than making eye movements in the service of extracting information from the scene.

Thus, current evidence regarding image-based versus object-based oculomotor control does not provide clear resolution of the core research question. The issue has been examined only for highly controlled saccades and in just two studies (Vishwanath & Kowler, 2004; Vishwanath et al., 2000). Under these orienting conditions, present evidence indicates that participants do not use object-based representations for the oculomotor selection of partially occluded objects, even when explicitly instructed to do so. However, some (but not all) participants may be able to use three-dimensional shape cues to select object-based COAs when instructed to execute a saccade to the center of an object region.

In the present study, we used occluders to dissociate the influence of image-level and object-level information on saccade landing positions, similar to the strategy of Vishwanath et al. (2000). However, we did so within the context of a free-viewing, visual search task that required multiple eye movements conducted in the service of locating a target. As shown in Figure 2, the displays consisted of eight black stimuli, half of which were full circles and half of which were partial circles. In the with-occluders condition, there were also four vertical gray rectangles that abutted the partial circles. These supported the perception of the partial circles as full circles that happened to be partially occluded by rectangular surfaces. In the without-occluders condition, there were no rectangles, and therefore there was no contextual support for the perceptual completion of the partial circles. Participants inspected each display to find a small target feature (red or green dot) among distractor features (blue dots) that appeared on each object in a gaze-contingent manner: that is, upon the entry of gaze into an object region. Note that participants were not informed about the stimulus manipulations, they were given no instruction about the execution of saccades, and they did not know that their saccade landing positions were of experimental interest. Thus, the paradigm was designed to embody key features of natural viewing, where multiple saccades are generated, and these are computed not as an end in themselves but as a means for extracting detailed perceptual information from local regions of a scene.

We recorded saccade landing positions within the black stimuli as participants searched for the red or green dot. If oculomotor control is image-based, then saccade landing positions should be biased toward the center of the image regions, independently of the presence of occluders. In contrast, if oculomotor control is object-based, then for the partial-circle stimuli, saccade landing positions should be shifted toward the center of the region defined by the full circle in the with-occluders condition, but toward the center of the partial circle in the without-occluders condition. This would be a compelling finding, because the image-level information, a partial circle, is identical in these two conditions.

Experiment 1

Method

Participants

Ten participants (6 female and 4 male; mean age = 18.4 years) completed Experiment 1. All participants were University of Iowa undergraduate students who received credit toward a research experience requirement in an introductory psychology course. All reported normal or corrected-to-normal visual acuity and color vision. No individual participated in more than one experiment. All procedures were approved by the University of Iowa Institutional Review Board. The number of participants was chosen based on the effect size in a pilot study ($N = 6$). The key result—landing position difference for partial circles as a function of occluder presence—had an effect size of $\eta_p^2 = 0.810$, indicating that four participants would be sufficient to achieve 0.8 power. Conservatively, we included 10 participants in each experiment.

Apparatus

Stimuli were presented on a 24-inch BenQ model XL2420T LCD monitor with a resolution of 1920 × 1080 pixels and a refresh rate of 100 Hz. Stimuli were restricted to a 1280 × 960-pixel central region of the monitor. Viewing distance was fixed at 77 cm using a chin and forehead rest to minimize head movement. The right eye was monitored by an SR Research Eyelink 1000 Plus eye-tracker sampling at 1000 Hz. Responses were entered using a USB button box. Experiments were programmed in E-Prime software (Schneider, Eschman, & Zuccolotto, 2002).

Stimuli

Stimuli were presented on a white background (26.01 degrees × 19.51 degrees), with a black 0.2 degrees × 0.2 degrees fixation cross presented at the center. Task displays consisted of four black circles (2.44 degrees diameter) and four black partial circles (2.03 degrees horizontally; see Figure 2). In the with-occluders blocks, the displays included four dark gray, vertically oriented rectangles (2.03 degrees × 19.51 degrees) that were centered horizontally at 3.86 degrees and 9.15 degrees to the left and right of the center of the display. In the without occluders blocks, the rectangles were also written to the screen, but in the same color as the background. One partial circle and one full circle were positioned along the vertical contour of each of the rectangles, one on the left side and one on the right side (randomly selected). The centers of the circles were positioned 0.41 degrees from the edge of the rectangle. The partial circles were placed in an equivalent horizontal location (defined relative to the full circle), so that the truncated side of the partial circle abutted the vertical contour of the rectangle. The vertical positions of the circles and partial circles were selected randomly with the following constraints: (1) circles could not be within 4.07 degrees of each other on the same rectangle, (2) circles could not be within 4.07 degrees of each other in the region between adjacent rectangles, (3) circles could not be within 3.25 degrees of the fixation cross, and (4) circles could not be within 2.03 degrees of either the top or bottom of the display.

The targets for the search task were small (0.08 degrees), colored dots that appeared at the centers of the circles and partial circles (the latter center defined relative to the full circle). To ensure that participants directed their gaze to the circular objects, rather than to the target dots, a dot was displayed only after the eyes entered a circle region. Specifically, a dot was drawn to the screen after the eye tracker recorded 12 consecutive samples within a circular region (2.85 degrees diameter) defined around each of the eight objects. The dot remained visible until the eyes entered a different object region, when it was erased simultaneously with the appearance of the new dot. The dots in all but one of the objects were blue. There was one target dot that appeared in a randomly selected object. This dot was either red or green, again selected randomly.

Task

The task was to find and report the color of the red or green dot (target), while ignoring blue dots (distractors), by pressing a corresponding button with the left or right index finger on a USB button box. Instructions emphasized that responses should be made as quickly as possible while making less than approximately 5% errors in each block.

Design

A 2 (occluder presence: with occluders, without occluders) × 2 (target shape: full circle, partial circle) within-subjects design was used. Target shape varied within each trial, with four full circles and four partial circles in each display. Occluder presence was blocked: two blocks of with-occluders trials and two blocks of without-occluders trials, interleaved. Block order was counter-balanced across participants.

Procedure

Each participant was tested in a single session. Following the informed consent process, they received task instructions. The participant was positioned comfortably in the chin and forehead rest with their index fingers on the two response buttons. The eye tracker was then calibrated using a nine-point procedure. The eye tracker was recalibrated during the experiment if the estimate of gaze position deviated by more than approximately 0.5 degrees from the central fixation reference.

Individual trials were initiated by the experimenter upon confirmation that the participant was fixating centrally. A blank screen was then displayed for 500 ms, replaced by the search display. Participants searched the display for the red or green dot among blue dots. Because dot appearance was contingent on circle fixation, this required moving the eyes from object to object. When the target dot was found, participants indicated red or green by pressing the appropriate button on the button box, at which point the search display was removed. If the response was incorrect, the word "incorrect" was then displayed for 1000 ms.

Participants completed a practice session of eight trials, followed by four blocks of 100 experimental trials, with short breaks between blocks. The entire session lasted approximately 45 minutes.

Data analysis

Eye-tracking data analysis was conducted offline. The continuous sample data were parsed into saccades and fixations using the standard Eyelink algorithm: saccades were defined by a combined velocity (30 degrees/s) and acceleration (8000 degrees/s^2) threshold. The critical data were the landing positions of saccades that resulted in a fixation in one of the eight target regions in each display. For all conditions, valid saccades were defined by the following four criteria: (1) the fixation position following the saccade was within 1.42 degrees of the center of the circle defined by a given circle stimulus, (2) the resulting fixation was the first fixation within that item, (3) the saccade amplitude was greater than 1.5 degrees, and (4) the preceding fixation duration was greater than 90 ms and less than 600 ms. The lower bounds on saccade amplitude and preceding fixation duration were designed to ensure that analyzed landing positions followed primary orienting saccades rather than secondary corrective saccades. The upper bound on preceding fixation duration was designed to limit the analysis to saccades that were generated naturally during visual search and were not delayed strategically to control landing position. Overall, the landing positions of 14,921 saccades were included in the analysis. There was an average of 3.73 included saccades per trial.

