

# On the limited effect of stimulus boundaries on saccade metrics

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How the endpoint of saccadic eye movements is determined out of many potential peripheral locations is a crucial issue in the field of vision. Models of saccade generation account for this seemingly selective process in terms of competitive interactions between populations of neurons that encode respectively for different saccade amplitudes and directions. However, these models do not specify which visual stimulus properties other than the relative location of the stimuli are involved and how these properties contribute to ultimately determine a single saccade endpoint. We addressed this issue by contrasting the respective contributions of the 2-D spatial extent of the stimuli and the location of their boundaries in a global-effect paradigm. Participants were presented a to-be-looked-at peripheral target stimulus with or without a less eccentric visually invariant distractor. The extent of the target stimulus was manipulated in either one or two dimensions, such that targets differed either by their 2-D spatial extent (small, medium, or large circle) or the location of their boundaries (circle vs. horizontal or vertical ellipse of medium size). Results showed that the distractor deviated the eyes away from the target with the deviation varying with the 2-D spatial extent of the target but not the location of its boundaries. This finding suggests that the spatial distribution of luminance contrast and/or the number of elementary features that compose the stimuli prevails over visual boundaries in specifying the saccade endpoint. Implications for models of saccade generation are discussed.

## Introduction

During the viewing of complex visual displays, each saccadic eye movement is directed toward only one of many potential locations in the visual periphery. How this seemingly selective process is achieved is a crucial issue in the field of vision. In models of saccade generation, determination of a single saccade endpoint presumably results from competitive interactions within the intermediate and deeper layers of the superior colliculus (SC), where sensory and endogenous signals (e.g., expectations) combine and shape the activity of populations of neurons coding for saccades of different amplitudes and directions (Arai, Keller, & Edelman, 1994; Findlay & Walker, 1999; van Opstal & van Gisbergen, 1989; Wilimzig, Schneider, & Schöner, 2006; see also Trappenberg, Dorris, Munoz, & Klein, 2001; Meeter, van der Stigchel, & Theeuwes, 2010). Visual input would first raise the activity of populations of neurons coding for potential saccades directed toward the displayed stimuli. Over time, the neuronal activity profile would reshape and ultimately result in one stronger peak of activity that would trigger a saccade to a particular location in the visual periphery. As further developed below, one key variable in this winner-take-all competition is the spatial arrangement of the stimuli. However, it remains unspecified which visual stimulus properties other than the relative location of the stimuli are involved and how these properties contribute to shaping the neuronal activity pattern that

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favors over time the emergence of a single saccade endpoint. Here, we addressed this issue by reinvestigating the respective roles of stimulus extent and stimulus boundary on the accuracy of saccades in a two-stimulus visual display.

### Role of stimulus location

The important role played by the spatial arrangement of the stimuli relies on the properties of the neuronal circuitry of the SC as exemplified in the framework of neural-field models (e.g., Amari, 1977; Kopecz & Schöner, 1995; Wilimzig et al., 2006; see also van Opstal & van Gisbergen, 1989). Neurons in the superficial and deeper layers of the SC have rather large and overlapping receptive/movement fields (e.g., Goldberg & Wurtz, 1972), and as a result of horizontal synaptic connections, they tend to spread their excitatory activity locally while inhibiting distant sites (for a review, see Isa & Hall, 2009). Thus, depending on the visual configuration formed by the stimuli, neuronal activity (re)shapes differently, and the resulting saccade brings the eyes to variable locations.

When stimuli are spatially close, overlapping populations of neurons become active. This, and possibly also mutual neuronal excitation, favors the buildup of neuronal activity at the center of the entire active population and, in turn, the execution of a saccade toward an intermediate location in visual space (i.e., the global effect; Coren & Hoenig, 1972; Findlay, 1982). Conversely, when stimuli are far apart (i.e., separated by an angle greater than about 20°–30°), competition, possibly relayed by long-range inhibition, favors one of the initially active populations and, hence, a saccade to one of the stimuli but at the cost of longer latencies (i.e., the remote distractor effect; Walker, Deubel, Schneider & Findlay, 1997; see also Ottes, van Gisbergen, & Eggermont, 1985).

### Role of stimulus extent

Several behavioral studies revealed that, besides stimulus location, the relative size as well as the relative luminance contrast of the displayed stimuli influences saccade metrics. In the framework of models of saccade generation, this suggests that neuronal activity in the SC is weighted differently depending on the relative size or intensity of the displayed stimuli. In the original studies, the simultaneous presentation of two spatially close stimuli of varying size or luminance contrast was found to favor the execution of an averaging saccade, which landed closer to the larger stimulus (Findlay, 1982) as well as

the more luminous stimulus of the pair (Deubel, Wolf, & Hauske, 1984). Further investigations suggested that the number and possibly the density of the elementary features that compose each stimulus could account for the effect of stimulus size, meaning therefore that the overall intensity would be one critical property that weights the contribution of each visual stimulus in the computation of saccade metrics (McGowan, Kowler, Sharma & Chubb, 1998; Tandonnet & Vitu, 2013).

In particular, in the study by Tandonnet and Vitu (2013), the materials and paradigm were very similar to those in experiments revealing an effect of stimulus size on the global effect. However, the distractor that appeared simultaneously with the saccade target, although being of variable size, was composed of a constant number of illuminated pixels irrespective of its size. Results showed that the distractor deviated the eyes away from the target but to the same extent irrespective of its size, thus suggesting indeed that the previously reported effect of stimulus size was an effect of the number of elementary features. Because the contour of larger distractors was defined by slightly more widely spaced pixels, one may argue that the lack of an effect of stimulus size was due to the boundaries of larger distractors being more poorly defined. However, this was rather unlikely as the difference in spacing (0.05°) was probably below visual resolution in the periphery. Furthermore, in the McGowan et al. (1998) study, the eyes landed on average near the center of random-dot patterns that were presented in isolation in the periphery, and none had sharp boundaries.

