Saccadic eye movements can only take the eyes to one spatial location at a time. The selection of their endpoint is presumed to occur at the level of the superior colliculus (SC), a midbrain structure involved in the generation of saccades (Gandhi & Katnani, 2011). The SC integrates visual inputs from both the retina and the visual cortex through its superficial layers, as well as afferent inputs from cortical (frontal and parietal) and subcortical (i.e., the basal ganglia) regions of the brain through its deeper layers (Isa & Sparks, 2006). The nature of the critical stimulus properties that determine where the eyes move has not been unambiguously determined. Here, we reexamined the role of local versus global visual features in the computation of saccade metrics.

Neurons in the superficial and deeper layers of the SC have large boundaries, thus supporting the notion that local contrasts are integrated and contribute to the computation of saccade metrics. However, the role of local visual features in the computation of saccade metrics has not been studied extensively. Here, we investigated the role of local visual features in the computation of saccade metrics by manipulating the visual properties of stimuli in a two-stimulus saccade task.

Stimulus Properties and Saccade Metrics: When Local Features Are More Critical Than Global Features

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One major issue in the field of vision is how stimulus properties contribute to determine where the eyes move. Here, we examined the role of local versus global visual features in the computation of saccade metrics in the light of the well-known tendency for saccade to vary with the size of the stimuli. We used a saccade-target task in which we varied the properties of a visual distractor simultaneously displayed with the target stimulus. Both the size and the luminance contrast of the distractor were varied but the number of elementary features that composed the distractor was held constant. Our results showed that under such controls mean saccades’ landing position remained unaffected by stimulus size irrespective of the level of luminance contrast. These findings suggest that the local visual features of a stimulus may be more critical than global features to specify a particular location to look at. These results are consistent with the notion that local features contribute to determine the amplitude and the width of the neuronal activity patterns associated with the visual stimulation and hence the computation of saccade metrics.

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grated into a global feature (i.e., stimulus boundary) in determining the saccadic endpoint. Another study suggested to the contrary a critical role of elementary features in the computation of saccade metrics. In this study, the distance between the boundaries of a single target stimulus was manipulated by randomly varying the spatial arrangement of the dots that composed the stimulus pattern (McGowan, Kowler, Sharma, & Chubb, 1998). Results showed that the participants’ eyes were equally likely to land near the center of gravity of the target stimulus irrespective of the extent of the dot patterns. This led the authors to propose that during the early phases of visual processing, saccade metrics are computed mainly based on the number and the intensity of the entire set of elementary features that compose the stimulus. Thus, the respective contributions of local versus global features to the computation of saccade metrics have not been fully determined.

In the present study, we investigated the role of local versus global visual features in saccade averaging and the computation of saccade metrics. To this aim, we assessed whether the effect of stimulus size can be accounted only based on global information related to the distance between stimulus boundaries. We measured the accuracy of saccades in a two-stimulus visual display, similar to those yielding clear effects of stimulus size (Findlay, 1982; Findlay et al., 1993). A to-be-looked-at peripheral target stimulus was presented with or without a less eccentric distractor stimulus. The novelty was that the distractor stimulus was composed of the same number of elementary features (i.e., dots) irrespective of the distance between their boundaries (see Figure 1). Both the local- and the global-feature hypotheses predicted that the distractor would deviate the participants’ eyes away from the target. However, only the global-feature hypothesis predicted that the deviation would be greater for larger distractors despite the number of elementary features being held constant. Our results showed, in accordance with the local-feature hypothesis, that mean saccades’ landing position remained unaffected by distractor size.

**Method**

Seven participants (on average 24-years old) viewed stimuli on a computer screen, while the movements of their right eye were recorded with a fifth-generation Dual-Purkinje-Image Eye-Tracker (Ward Electro-Optics, Inc.) and analyzed online (Van Rensbergen & de Troy, 1993). Each trial started with the presentation of a fixation cross (0.3 deg; 2.2 cd/m², as measured by displaying a single patch of illumination) on a black background. When the participant’s eye was within a 1 by 0.3 deg vertical-rectangle zone centered on the cross, this was switched off and a target stimulus (i.e., a circle; 0.1 deg in diameter; 2.2 cd/m²) was presented 6 or 7.5 deg to the right of fixation on the horizontal axis. Participants were asked to fixate the target (i.e., a small peripheral circle) as quickly and as accurately as possible. On 80% of the trials, a distractor stimulus was displayed simultaneously with the target at a location, which was three degrees less eccentric; both the eccentricity of the stimuli and the interstimulus distance were expressed relative to their centers. The distractor was a dotted circle composed of 18 pixels (see Figure 1), whose size was varied (0.6 vs. 1.2 deg in diameter; spacing between two adjacent pixels: 0.05 and 0.1 deg respectively). The luminance of the pixels that composed the distractor was also manipulated (1.1 vs. 3.4 cd/m²); the overall luminance of the distractor, when measured by displaying the 18-pixel dotted circle on the dark background was less than 0.1 cd/m² in all conditions of size and luminance. Stimuli remained on the screen for 500 ms; the intertrial interval lasted 1,000 ms. After 30 practice trials, participants ran 10 blocks of 100 trials in which each condition occurred 10 times in a random sequence. A 15-point calibration procedure preceded each block (Vitu, Lancelin, Jean, & Farioli, 2006).