The main dependent measure was the horizontal spatial deviation of saccade landing position from the center of the circle defined by the circular item in which the saccade landed. We report only horizontal deviation, because the manipulations were on the horizontal dimension, and there were no reliable effects of condition on the vertical component of landing position. Data were normalized such that (1) the zero point was defined by the center of the full-circle region of a given item and (2) positive values reflect deviation away from the contour of the rectangle and negative values reflect deviation toward the contour of the rectangle (see Figure 1C). For statistical comparisons, alpha was set at 0.05 throughout. Effect sizes are reported as adjusted partial eta-squared (*adj* η_p^2), which corrects for the positive bias inherent in standard partial eta-squared (Mordkoff, 2019).

Results and discussion

Figure 3 shows a sample scanpath during a search trial. Figure 4A shows the distribution of horizontal deviation in saccade landing position for each of the four conditions. Figure 4B shows the mean landing position data for each of the participants and the grand means. The Table contains the mean landing position values in each condition, along with mean saccade amplitude and latency.

As is evident in Figure 4, saccade landing position was centered near the zero point for full circles, independently of occluder presence (left graphs). In contrast, for saccades to partial circles, saccade landing position varied depending on whether occluders were present or not (see Figure 4, right graphs). Specifically, landing position was closer to the center of the partial circle when there were no occluders, and closer to the center of the inferred full circle (zero) when occluders were present.

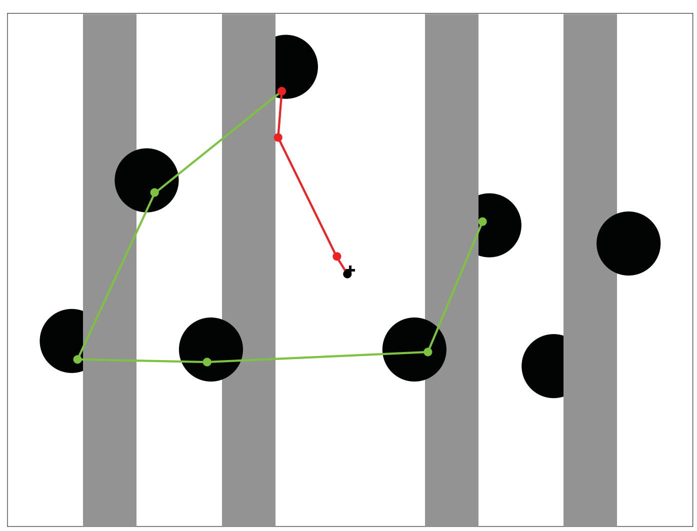

Figure 3. Eye movement scanpath for a representative trial. The small circles represent fixations, and the lines represent saccades. The saccades marked in *green* were included in the analysis. The saccades marked in *red* did not meet criteria for inclusion in the analysis.

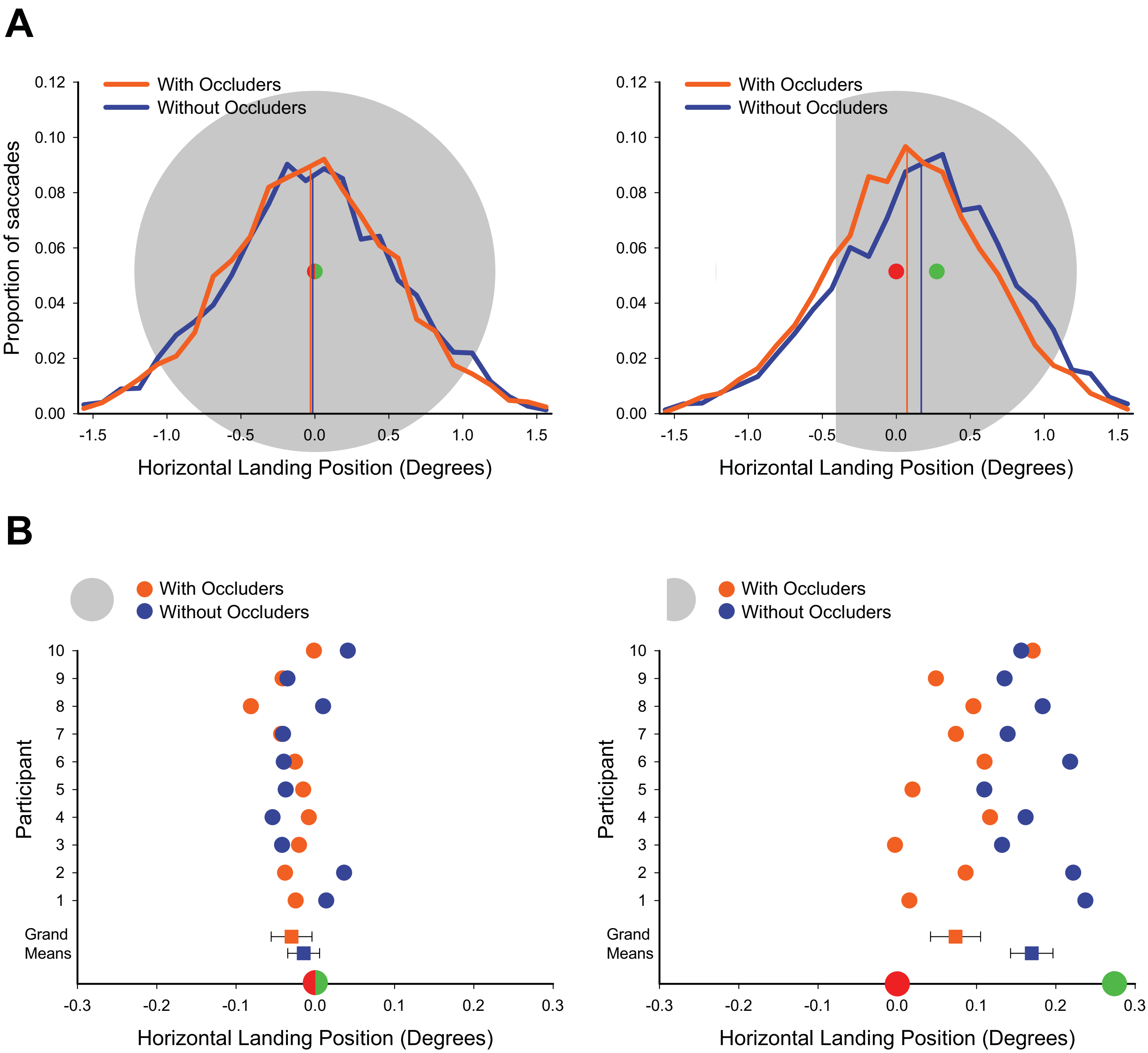

Figure 4. (**A**) Distributions of horizontal landing position in Experiment 1, aggregated across all participants, relative to the center of the full-circle region. Data for full circles are presented in the left graph and data for partial circles in the right graph. The *orange lines* represent the with-occluders condition and *blue lines* the without-occluders condition. *Vertical lines* indicate the mean of the individual participants' mean landing positions. The *red circle* represents the center of the perceptual object and the *green circle* the center of the image region. Panel (**B**) shows the mean landing positions for each of the 10 participants for full circles (*left graph*) and partial circles (*right graph*) as a function of occluder presence. Again, the *red reference circle* represents the center of the perceptual object and the *green reference circle* the center of the image region. *Square symbols* are the grand means. Error bars are condition-specific, within-participant 95% confidence intervals (Morey, 2008).