### Role of stimulus boundaries

In contrast with the stimulus-extent hypothesis, several findings suggested that the extraction of visual boundaries as relayed by the global integration of local luminance-contrast information underlies the effect of stimulus size on saccade metrics. In particular, Findlay, Brogan, and Wenban-Smith (1993) reported similar variations of the global effect with stimulus size whether or not the area occupied by the stimulus shape was filled or left empty (see also Guez, Marchal, Le Gargasson, Grall, and O'Regan, 1994). This result may thus indicate that where the eyes move is determined by the distance between stimulus boundaries but not the respective overall intensity of the stimuli (see also Deubel, Findlay, Jacobs, and Brogan, 1988; Melcher & Kowler, 1999). It still remains that, in the Findlay et al. (1993) study, larger stimuli, whether filled or empty, were composed of a greater number of illuminated pixels than smaller ones; this may have formed the basis of the effect of stimulus size the authors reported.

## Prevalence of stimulus boundaries or stimulus extent?

Thus, so far, it has not been unambiguously determined whether stimulus boundaries prevail over stimulus extent in accounting for saccade metrics and their variations with stimulus size. We addressed this issue by using saccade averaging as an index of the impact of stimulus properties on saccade endpoints. We tested whether saccade accuracy in a global-effect paradigm depends on the relative location of stimulus boundaries or alternatively their 2-D spatial extent. Participants were presented with a to-be-looked-at peripheral target stimulus, with or without a spatially proximal visual distractor, which was always less eccentric than the target; these conditions were previously found to yield a global effect as well as clear effects of stimulus size (Findlay et al., 1993). While the distractor (i.e., a small circle) had the same properties all throughout the experiment, the spatial extent of the target stimulus was manipulated in either one or two dimensions, being either a horizontally or vertically oriented ellipse or a circle of varying size. Note that the luminance contrast of each pixel that composed the target stimulus was constant across size variations. Critically, the 2-D area subtended by horizontal and vertical ellipses was the same as that of the medium-size circle stimuli while the location, on the horizontal axis, of the boundaries of the horizontal and vertical ellipses matched the location of the boundaries of large- and small-circle targets, respectively (see Figure 1). This allowed the effect of the distance between distractor and target boundaries to be directly contrasted with the effect of the 2-D spatial extent of the target.

According to both the stimulus-extent and boundary hypotheses, the distractor was expected to deviate the eyes away from the target. However, under the stimulus-extent hypothesis, the deviation was expected to become smaller as the 2-D spatial extent of the target stimulus increased, irrespective of the location of its boundaries; in the medium-size condition, the eyes were thus expected to land at the same location whether the target was a circle, a horizontal ellipse, or a vertical ellipse. In contrast, according to the boundary hypothesis, the eye deviation was predicted to depend on the location of the target boundaries. The deviation was thus expected to be of the same extent for target stimuli whose boundaries were matched (i.e., horizontal ellipse vs. large-size circle and vertical ellipse vs. small-size circle) but to differ between targets whose boundaries were not matched (e.g., circles of different sizes; horizontal vs. vertical ellipses).

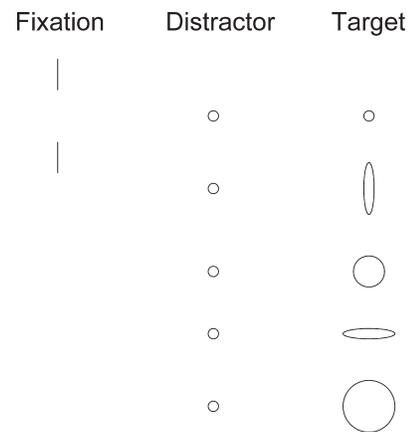


Figure 1. Illustration of the five possible configurations of the stimuli in the distractor condition. The relative sizes (diameter, in degrees of visual angle) of fixation cross ( $0.3^\circ$ ), distractor circle ( $0.1^\circ$ ), and the smallest target circle ( $0.1^\circ$ ) were scaled as well as the relative distance between them; target eccentricity was  $4^\circ$  or  $5^\circ$ , and the distance between distractor and target was  $2^\circ$  (center to center). The five conditions differed by the type of target stimulus (presented on the right, from top to bottom): small circle ( $0.1^\circ$  by  $0.1^\circ$ ), medium vertical ellipse ( $0.1^\circ$  by  $0.5^\circ$ ), medium circle ( $0.3^\circ$  by  $0.3^\circ$ ), medium horizontal ellipse ( $0.5^\circ$  by  $0.1^\circ$ ), and large circle ( $0.5^\circ$  by  $0.5^\circ$ ). Note that the boundaries of the vertical ellipse were aligned with the boundaries of the small circle, and the boundaries of the horizontal ellipse were aligned with the boundaries of the large circle.

## Methods

### Participants

Informed consent was obtained from participants; investigation was conducted according to the principles expressed in the Declaration of Helsinki. Eight participants (on average 27 years old) viewed stimuli on a computer screen while the movements of their right eye, recorded with a fifth-generation Dual-Purkinje-Image eye-tracker (Ward Electro-Optics, Inc., Jamestown, MO), were analyzed online (van Rensbergen & de Troy, 1993).