To confirm these observations, mean horizontal deviations for each subject were submitted to a two (occluder presence) by two (target shape) repeated-measures ANOVA. There was a reliable main effect of occluder presence, $F(1, 9) = 18.47$, $p = 0.001$, adj $\eta_p^2 = 0.636$, as well as a reliable main effect of target shape, $F(1, 9) = 184.6$, $p < 0.001$, adj $\eta_p^2 = 0.949$. Critically, the interaction between occluder presence and target shape was also reliable, $F(1, 9) = 12.78$, $p = 0.006$, adj $\eta_p^2 = 0.541$, indicating that the presence of occluders

	Full circles		Partial circles	
	With occluders	Without occluders	With occluders	Without occluders
Experiment 1				
Landing position (degrees)	−0.030 (0.007)	−0.015 (0.011)	0.074 (0.017)	0.170 (0.014)
Latency (ms)	224.5 (4.7)	224.7 (4.6)	223.2 (5.0)	227.9 (5.0)
Amplitude (degrees)	6.56 (0.17)	6.42 (0.09)	6.46 (0.14)	6.46 (0.12)
Experiment 2				
Landing position (degrees)	−0.005 (0.020)	−0.021 (0.019)	0.115 (0.013)	0.210 (0.015)
Latency (ms)	221.1 (4.7)	223.7 (3.8)	221.5 (3.8)	225.0 (4.3)
Amplitude (degrees)	6.54 (0.07)	6.67 (0.10)	6.50 (0.07)	6.68 (0.10)
Experiment 3				
White occluders				
Landing position (degrees)	−0.034 (0.019)	−0.010 (0.016)	0.118 (0.018)	0.185 (0.012)
Latency (ms)	223.2 (5.2)	226.7 (7.1)	221.6 (5.4)	225.9 (5.4)
Amplitude (degrees)	6.38 (0.16)	6.24 (0.13)	6.45 (0.17)	6.10 (0.11)
Gray occluders				
Landing position (degrees)	0.018 (0.021)	0.016 (0.015)	0.100 (0.022)	0.183 (0.017)
Latency (ms)	227.2 (5.4)	226.8 (5.4)	223.1 (5.5)	225.7 (5.8)
Amplitude (degrees)	6.33 (0.10)	6.53 (0.23)	6.29 (0.15)	6.38 (0.15)

Table. Mean horizontal landing position (relative to the full circle center), mean saccade latency, and mean saccade amplitude for Experiments 1, 2, and 3 as a function of occluder presence and target shape (partial circle, full circle). Standard errors are in parentheses.

modulated the effect of full versus partial circles on saccade landing position.

We then conducted a series of planned contrasts. In the first, we examined saccades to full circles as a function of occluder presence. As is evident in the left graphs of Figure 4, the mean landing position was very close to the center of the full circles in both with- and without-occluders conditions. Mean landing positions for full-circle stimuli in the with-occluders and without-occluders conditions were −0.030 degrees and −0.015 degrees, respectively. These did not differ statistically, $t(9) = 0.514$, $p = 0.310$, adj $\eta_p^2 = 0.016$. Thus, adding gray rectangles to the display had no observable effect on landing position when the full circle shapes were explicitly available within the image.

Second, we compared landing position between the full and partial circles when there were no occluders present in the display (represented in blue in Figure 4). There was a reliable difference in horizontal deviation, $t(9) = 13.40$, $p < 0.001$, adj $\eta_p^2 = 0.954$. Horizontal landing positions for the partial circles (M = 0.170 degrees) were reliably shifted an average of 63.0% of the distance from the center of the circular region to the COA of the partial-circle region, indicating that they were sensitive to the shape of the target region. The deviation toward the center of the partial circle without occluders provides a baseline against which to compare landing position for partial circles when the presence of occluders allowed for perceptual completion.

The third and critical contrast was between landing position for partial circles as a function of occluder presence (see the right graphs in Figure 4). Saccade landing position was significantly closer to the zero point (i.e. the center of the full circle) in the with-occluders condition (M = 0.074 degrees) than in the without-occluders condition, $t(9) = 4.38$, $p < 0.001$, adj $\eta_p^2 = 0.694$. This was an average of 56.5% of the distance from the mean landing position on partial circles without occluders back to the center of the full-circle region. Thus, for object regions that were identical at an image level, we found a robust difference in landing position, consistent with a bias toward the center of the completed circle when the scene context supported the interpretation of a partially occluded object.

The fourth and final contrast was between full and partial circles in the with-occluders condition (represented in orange in Figure 4). There was a reliable difference, $t(9) = 5.26$, $p < 0.001$, adj $\eta_p^2 = 0.766$. Although partial circles in the presence of occluders led to a shift toward the center of the inferred circle, this shift was not complete. We address possible reasons for this incomplete shift in the General Discussion.

In addition to the main analyses on landing position, we conducted exploratory analyses to examine whether the bias toward the center of partially occluded circles was influenced by the latency and/or amplitude of the saccade. For the latency analysis, the data from all participants' saccades to partially occluded circles were combined and binned into 20 latency quantiles. Mean latency and mean landing position within each quantile were calculated and entered into a regression analysis. There was no reliable relationship between saccade latency and landing position for partially occluded circles, $r = -0.174$, $t(19) = -0.751$, $p = 0.462$. Using the same approach, we found that there was also no reliable relationship between saccade amplitude and landing position, $r = -0.117$, $t(19) = -0.502$, $p = 0.622$.

Overall, the results indicate that saccade landing positions in partial-circle targets were biased toward the center of the region defined by a full circle when there were occluders present to support perceptual completion. Perceived object shape influenced saccade landing position.

Experiment 2

Experiment 1 provided evidence that oculomotor control can operate over object-based representations. However, it is possible that the design of Experiment 1 encouraged a strategic engagement of object-based control, rather than object-based control being intrinsic to saccade target computation. Specifically, the colored dots always appeared in the center of the full-circle region, regardless of whether the target shape was a full circle or a partial circle. This may have encouraged participants to strategically program saccades to land at the center of the full-circle region, even for partial-circle targets. Note that this possibility cannot account for the full pattern of results in Experiment 1, because saccade landing positions were in fact biased away from the center of the full-circle region, toward the center of the partial-circle region, when there were no occluders to support perceptual completion. Nonetheless, landing positions in partial circles without occluders were shifted 63%, not 100%, toward the partial-circle COA. This may have reflected a strategic bias to target the center of the full-circle region.

In Experiment 2, we eliminated any incentive to strategically bias saccade landing position toward the center of the full-circle regions. The colored dots were always presented at the center of the visible portion of each target shape. Thus, for full circles, the colored dots were presented at the center of the full-circle region (as in Experiment 1) but for partial circles, the colored dots were presented at the COA of the partial-circle region, regardless of whether or not occluders were present. If participants can use image-level information to guide the landing position of their saccades, then it would be to their strategic advantage to do so in this experiment.

Method

The method was the same as in Experiment 1, with the following exceptions.

Participants

Ten participants (6 female and 4 male; mean age = 18.7 years), drawn from the same pool as Experiment 1, completed Experiment 2. All reported normal or corrected-to-normal visual acuity and color vision. None had participated in Experiment 1.

Stimuli

The target dots were presented at the centers of the visible portions of the object stimuli. For partial circles, this was 0.27 degrees to the left or right of the center of the full circle, depending on whether the right or the left side of the circle was truncated, respectively.

Data analysis

The data were processed in the same manner as in Experiment 1. The landing positions of 14,805 saccades were included in the analysis, an average of 3.70 included saccades per trial.

Results and discussion

Figure 5 shows the landing position data for each of the four conditions. The Table contains the mean landing position values in each condition, along with mean saccade amplitude and latency.

As in Experiment 1, saccade landing position was centered near the zero point for the full circles, independently of occluder presence (see the left graphs in Figure 5), whereas for saccades to partial circles (see the right graphs in Figure 5), landing position was closer to the center of the partial circle when there were no occluders and closer to the center of the inferred full circle (0 degrees) when occluders were present. To confirm these observations, subject data were submitted to a 2 (occluder presence) × 2 (target shape) repeated-measures ANOVA. There was a reliable main effect of occluder presence, $F(1, 9) = 13.81$, $p = 0.005$, adj $\eta_p^2 = 0.562$, as well as a reliable main effect of target shape, $F(1, 9) = 311.4$, $p < 0.001$, adj $\eta_p^2 = 0.969$. Critically, the interaction between occluder presence and target shape was reliable, $F(1, 9) = 10.73$, $p = 0.010$, adj $\eta_p^2 = 0.493$, indicating that the presence of occluders modulated the effect of full versus partial circles on landing position.

We then conducted the series of planned contrasts. In the first, we examined saccades to full circles as

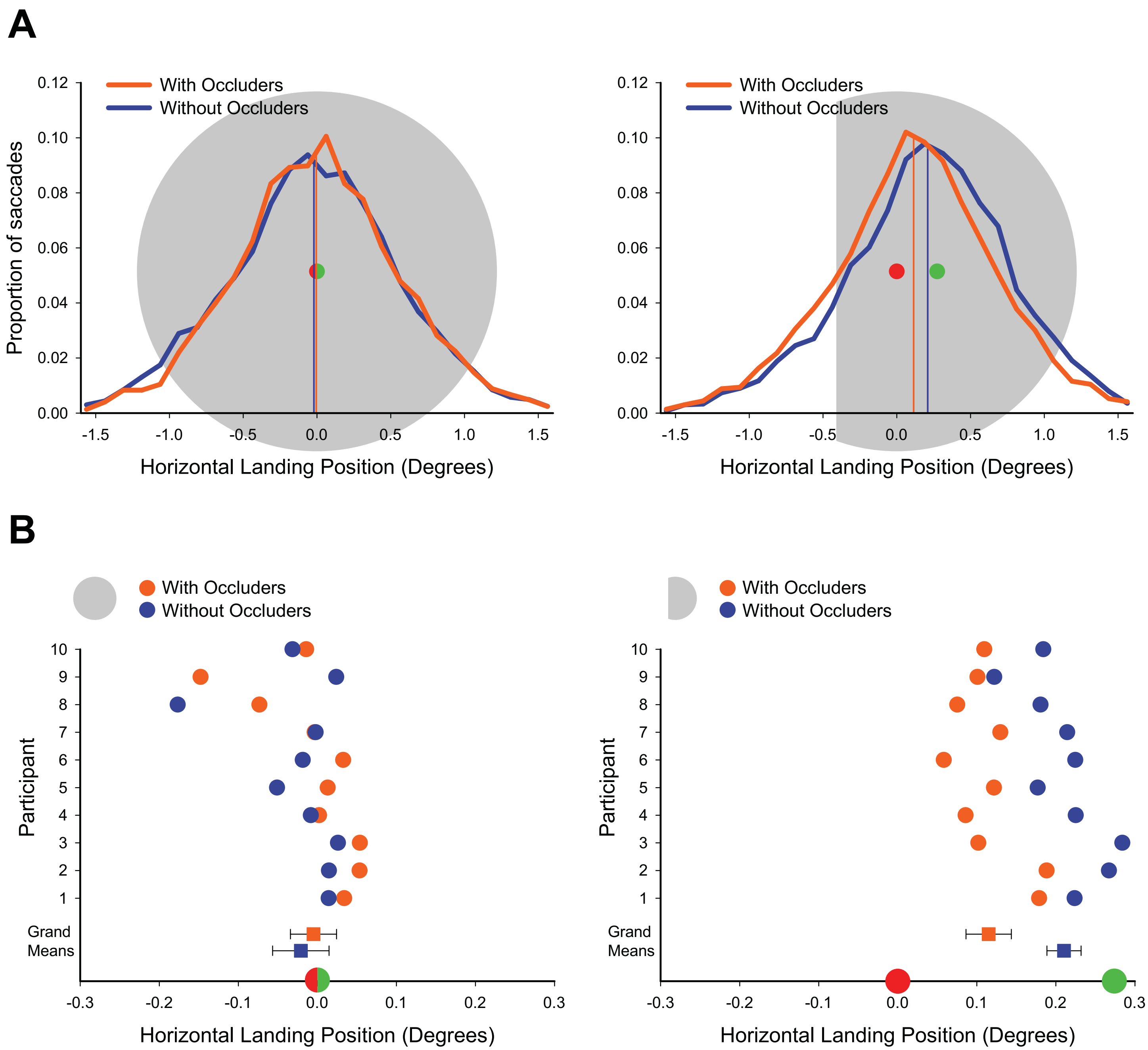

Figure 5. Panel (**A**) shows distributions of horizontal landing position in Experiment 2, aggregated across all participants, relative to the center of the full-circle region. Data for full circles are presented in the *left graph* and data for partial circles in the *right graph*. The *orange lines* represent the with-occluders condition and the *blue lines* the without-occluders condition. The *vertical lines* indicate the mean of the individual participants' mean landing positions. The *red circle* represents the center of the perceptual object and the *green circle* the center of the image region. Panel (**B**) shows the mean landing positions for each of the 10 participants for full circles (*left graph*) and partial circles (*right graph*) as a function of occluder presence. Again, the *red reference circle* represents the center of the perceptual object and the *green reference circle* the center of the image region. *Square symbols* are the grand means. Error bars are condition-specific, within-participant 95% confidence intervals (Morey, 2008).

a function of occluder presence. As is evident in the left graphs of Figure 5, mean landing position was very close to the center of the full circles in both with- and without-occluders conditions. Mean landing positions for full-circle stimuli in the with-occluders and without-occluders conditions were −0.005 degrees and −0.021 degrees, respectively. These did not differ statistically, $t(9) = 0.010$, $p = 0.504$, adj $\eta_p^2 = -0.054$. Thus, adding gray rectangles to the display had no observable effect on landing position when the full circle shapes were explicitly available within the image.

Second, we compared landing position between the full and partial circles when there were no occluders present in the display (represented in blue in Figure 5). There was a reliable difference in horizontal deviation, $t(9) = 10.67$, $p < 0.001$, adj $\eta_p^2 = 0.930$. Horizontal landing positions for the partial circles (M = 0.210 degrees) were reliably shifted an average of 77.8% of the distance from the center of the circular region to the COA of the partial-circle region, indicating that they were sensitive to the shape of the target region.

The third and critical contrast was between landing position for partial circles as a function of occluder presence (see the right graphs in Figure 5). Saccade landing position was significantly closer to the zero point (i.e. the center of the full circle) in the with-occluders condition (M = 0.115 degrees) than in the without-occluders condition, $t(9) = 5.18$, $p < 0.001$, adj $\eta_p^2 = 0.760$. This was an average of 45.2% of the distance from the mean landing position on partial circles without occluders back to the center of the full-circle region. The difference in landing position is consistent with a bias toward the center of the completed circle when the scene context supported the interpretation of a partially occluded object.