### Procedure and design

Each trial started with the presentation of a white fixation bar (two aligned vertical lines of length  $0.3^\circ$  separated by a  $0.5^\circ$  space and of luminance  $2.2 \text{ cd/m}^2$  as measured by displaying a single patch of illumination) on a black background ( $<0.1 \text{ cd/m}^2$ ). When the participant's eye was detected to be within a  $1^\circ$ -by- $0.3^\circ$  vertical-rectangle zone centered on the bar, this was

switched off, and a target stimulus was presented to the right of fixation on the horizontal axis; stimulus eccentricities and interstimulus distance are expressed relative to the center of the stimuli. The target was either a circle of varying size ( $0.1^\circ$ ,  $0.3^\circ$ , or  $0.5^\circ$  in diameter;  $2.2 \text{ cd/m}^2$ ) or an ellipse ( $0.1^\circ$ -by- $0.5^\circ$ ;  $2.2 \text{ cd/m}^2$ ), which was oriented either horizontally or vertically (see Figure 1). On half the trials, it contained a small gap (one pixel wide, about  $0.03^\circ$ ). Participants were asked to first fixate the target as quickly and as accurately as possible and then to indicate the presence or absence of the gap by pressing the left or the right button. On test trials (90% of all trials), the target was displayed at an eccentricity of  $4^\circ$  or  $5^\circ$ , and on half the test trials, it appeared with a  $2^\circ$  less eccentric distractor (circle,  $0.1^\circ$  in diameter,  $2.2 \text{ cd/m}^2$ ), which participants were asked to ignore. On additional, “catch” trials (10% of all trials), the target appeared with no distractor at an eccentricity of  $2^\circ$  or  $3^\circ$ , thus, at the same eccentricity as the potential distractor on the test trials; this was done to avoid anticipations by encouraging participants to locate the target stimulus (the only displayed stimulus vs. the most eccentric stimulus in the display) before initiating their saccade. Stimuli remained on the screen until participants pressed one of two response buttons. A letter “C” or “F” (for “correct” and “false”) was then displayed at the bottom of the screen, which indicated to participants whether or not their response to the gap detection task was correct; the current trial number was displayed simultaneously for 2 s (intertrial interval).

After a few practice trials, participants ran 10 blocks of 88 trials. In 80 test trials, each possible target stimulus occurred five times in a random sequence at a location of  $4^\circ$  or  $5^\circ$  with or without a less eccentric distractor; in eight catch trials (10% of the trials of the block), the smallest target was displayed alone at a location of  $2^\circ$  or  $3^\circ$ . A 15-point calibration procedure preceded each block (Vitu, Lancelin, Jean, & Farioli, 2006).

## Data selection and analysis

Trials with blinks, anticipatory saccades (latency less than 80 ms), or saccades landing no further than  $0.5^\circ$  to the right of fixation were rejected ( $17.3 \pm 1.1\%$ ). Note that rejection percentages in the range of 20% are commonly observed in this type of task and mostly result from the very first saccades initiated after stimulus onset being very small and keeping the eyes in the fixation area (Vitu et al., 2006). The mean landing positions and the latencies of the initial saccades were submitted to separate ANOVAs in a 5 (target type)  $\times$  2 (eccentricity)  $\times$  2 (distractor; presence vs. absence) within-subject design. Reported values were expressed

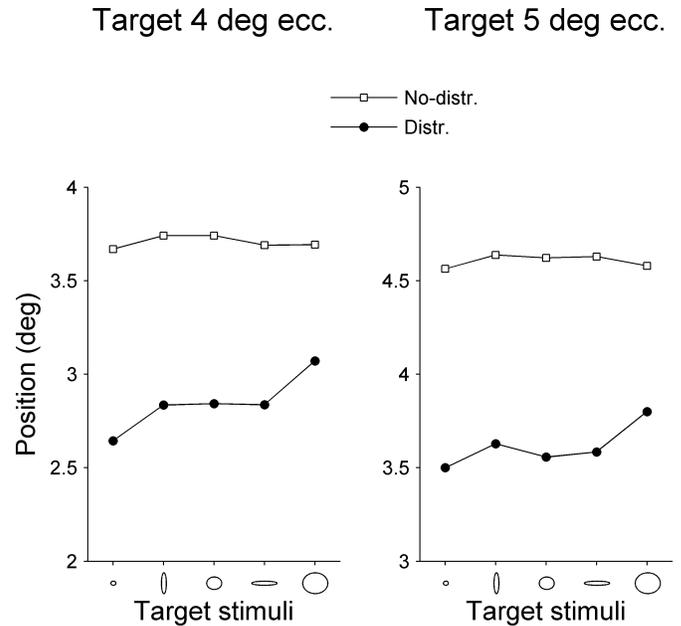


Figure 2. Mean eye landing positions (in degrees of visual angle) averaged across participants. The empty squares represent the target-only (No-distr.) conditions, and the filled circles represent the distractor (Distr.) conditions: small circle, medium vertical ellipse, medium circle, medium horizontal ellipse, and large circle. The eye deviation away from the target was less pronounced for larger target stimuli irrespective of the location of their boundaries. Left panel: target stimulus presented at  $4^\circ$  and visual distractor at  $2^\circ$  from fixation. Right panel: target stimulus presented at  $5^\circ$  and visual distractor at  $3^\circ$ .

as means  $\pm$  standard errors of the mean; visual angles were expressed in degrees. Newman-Keuls was used as a post hoc test.