The fourth and final contrast was between full and partial circles in the with-occluders condition (represented in orange in Figure 5). There was a reliable difference, $t(9) = 5.62$, $p < 0.001$, adj $\eta_p^2 = 0.788$. As in Experiment 1, although partial circles in the presence of occluders led to a shift toward the center of the inferred circle, this shift was not complete.

In addition to our main analyses, we conducted the same set of exploratory analyses, as in Experiment 1, testing whether the bias toward the center of partially occluded circles was influenced by saccade latency and/or amplitude. There was no reliable relationship between latency and landing position, $r = 0.175$, $t(19) = 0.755$, $p = 0.460$, or between saccade amplitude and landing position, $r = -0.315$, $t(19) = -1.41$, $p = 0.177$.

In sum, the results of Experiment 2 provide evidence that oculomotor control operates over object-based representations even when the task-incentive structure favors image-level control. Specifically, the bias toward the center of the completed circle was observed for partially occluded objects even though the target dot always appeared at the center of the partial-circle region.

Experiment 3

To test for an object-level influence on saccade landing position, we have manipulated the presence or absence of rectangular contrast regions in the displays (i.e. occluders). It is possible that the image-level differences created by those contrast regions influenced the pattern of results by, for example, causing attraction or repulsion of saccades toward or away from contrast edges. To address this possibility, we conducted a third experiment with two types of displays that, together, controlled for local edge differences across conditions.

Figure 6 illustrates the logic and design of Experiment 3. Two different background contrasts and two different occluder contrasts were used. For any given block of trials, the background was either white or gray, and the occluders were the reverse. This created two different versions of the 2 (occluder presence) × 2 (target shape) design that we used in previous experiments. The white-occluders version is illustrated in the top row of Figure 6 (panels A and B) and the gray-occluders version is illustrated in the bottom row of Figure 6 (panels C and D). Notice that in both versions, the local edges between partial-circle targets and occluders are identical to the local edges between partial-circle targets and the background in their respective without-occluders condition. In addition, the two versions of the design control for differences between the contrast-edge strengths on either side of partial-circle targets. For example, in the version with white occluders (see Figure 6A), the contrast edge for partial circles is stronger on the occluded side of that object (black to white) than it is on the unoccluded side (black to gray). However, this relative difference is reversed in the version with gray occluders (see Figure 6C), with a weaker contrast edge on the occluded side than on the unoccluded side. If the strength of contrast edge biases saccade landing position, then it should do so in opposite directions for the two versions of the design. If we were to find the same pattern of results across versions, this would eliminate concern that image-level differences in contrast edges—whether attractive or repulsive—are an important cause of the effect of occluders on landing position for partial circles.

Method

Participants

Twelve participants (8 female and 4 male; mean age = 18.5 years), drawn from the same pool as

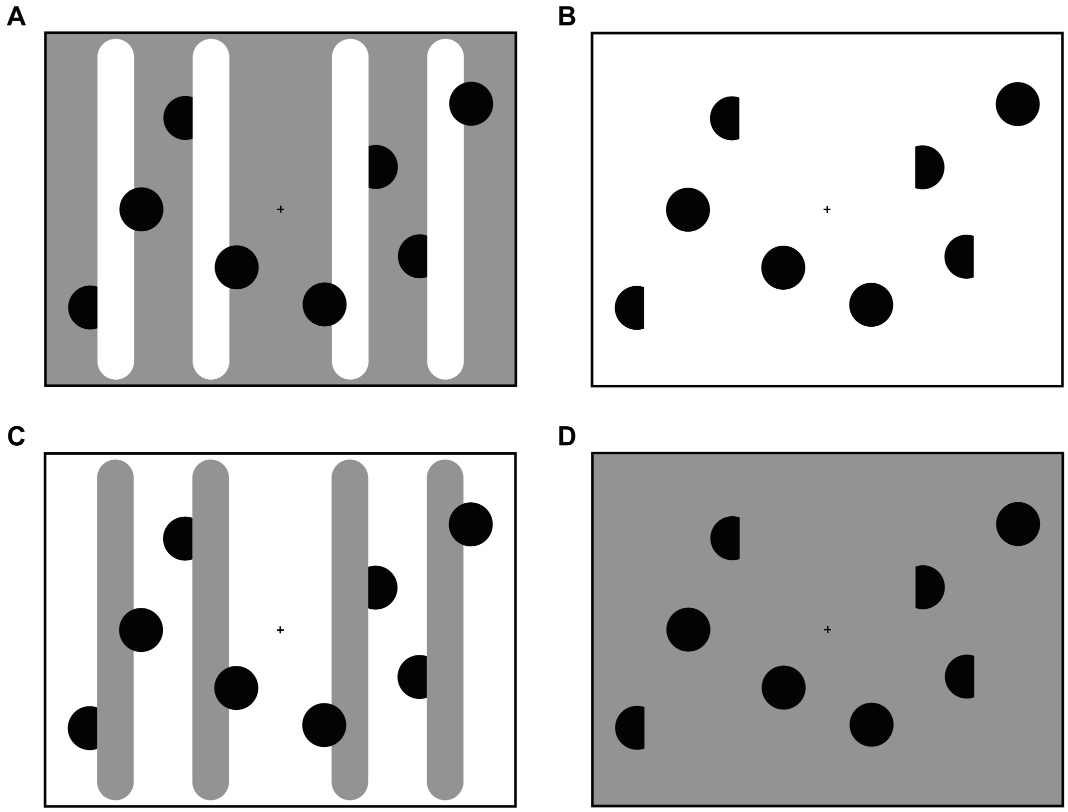

Figure 6. Illustrations of each of the four display types in Experiment 3. The white-occluder condition consists of displays **A** and **B**, with a gray background with white occluders for the with occluder condition and a white background with no occluders for the without occluder condition. The gray-occluder condition consists of displays **C** and **D**, with a white background with gray occluders for the with occluder condition and a gray background with no occluders for the without occluder conditions.

Experiments 1 and 2, completed Experiment 3. All reported normal or corrected-to-normal visual acuity and color vision. None had participated in Experiments 1 or 2.

Stimuli

The stimuli were the same as in Experiment 1, with the following exceptions. Occluders had circular endcaps and were 2% shorter than the display area, so that their top and bottom edges were visible. This provided additional cues that the occluders were discrete objects. In addition, the range of possible locations of the target shapes was reduced by 5% to avoid overlap with the curved edges of the endcaps. For half of the blocks, backgrounds were white, and occluders were gray. For the other half, backgrounds were gray, and occluders were white. Block type was alternated and counterbalanced across participants.

Procedure

Participants completed a practice session of eight trials, followed by four blocks of 125 experimental trials, with short breaks between blocks. The entire session lasted approximately 1 hour.

Design and data analysis

The data were analyzed in terms of the two versions of the design illustrated in Figure 6. The conditions illustrated in Figures 6A and 6B constituted the white-occluders version of the 2 (occluder presence) × 2 (target shape) design, and the conditions illustrated in Figures 6C and 6D constituted the gray-occluders version. The full design, therefore, was a 2 (version: white occluders, gray occluders) × 2 (occluder presence: with occluders, without occluders) × 2 (target shape: full circle, partial circle) within-subjects design. The landing positions of 22,570 saccades were included in the analysis, with an average of 3.76 included saccades per trial.