## Results

### Saccade accuracy

Figures 2 and 3 present the landing positions of the initial saccades on test trials. Figure 2 presents the mean landing position averaged across participants for the five different target stimuli and for distractor versus no-distractor trials. This shows that saccades in the no-distractor, control condition were relatively accurate, undershooting the center of the target by a little less than 10% of its eccentricity (for a review, see Becker, 1989), irrespective of its size and shape (see also Kowler & Blaser, 1995). Saccade endpoints in distractor trials were less accurate, thus confirming the presence of a global effect, and quite importantly, it varied with the 2-D spatial extent but not with the shape of the target. This result thus suggests, in

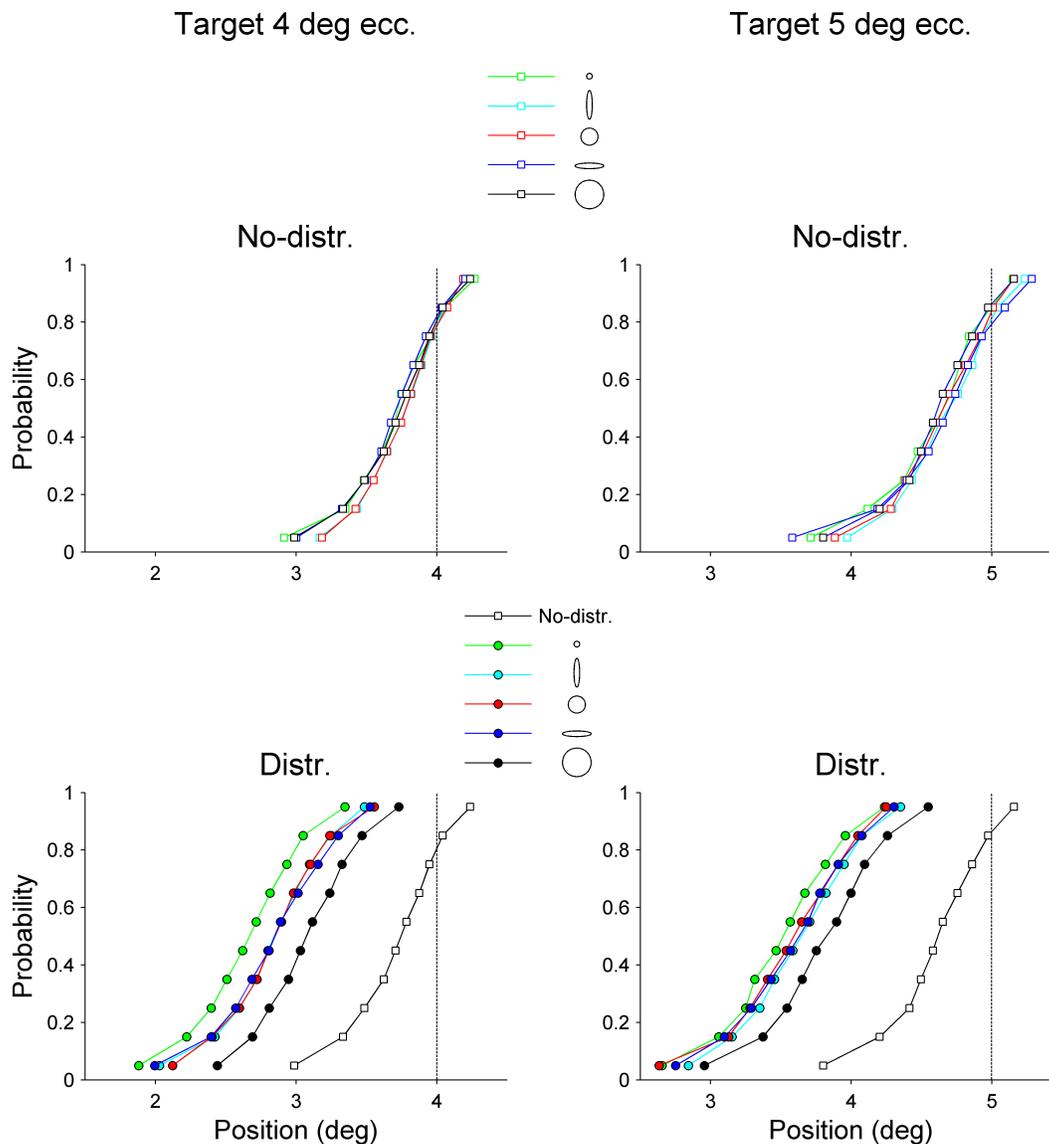


Figure 3. Distributions of the eye's landing positions (in degrees of visual angle) averaged across all participants. Each point corresponds to the average of the deciles of the individuals' distributions in a given test condition: small circle (green), medium vertical ellipse (light blue), medium circle (red), medium horizontal ellipse (dark blue), and large circle (black). Top: no-distractor condition (empty squares). Bottom: distractor conditions (filled dots) compared with one example of the no-distractor condition (empty squares, representing the largest circle). Left panels: target stimulus presented at  $4^\circ$  and visual distractor at  $2^\circ$  from fixation. Right panels: target stimulus presented at  $5^\circ$  and visual distractor at  $3^\circ$ . Note that the effect of stimulus size for the distractor condition was consistent across the deciles of the distributions, but there were no systematic modulations as a function of the location of stimulus boundaries.

contrast with the boundary hypothesis, that where stimulus boundaries were located did not matter. The deviation of the eyes' landing position away from the center of the target became greater as the circle target became smaller in size, but it was of about the same extent for the medium circle and both horizontal and vertical ellipsoid targets. Figure 3, which presents the distributions of the landing positions, illustrates the consistency of the effect of stimulus size across the different bins as well as a lack of clear modulations of

landing positions with the location of stimulus boundaries.

The analysis of variance confirmed this pattern. It first indicated a significant effect of target eccentricity,  $F(1, 7) = 444.00$ ,  $p < 0.01$ , as well as a main effect of the distractor condition, thus confirming that when a visual distractor was presented along with the target, the eyes were deviated away from the target,  $F(1, 7) = 100.70$ ,  $p < 0.01$ . There was a trend for an interaction between distractor condition and target eccentricity,  $F(1, 7) =$

4.23  $p = 0.079$ . However, post hoc tests indicated that the undershoot classically observed when the target is presented in isolation tended to be more pronounced for  $6^\circ$  compared to  $4^\circ$  target eccentricities ( $0.44^\circ \pm 0.10^\circ$  vs.  $0.33^\circ \pm 0.05^\circ$ , respectively;  $p = 0.062$ ). They also showed that in distractor conditions the deviation away from the target was more pronounced for  $6^\circ$  compared to  $4^\circ$  targets ( $1.50^\circ \pm 0.09^\circ$  vs.  $1.36^\circ \pm 0.08^\circ$ , respectively;  $p < 0.01$ ).

The visual properties of the target stimulus also influenced the saccades' landing position as indicated by a significant effect of target type,  $F(4, 28) = 14.42$ ,  $p < 0.01$ . However, the significant interaction between target type and distractor condition,  $F(4, 28) = 18.92$ ,  $p < 0.01$ , suggested that the target properties influenced where the eyes landed only when a distractor was present. Post hoc tests confirmed that there were no significant differences between the different target stimuli when presented in isolation ( $ps \geq 0.14$ ).

Planned comparisons were conducted in the distractor condition in order to test the predictions of the stimulus-extent and boundary hypotheses. First, the medium-circle target was contrasted with the two medium, ellipsoid target stimuli. Then, all three medium-size targets were contrasted with both the small- and the large-circle target. These planned comparisons revealed that the deviation was not significantly different between the medium circle and the two ellipses, whatever their orientation, vertical:  $F(1, 7) = 3.21$ ,  $p = 0.12$ ; horizontal:  $F(1, 7) < 1$ . However, the deviation was greater for the small circle,  $F(1, 7) = 14.52$ ,  $p < 0.01$ , and smaller for the large circle compared to all three medium-size targets,  $F(1, 7) = 35.95$ ,  $p < 0.01$ . Post hoc comparisons further indicated that the deviation was more pronounced for the small circle than for the vertical ellipse ( $p < 0.01$ ) and less pronounced for the large circle than for the horizontal ellipse ( $p < .01$ ). The two-way interaction between target type and eccentricity as well as the three-way interaction between all three manipulated variables were not significant,  $F(4, 28) = 1.28$ ,  $p = 0.30$  and  $F(4, 28) < 1$ , respectively, suggesting that these effects of target properties were comparable for both eccentricities.

## Saccade latency

Figures 4 and 5 present saccadic reaction times. Figure 4 presents the mean reaction time averaged across participants for the five different target stimuli and for distractor versus no-distractor trials. This shows that mean reaction times, of the order of about 175 ms on average, did not vary consistently between distractor and no-distractor trials and the two target eccentricities. However, they tended to be slightly longer for small-circle targets compared to other target stimuli, and they were reduced for large-circle

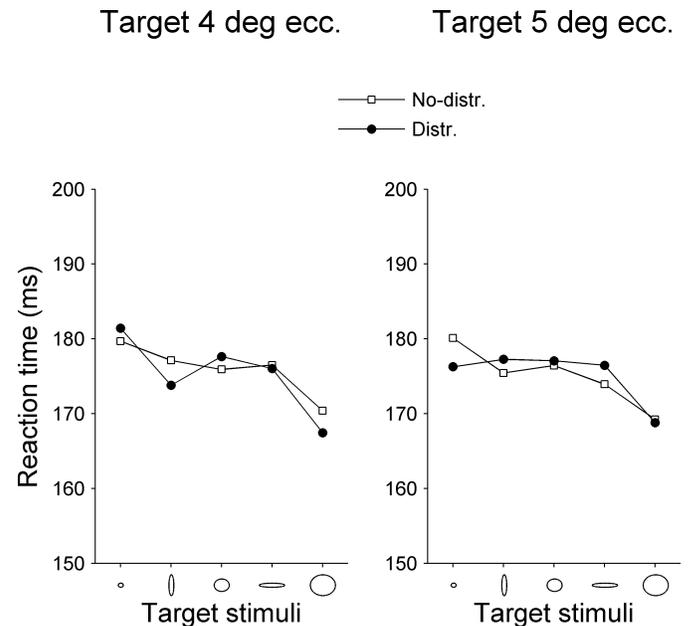


Figure 4. Mean reaction times (in ms) averaged across participants. The empty squares represent the target-only (No distr.) conditions, and the filled dots represent the distractor (Distr.) conditions: small circle, medium vertical ellipse, medium circle, medium horizontal ellipse, and large circle. Left panel: target stimulus presented at  $4^\circ$  and visual distractor at  $2^\circ$  from fixation. Right panel: target stimulus presented at  $5^\circ$  and visual distractor at  $3^\circ$ .

targets in both the distractor and the no-distractor conditions. In Figure 5, the deciles of the reaction time distributions were presented; the distribution associated with large-circle targets showed a consistent shift toward shorter latencies, thus indicating that this trend was consistent across the different time bins.