Results and discussion

Figures 7 and 8 show the landing position data in the four conditions of the two versions of the design,

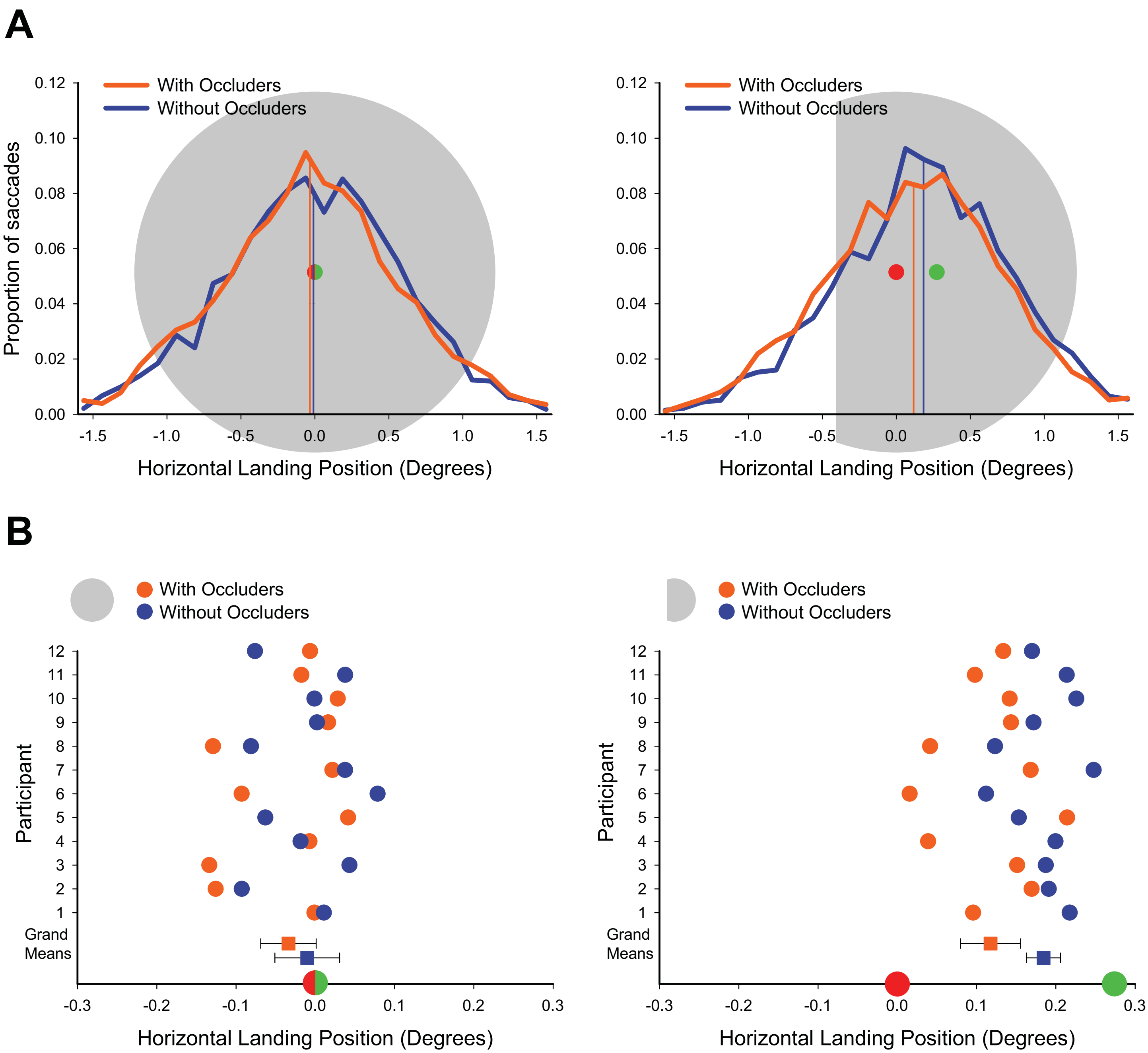

Figure 7. Panel (**A**) shows the distributions of horizontal landing position in Experiment 3 white-occluders version, aggregated across all participants, relative to the center of the full-circle region. Data for full circles are presented in the *left graph* and data for partial circles in the *right graph*. The *orange lines* represent the with-occluders condition and blue lines the without-occluders condition. *Vertical lines* indicate the mean of the individual participants' mean landing positions. The *red circle* represents the center of the perceptual object and the *green circle* the center of the image region. Panel (**B**) shows the mean landing positions for each of the 12 participants for full circles (*left graph*) and partial circles (*right graph*) as a function of occlude presence. Again, the *red reference circle* represents the center of the perceptual object and the *green reference circle* the center of the image region. *Square symbols* are the grand means. Error bars are condition-specific, within-participant 95% confidence intervals (Morey, 2008).