The analysis of variance showed that saccade latency did not differ between the target-alone ( $175 \pm 15$  ms) and the distractor conditions ( $175 \pm 16$  ms),  $F(1, 7) < 1$ . It remained unaffected by eccentricity,  $F(1, 7) < 1$ , but varied significantly with the properties of the target stimulus,  $F(4, 28) = 14.92$ ,  $p < 0.01$ . Post hoc tests further showed that the small-circle target tended to lead to longer reaction times compared to other stimuli ( $ps < 0.08$ ) whereas the large-circle target led to significantly shorter reaction times ( $p < 0.01$ ). However, the interaction between target type and distractor condition was not significant, thus indicating that these differences did not depend on whether or not the target stimulus was presented with a distractor,  $F(4, 28) < 1$ . The two-way interaction between target type and eccentricity was not significant,  $F(4, 28) = 1.10$ ,  $p = 0.37$ , as well as the other two- and three-way interactions,  $F(1, 7) < 1$ ;  $F(4, 28) = 1.37$ ,  $p = 0.27$ . The fact that reaction times were overall shortest for the largest target stimuli and tended to be overall longest for the smallest targets could not account for the

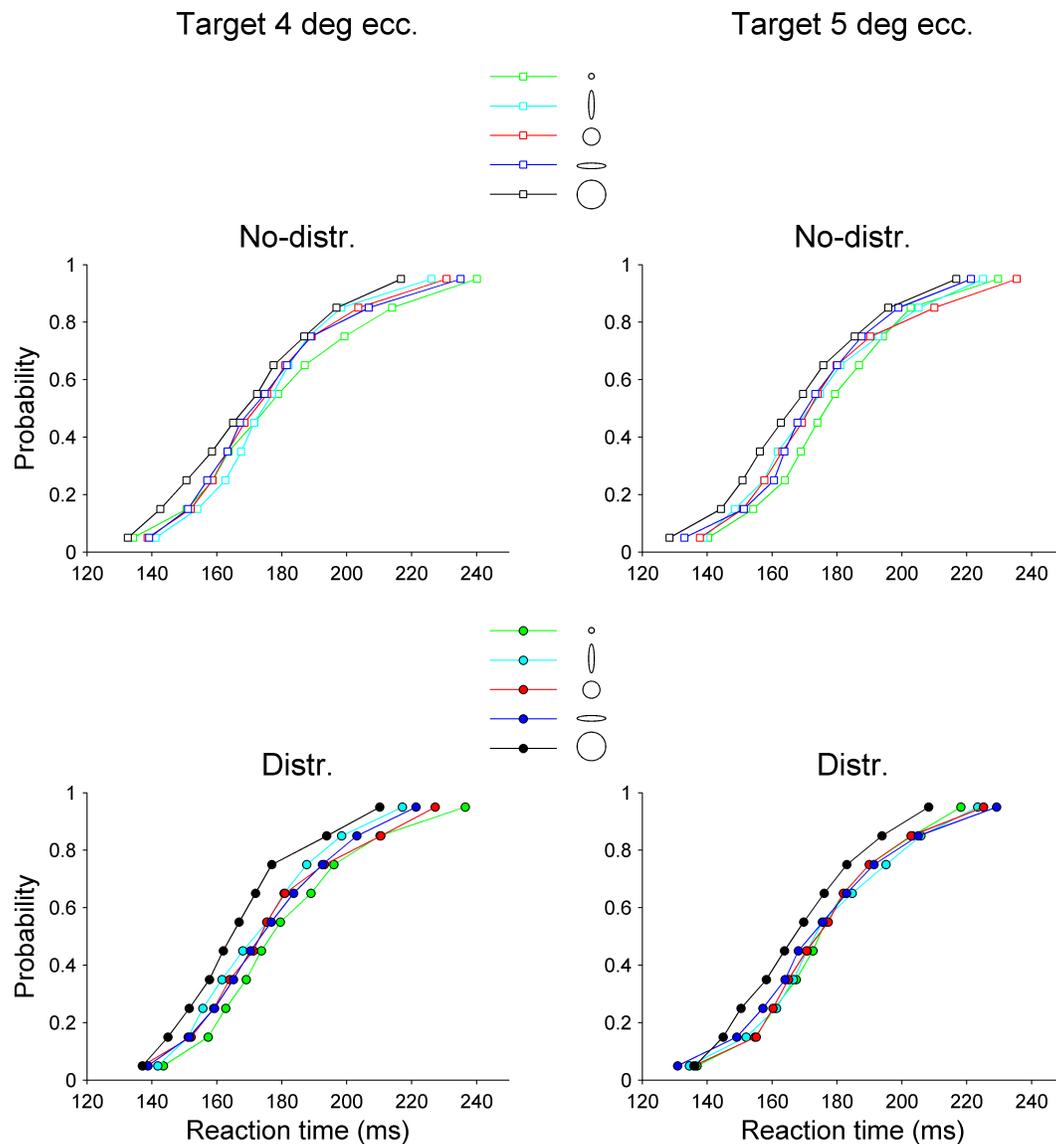


Figure 5. Distributions of reaction times (in ms) averaged across all participants. Each point corresponds to the average of the deciles of individuals' distributions in a given test condition: small circle (green), medium vertical ellipse (light blue), medium circle (red), medium horizontal ellipse (dark blue), and large circle (black). Top: no-distractor condition (empty squares). Bottom: distractor conditions (filled dots). Left panels: target stimulus presented at  $4^\circ$  and visual distractor at  $2^\circ$  from fixation. Right panels: target stimulus presented at  $5^\circ$  and visual distractor at  $3^\circ$ .

above-reported variations of the saccades' landing positions with target type. Indeed, the deviation of the eyes from the target was greatest for the smallest targets (and smallest for the largest targets) but only in distractor conditions. Thus, this could not be the effect of a speed-accuracy trade-off.