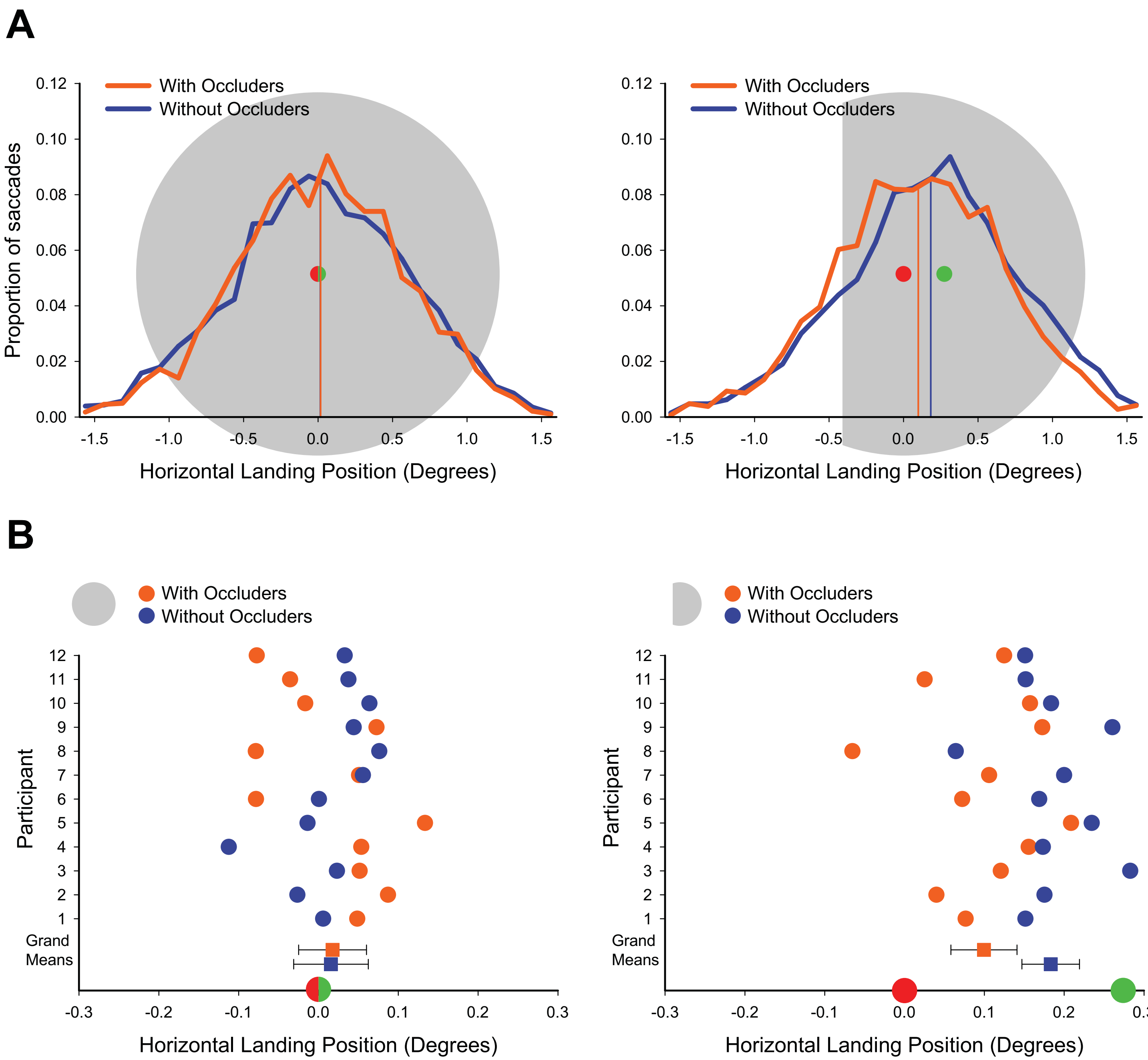

Figure 8. Panel (**A**) shows the distributions of horizontal landing position in Experiment 3 gray-occluders version, aggregated across all participants, relative to the center of the full-circle region. Data for full circles are presented in the *left graph* and data for partial circles in the *right graph*. The *orange lines* represent the with-occluders condition and blue lines the without-occluders condition. *Vertical lines* indicate the mean of the individual participants' mean landing positions. The *red circle* represents the center of the perceptual object and the *green circle* the center of the image region. Panel (**B**) shows the mean landing positions for each of the 12 participants for full circles (*left graph*) and partial circles (*right graph*) as a function of occluder presence. Again, the *red reference circle* represents the center of the perceptual object and the *green reference circle* the center of the image region. *Square symbols* are the grand means. Error bars are condition-specific, within-participant 95% confidence intervals (Morey, 2008).

with the white-occluders version displayed in Figure 7 and the gray-occluders version displayed in Figure 8. The Table contains the mean landing positions for each condition, along with mean saccade amplitude and latency.

Participant data were submitted to a two (version) by two (occluder presence) by two (target shape) repeated-measures ANOVA. There were reliable main effects of both occluder presence, $F(1, 11) = 8.38$, $p < 0.05$, adj $\eta_p^2 = -0.381$ and target shape, $F(1, 11) = 267.65$, $p < 0.001$, adj $\eta_p^2 = 0.957$, but no main effect of version, $F(1, 11) = 2.75$, $p = 0.126$, adj $\eta_p^2 = 0.127$. As in previous experiments, the two-way interaction between occluder presence and target shape was significant, $F(1, 11) = 14.17$, $p < 0.01$, adj $\eta_p^2 = 0.523$, indicating that the presence of occluders modulated the effect of full versus partial circles on landing position. Critically, the three-way interaction was not significant, $F(1, 11) = 0.933$, $p = 0.355$, adj $\eta_p^2 = -0.0056$, nor were either of the two-way interactions involving version: version X occluder presence, $F(1, 11) = 0.060$, $p = 0.811$, adj $\eta_p^2 = -0.085$; version X target shape, $F(1, 11) = 3.75$, $p = 0.079$, adj $\eta_p^2 = 0.187$, Thus, version had no modulating effect on any of the other effects.

For completeness, we conducted the same four contrasts that we conducted in previous experiments for both the white-occluders and gray-occluders versions of the main occluder presence X target shape design.

For the white-occluders version, the landing position for full-circle targets was not significantly different with occluders (M = −0.034 degrees) compared to without occluders (M = −0.010 degrees), $t(11) = 0.975$, $p = 0.351$, adj $\eta_p^2 = -0.004$, and was very near zero in both cases (see the left graphs of Figure 7). Second, the landing positions for partial circles without occluders (M = 0.185 degrees) was reliably biased toward the center of the partial-circle region compared to the landing positions for full circles without occluders (M = −0.010 degrees), $t(11) = 10.82$, $p < 0.001$, reflecting a shift of 68.5% of the distance from the center of the circular region to the center of the partial-circle region (represented in blue in Figure 7). Third, landing positions for partial circles with occluders (M = 0.118) was closer to the center of the full-circle region than for partial circles without occluders (M = 0.185 degrees), $t(11) = 3.96$, $p < 0.05$, adj $\eta_p^2 = 0.551$, an average shift of 36.2% of the distance from the mean landing position on partial circles without occluders back to the center of the full-circle region (see the right graphs of Figure 7). Finally, landing positions were reliably different for partial circles with occluders (M = 0.118) compared to full circles with occluders (M = −0.034 degrees), $t(11) = 7.19$, $p < 0.001$, adj $\eta_p^2 = 0.809$, confirming that the shift of landing position back toward the center of the full-circle region for partial-circle targets with occluders was not complete (represented in orange in Figure 7).

For the gray-occluders version, landing position for full-circle targets was not significantly different with occluders (M = 0.018 degrees) compared to without occluders (M = 0.016 degrees), $t(11) = 0.067$, $p = 0.948$, adj $\eta_p^2 = -0.090$, and was very near zero in both cases (see the left graphs of Figure 8). Second, landing positions for partial circles without occluders (M = 0.183 degrees) was reliably biased toward the center of the partial-circle region compared to the landing positions for full circles without occluders (M = 0.016 degrees), $t(11) = 7.11$, $p < 0.001$, adj $\eta_p^2 = 0.805$, reflecting a shift of 67.7% of the distance from the center of the circular region to the center of the partial-circle region (represented in blue in Figure 8). Third, landing positions for partial circles with occluders (M = 0.100) was closer to the center of the full-circle region than for partial circles without occluders (M = 0.183 degrees), $t(11) = 5.80$, $p < 0.001$, adj $\eta_p^2 = 0.732$, an average shift of 45.3% of the distance from the mean landing position on partial circles without occluders back to the center of the full-circle region (see the right graphs of Figure 8). Finally, landing positions were reliably different for partial circles with occluders (M = 0.100) compared to full circles with occluders (M = 0.018 degrees), $t(11) = 4.05$, $p < 0.05$, adj $\eta_p^2 = 0.563$, confirming that the shift of landing position back toward the center of the full-circle region for partial-circle targets with occluders was not complete (represented in orange in Figure 8).

Finally, we conducted the same set of exploratory analyses that we did for the previous experiments testing whether the bias toward the center of partially occluded circles was influenced by the saccade latency and/or amplitude. There was no reliable relationship between latency and landing position for either the white-occluders version, $r = -0.009$, $t(23) = -1.00$, $p = 0.315$ or the gray-occluders version, $r = 0.090$, $t(23) = 0.954$, $p = 0.340$. There was, however, a reliable effect of saccade amplitude on landing position within occluded partial circles in the gray-occluders version, $r = -0.029$, $t(23) = -3.12$, $p < 0.01$, and a trend in the white-occluders condition, $r = -0.017$, $t(23) = -1.78$, $p = 0.075$. The nature of the relationship was that the bias of saccade landing positions toward the center of the implied, full-circle region, decreased with larger saccade amplitudes. This might be expected if the information needed to engage the perceptual completion processes were compromised at more peripheral locations, and therefore the partial circles were not perceived as being perceptually extended behind occluding surfaces at those distances.

In sum, Experiment 3 produced the same pattern of results as Experiments 1 and 2, providing evidence that oculomotor control operates over object-level representations. Moreover, given the design of Experiment 3, the critical pattern of results—that is, the change in saccade landing position within partial-circle regions depending on whether occluders were present or not—cannot be attributed to imbalances in image-contrast regions introduced by the occluders.