## Discussion

In the present study, the goal was to determine the respective contributions of the 2-D spatial extent of the

stimuli and stimulus boundaries to the computation of saccade metrics in complex visual displays. To this end, the well-known influence of stimulus size on the global effect was revisited by contrasting the influence of a visually invariant distractor on the accuracy of saccades to target stimuli that differed either by their 2-D spatial extent or the location of their boundaries. To this aim, the spatial extent of the target stimulus was manipulated in either one or two dimensions, being either a horizontally or vertically oriented ellipse or a circle of varying size. Results showed that the eye deviation away from the saccade target that was induced by the distractor depended on the 2-D spatial

extent of the target but not on the location of the target boundaries. The present findings suggest that the 2-D spatial extent of the stimuli, possibly reflecting the overall intensity of the stimuli, is more critical than visual boundaries in accounting for saccade metrics in complex visual displays.

### The effect of stimulus size

Two alternative hypotheses were proposed to account for the tendency to move the eyes closest to the largest stimulus of a display. The first attributed the effect to the relative weight of the stimuli, thus assuming that larger stimuli contribute with a larger weight to the computation of saccade metrics (Findlay, 1982). The second attributed the effect to the extraction of stimulus boundaries and how far they lay from one another (Findlay et al., 1993). Here, we provided evidence for the stimulus-extent hypothesis and against the boundary hypothesis. We found that the eye deviation away from the center of the peripheral target stimulus on distractor trials remained unaffected by the shape of the target, and hence the location of its boundaries, when the 2-D spatial extent of the target was held constant (i.e., circles vs. horizontal and vertical ellipses of medium size). It may still be argued that the present manipulation was too subtle to give rise to significantly different landing positions. Indeed, the boundaries of the medium-size vertical ellipses were shifted respectively by only  $0.2^\circ$  and  $0.4^\circ$  relative to the boundaries of the circles and horizontal ellipses of corresponding size. However, the diameter of the large-circle targets was only  $0.2^\circ$  and  $0.4^\circ$  greater than the diameter of the medium and small circles respectively, and still the eyes landed significantly closer to the large-circle targets (for similar stimulus sizes and effects, see Findlay, 1982). Thus, it appears unlikely that the present manipulation was inappropriate to reveal an effect of stimulus boundaries. The lack of an effect of shape and orientation for medium-size targets should instead be attributed to the spatial extent of the stimuli being equated.

The finding that the global effect depends on the spatial extent of the stimuli in two dimensions suggests that the effect of stimulus size is due to larger stimuli contributing with larger weights to the integration of spatially proximal stimuli (Findlay, 1982) in the same way as more luminous stimuli do (Deubel et al., 1984). McGowan et al. (1998) proposed that the computation of saccade metrics to a single target object depends mainly on the number and the intensity of the elementary features that compose the stimulus within the integration area. In line with this assumption, we showed, in a two-stimulus visual display, that large and small distractors produced similar eye deviations away

from the saccade target when they were composed of the same number of illuminated pixels (Tandonnet & Vitu, 2013). We thus raised the possibility that the effect of stimulus size may merely reflect an effect of the overall intensity of the stimuli. The present findings are consistent with this view. Indeed, they suggest that a target stimulus contributes with the same weight to the computation of saccade metrics, irrespective of its shape and the proximity of its boundaries to the boundaries of the distractor stimulus at least as long as its 2-D spatial extent (and hence its overall intensity) is held constant. However, when the target is larger and hence contains more (illuminated) pixels its contribution is greater, and the eyes land closer to it while the reverse is true for smaller targets.

An intensity-type interpretation may hold for the apparently contradictory findings of Findlay et al. (1993). The authors reported similar effects of stimulus size on the eyes' landing position in a two-stimulus visual display whether stimuli were filled or empty. However, larger stimuli, whether filled or empty, were still composed of more elementary features compared to smaller stimuli. This is probably what prevented the authors from observing differential effects of stimulus size with frame-only versus filled stimuli. Thus, the effect of stimulus size may be merely an effect of the overall intensity of the stimuli. This suggests that the spatial integration of neighboring signals in the SC, which presumably underlies the global effect, is mainly based on the extraction of rather primitive features. We will describe below how this integration may be implemented in models of saccade generation while discussing whether and how higher-level factors may intervene.

### On the computation of saccade metrics

It is generally assumed that the metrical properties of saccadic eye movements are computed at the level of the SC (Arai et al., 1994; Findlay & Walker, 1999; van Opstal & van Gisbergen, 1989; Wilimzig et al., 2006; see also Meeter et al., 2010; Trappenberg et al., 2001). The SC integrates visual inputs from the retina and the visual cortex as well as cortical (frontal and parietal cortices) and subcortical (basal ganglia) afferent inputs (Isa & Sparks, 2006). Local mechanisms occurring within the SC are assumed to constrain where the eyes move, being responsible for the relative accuracy of saccades to single targets or targets displayed with remote distractors as well as the deviation of the eyes to an intermediate location between spatially close distractor and target stimuli (i.e., the global effect). These mechanisms rely on the large and overlapping receptive/movement fields of SC neurons (Goldberg & Wurtz, 1972; McIlwain, 1975) and/or the interplay of short-range excitatory and (possibly) long-range in-

hibitory interactions within the different layers of the SC (see Isa & Hall, 2009, for a review). Over time, neuronal activity would build up at the center of the entire active neuronal population(s) (Edelman & Keller, 1998; see also Robinson, 1972), which would, in turn, favor the execution of a saccade to the center of the stimulus pattern when this is made of one or several proximal stimuli. The stimulus properties or visual features that influence the spatial integration of neighboring signals remain, however, not unambiguously determined. The present findings informed this question. They suggested that rather primitive visual features that determine the 2-D spatial extent of the stimuli play a more crucial role than the extraction of stimulus boundaries.