General discussion

In this study, we probed the nature of the visual representations that underlie the computation of saccade landing position for spatially extended targets. Specifically, we contrasted the hypothesis that control is based solely on image-based representations and the alternative hypothesis that control operates over object-based representations. Using a naturalistic orienting task in which participants made multiple eye movements to spatially extended target regions while searching for a small target stimulus that appeared inside of them, we found evidence of object-based programming of saccades. Specifically, we found that the locations of saccades that landed inside of partial-circle targets were biased toward the center of those shapes, consistent with known properties of saccade targeting (e.g. Melcher & Kowler, 1999). However, adding rectangles that abutted the partial circles, so that they supported the perceptual completion of an extended object behind an occluding surface, caused saccade landing positions to be biased away from the center of the partial-circle image region and toward the center of the full-circle region defined by a perceptually completed circle. This pattern suggests that saccade landing position is computed based on perceptually completed objects, rather than solely based on the shape of the image contrast region. We observed this basic pattern four separate times: once each in Experiments 1 and 2, and twice in Experiment 3. Moreover, it occurred even when the task incentives favored the use of image-based information (Experiment 2). Finally, we confirmed that the result cannot be explained by differences in the relative strength of contrast edges where the object stimuli meet the occluder or the background (Experiment 3). Together these findings indicate that oculomotor control, like the guidance of covert attention, is mediated by object-level representations of the scene.

Although we consistently found that saccade landing position was biased toward the inferred center of partially occluded circles, the bias was not complete, as the mean landing position never shifted all the way back to the center of the full-circle region. There are several possible explanations for this finding. First, partially occluded objects tend to be perceived as smaller than the same objects when they are unoccluded (Kanizsa, 1979; see also Vezzani, 1999), which would influence the perceived center of the inferred circle in the direction observed here. Second, mean landing position results might have reflected a mixture of trials, such that saccades were based on image-level shape on some trials and object-level shape on other trials. Logically, this would predict a bimodal distribution of saccade landing positions, which is not apparent in the data, but given the magnitude of expected differences, such bimodality would be extremely difficult to detect. Third, individual saccades may have been influenced by both image-level and object-level shape information. All of these possibilities involve some degree of object-level influence on saccade targeting, either fully or partially, and so our conclusion at this stage is that the present data indicate that saccade targeting can be influenced by object-level information.

The present research question concerns the effect of multiple stimuli on saccade landing position (i.e. landing position within an extended target, with and without occluders). It is therefore reminiscent of another known oculomotor bias, termed the "global effect" (e.g. Coren & Hoenig, 1972; Findlay, 1982). When participants make a speeded saccade to an abruptly appearing target stimulus, simultaneous presentation of a second (non-target) stimulus in close proximity to the target causes the saccade to land at an intermediate position between the two stimuli. The global effect is understood in terms of interactions between representations of stimuli in spatially organized oculomotor control systems. Two nearby peaks of activation, for example, can end up functioning as though there were a single peak of activation at an intermediate location between the two. Under this view, the global effect reflects stimulus-level interactions that unfold without regard to object-level structure.

Despite the prima facie similarity of the effects of multiple stimuli (occluders and targets) on saccade landing position and interactions between multiple stimuli causing global effects, it is unlikely that a global effect contributed to the pattern of results reported in the current study. The global effect is observed for small numbers of stimuli (usually two) that appear abruptly, creating dynamic input to oclumotor systems that lead to rapid, reflexive saccades. The global effect is not typically observed if displays are complex and consist of a relatively large number of objects (McSorley & Findlay, 2003) or if participants are not required to generate speeded saccades, leading to longer latencies (Ottes, Van Gisbergen, & Eggermont, 1985; Coëffé & O'Regan, 1987). Here, we used complex displays containing a relatively large number of objects, the displays were typically static when critical saccades were generated (first saccades following stimulus onset constituted less than 1% of analyzed saccades), and the timing of saccades was self-paced, with no latency demand. Finally, if a global effect contributed to the observed influence of occluder presence on landing position for partial circles, we should have observed a similar effect of occluder presence for full circles. Yet, there was no reliable difference in saccade landing positions within full-circle targets when occluders were present (creating the potential for a global effect) compared with when occluders were absent (no potential for a global effect).

We next consider an apparent conflict between the findings of the current study and the Vishwanath et al. (2000) study that was reviewed in the Introduction. Targets in that study were different sized solid black scalene triangles with two vertices occluded by outline polygons. In a control condition, the visible polygon-shaped regions of the triangles were rendered with a small area of overlap in front of the outline polygons, thereby disrupting image-level support for occlusion and perceptual completion of the triangles. The question, similar to that of the current study, was whether in the occlusion condition, saccade landing position would be determined by the size of perceptually completed triangles or by the size and shape of the visible polygonal portions (i.e. the image-level information). Saccade landing positions were predicted by the visible polygons, not the implied triangles, in both the occlusion condition and the control condition, indicating that saccade targeting was computed based on image-level information in both conditions. These results appear to conflict with our finding that saccade landing position was biased toward the center of perceptually completed shapes.

There are many differences between the current study and the Vishwanath et al. (2000) study that might account for the different findings. First, it is possible that the stimuli used in the two studies determined the difference. The triangle stimuli in Vishwanath et al. were occluded by outlined polygons that were similar in shape to the shape of the visible image region of the triangle. Shape similarity between the occluders and the visible potion of occluded object may have led participants to parse the display into a set of similar polygons rather than to infer a completed triangle behind polygons. In addition, there were broad differences in the nature of the orienting tasks used in the two studies. In the present study, participants were naïve to the question being addressed and were not given any instructions regarding how they should orient their gaze. They executed multiple saccades within a scene of multiple objects in order to find a target stimulus. In contrast, because the goal of the Vishwanath et al. (2000) study was different—that is, to examine how conscious perception is related to the strategic control of gaze—they used a controlled orienting paradigm which required the strategic execution of a single saccade to a prespecified target. Moreover, participants were aware of the question being addressed and the nature of the stimuli. They were instructed 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" or, in a second condition, to "…look at the visible fragment alone, and not attempt to infer the triangle." Saccade latencies were long (between 450 and 1400 ms) compared to those in the present study (approximately 250 ms), reflecting adherence to those instructions.

It is plausible that these differences in stimuli, task demands, instructions, and participant knowledge contributed to the difference in results across studies. For example, in a later study in which three-dimensional rendered objects were used to dissociate the center of image-region shapes and object-level shapes, Vishwanath and Kowler (2004) found that some participants' saccades were biased toward the center of the image region, whereas others were biased toward the center of the object-based shape. It seems likely that these individual differences reflect different interpretations of the strategic demands of the controlled orienting task. In sum, the extensive differences in goals, stimuli, and task, allow for many possible causes of the apparent discrepancy between the current study and the earlier studies. Isolating the critical factors that produced the empirical difference between the present and previous work will require additional research.

Finally, a broad motivation for this study was to begin to connect the oculomotor control literature with the attentional guidance literature. People perceive and act on objects in three dimensions. This fact is reflected in how attention is guided within scenes and the higher-level goals that are used to select the objects of attention and gaze (e.g. orient to the white item on the top shelf of the refrigerator when looking for the milk). In this study, we have shown that, like covert attentional selection, oculomotor control is influenced by the object-level structure of the scene: specifically, the completion of objects behind occluding surfaces. Ultimately, individual saccades are triggered based on activity in neurons that embody a functional motor map of the two-dimensional visual field. The question therefore remains open as to how object-based control processes that underlie attentional guidance and saccade-target selection within scenes interface with the retinotopic mechanisms that are most proximal to the execution of individual saccades.

Keywords: eye movements, oculomotor control, object-based attention, perceptual completion

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