We speculate that as stimuli become larger and their elementary features (e.g., the illuminated pixels that compose them) are more widely spread they may activate larger populations of neurons in the SC. Note that this would lead to larger peaks of activity and also higher peaks of activity when stimuli have higher overall intensity as recently proposed (Tandonnet & Vitu, 2013). When the target stimulus is presented in isolation, this has little repercussion on saccadic behavior as shown in the no-distractor condition of the present experiment. As long as the spatial extent of the stimulus is below the extent of the neurons' receptive fields and within the range of short-range excitation, neuronal activity would build up at the center of the entire active population. The eyes would thus land near the center of the stimulus pattern irrespective of its shape or its 2-D spatial extent (see also Kowler & Blaser, 1995; McGowan et al., 1998). In multiple-stimulus visual displays, the extended activity pattern associated with a larger stimulus would likely overlap with the neuronal activity patterns associated with other spatially close stimuli in the display. Moreover, the stronger weight of a larger stimulus may further bias saccade averaging toward it and hence pull the eyes to greater extents. The interplay of short-range excitation and long-range inhibition may be the key mechanism that weights the contribution of each stimulus in the display, depending notably on its spatial extent (e.g., Amari, 1977; Kopecz & Schöner, 1995; Wilimzig et al., 2006). However, the present data do not allow us to confirm or reject a role of lateral interactions in this spatial integration. Still, they are consistent with our recent behavioral estimation of the range of putative lateral inhibition in humans (Tandonnet, Massendari, & Vitu, 2012). In this experiment, we observed that the eyes were deviated away from the target stimulus (i.e., a tiny circle) when this was presented with a vertical distractor line. Importantly, the deviation became greater as the length of the line increased from 0.3° to 0.8° while becoming smaller as the line's length was further increased from 0.8° to 4°.

We interpreted the latter, reverse effect of stimulus size as possible evidence for lateral inhibition. Here, stimuli had diameters varying between 0.1° and 0.4°, which is below the presumed range of lateral inhibition. That may explain why we observed a conventional but not a reversed effect of stimulus size.

Although the present study suggests that low-level visual features play a key role in the integration of neighboring signals, a contribution of visual boundaries or more integrated contour information cannot be completely ruled out. As the SC receives afferent projections from various cortical areas, elaborated visual information may thus also contribute to shape the neuronal activity profile in the SC. In fact, Deubel et al. (1988) found a global effect with texture-defined distractor and target stimuli. The distractor differed from the background by the orientation of its composing elements but not by the luminance contrast of the elements, thus suggesting that visual cortical processes may be involved in the integration of neighboring signals (see also Melcher & Kowler, 1999). However, saccade latencies were overall longer than in the present study (i.e., about 216 ms on average compared to 175 ms here), and it may be that such visual cortical influences take time to emerge and only intervene later to determine where the eyes move. This may explain why visual boundaries did not modulate the global effect in our study.

On the other hand, several studies suggested that the visual similarity between simultaneously displayed stimuli influences the generation of saccadic eye movements. For instance, Born and Kerzel (2009) found that the lengthening of saccade latency, which is typically observed when the target is presented with a remote distractor (e.g., Walker et al., 1997), is greater for physically congruent distractor and target stimuli. Thus, small differences between the visual properties of target and distractor stimuli may delay selection of the saccadic eye movement. On this basis, we would expect that when the visual distractor is displayed near the target stimulus, the difficulty in discriminating both stimuli is further enhanced due to visual crowding (e.g., Pelli et al., 2007), which should, in turn, lengthen saccadic reaction times and/or reduce the accuracy of saccades. To our knowledge, there has been so far no evidence for this assumption (e.g., Tandonnet et al., 2012). In the present study, the greater distractor-related eye deviation that was observed for small-circle compared to large-circle targets could potentially reflect an effect of the visual similarity between distractor and target. However, this was rather unlikely as medium-size ellipses differed from the distractor in both size and shape, and yet the eyes' initial landing position was no different than with medium-circle targets, which only slightly differed from the distractor by their size. Note, in addition, that saccade latency

was reduced for large-circle targets in both distractor and no-distractor trials. This argues against an account in terms of visual discrimination and rather suggests an effect of stimulus detection. Thus, although visual similarity may also influence, through descending projections, the neural activity profile in the SC, it does not seem to contribute to the integration of neighboring signals—at least not within the range of saccade latencies observed in the present study (175 ms on average).

## Conclusion

The present study showed that the large spatial integration of neighboring visual inputs depended on the 2-D spatial extent of the stimuli but not on the distance between stimulus boundaries. This suggests that the spatial distribution and/or the number of elementary features that compose the stimuli in complex visual displays may be more critical than visual boundaries in determining a single saccade endpoint out of many potential locations in the visual periphery. It will be the work of future research to investigate the contribution and time course of more elaborated visual processes.

*Keywords:* human, eye movement, saccade metrics, global effect, size, salience, visual boundaries

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