Trials with blinks, anticipatory saccades (latency less than 80 ms) or saccades landing no further than 1 deg to the right of fixation were rejected (24.3 ± 7.5%). 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). For each participant and each experimental condition, the cumulative distribution of the saccades’ landing positions was split in 10 bins (same number of trials); these individual deciles were then used to provide an average cumulative distribution using the procedure described in Ratcliff (1979; see Figure 2). This procedure allows keeping the shape properties of the individual cumulative distributions, and hence provides a reliable representation of the intrasubject variability whatever the intersubject variability (individual differences). Statistical analysis of variability relied on an estimate of the slope of the linear part of the individual cumulative distributions, the difference between the second and the ninth decile of the distribution, computed for each participant and each experimental condition. Corresponding values were used as an index of intra-

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**Figure 1.** Distractor stimuli and mean eye’s landing positions. Positions (in degrees of visual angle) for all participants are expressed for distractor trials relative to no-distractor (control) trials as a function of contrast (weak vs. strong) and size (small vs. large) of the distractor stimulus, for 6 (dots) and 7.5-degree (triangles) target eccentricities. The ordinate origin corresponds to the mean saccade landing position in the no-distractor (control) trials (horizontal dotted line). Each distractor stimulus was a dotted circle with a diameter of either 0.6 or 1.2 deg. Small and large distractor stimuli were composed of 18 pixels; interpixel spacing: 0.05 and 0.1 deg, respectively.
STIMULUS PROPERTIES AND SACCADE METRICS

subject variability. In the analyses reported below, mean landing positions, measures of the variability of landing positions, and mean saccade latencies for each individual and each distractor condition were expressed relative to the corresponding measures in the target-only (control) condition. Reported values were expressed as means \pm standard errors of the mean; visual angles were expressed in degrees. Mean landing position, landing position variability, and saccade latency were submitted to separate ANOVAs in a 2 (size) \times 2 (luminance) \times 2 (eccentricity) within-subject design.

Results

When the target was presented in isolation, saccades showed the usual pattern of high accuracy with on average a slight undershoot (0.02 \pm 0.06°) despite some individual differences (+0.04 \pm 0.12 at 6- and −0.08 \pm 0.08° at 7.5-degree target eccentricities). The distractor deviated the eyes away from the target, but to a greater extent for more eccentric targets, 0.21 \pm 0.18°, \(F(1, 6) = 44.18, p < .01\); Figure 2. The deviation was also more pronounced when the distractor was brighter, 0.20 \pm 0.07°, \(F(1, 6) = 7.50, p = .03\). However, and most importantly, the size of the distractor had no significant effect, \(F(1, 6) = 2.51\) and did not interact with luminance contrast, \(F(1, 6) < 1\); other interactions were also nonsignificant, \(F_{S}(1, 6) < 1\).

Deciles of landing positions showed the consistency of the effect of luminance contrast across the distribution but no tendency at all for a stronger deviation with larger distractors (see Figure 2). Analysis of the variability of landing positions showed that the slope of the cumulative density of the saccades’ landing positions was affected by luminance contrast, \(F(1, 6) = 18.20, p < .01\) and size, \(F(1, 6) = 6.29, p = .046\), but not by eccentricity, \(F(1, 6) < 1\), indicating that brighter or larger distractors led to more variable saccades’ landing positions. None of the interactions were significant, \(F_{S}(1, 6) < 1\).

Saccade latency did not differ between the target-only (230 \pm 13 ms) and the distractor conditions (230 \pm 12 ms), and in the latter case it remained unaffected by size, \(F(1, 6) = 1.42\), luminance, \(F(1, 6) = 1.84\), and eccentricity, \(F(1, 6) < 1\). None of the interactions were significant, \(F_{S}(1, 6) < 1.86\). These results rule out the possibility that the above-reported differences in landing positions were due to speed-accuracy trade-offs.

Discussion

The present study investigated the contribution of local versus global stimulus features to saccade metrics. Overall, our results favored a main role of local visual features. First, in line with previous findings (Deubel et al., 1984), the luminance contrast of the distractor stimulus influenced where the eyes moved. In all distractor conditions, the eyes were deviated away from the target stimulus (i.e., the global effect), but to greater extents with brighter distractors; it thus confirmed that luminance contrast is a first important variable that needs to be controlled for (Findlay, 1982; Findlay et al., 1993). The novel finding was that stimulus size did not matter when the number of lighted pixels was held constant. With such controls, the mean eye deviation induced by the distractor was found to be no greater for larger distractors. Note that an influence of stimulus size on saccade metrics was previously evidenced in conditions comparable to ours, that is in two-stimulus visual displays and when extraction of stimulus size was not relevant for the task (Findlay, 1982; Findlay et al., 1993;
Tandonnet, Massendari, & Vitu, 2012). Importantly, the range of distractor sizes (0.6°) in the present study was slightly larger than the ranges which repeatedly yielded effects of stimulus size in previous studies (0.3°, Findlay, 1982; Findlay et al., 1993; 0.5°, Tandonnet et al., 2012). Thus, it appears unlikely that the lack of an effect of stimulus size in the present study was specific to our particular set-up.

The present results suggest that previously reported effects of stimulus size on averaging saccades were not due to the distance between stimulus boundaries, and hence global visual features. Instead, in previous studies, the increased weight of larger stimuli likely reflected the greater number of elementary features (or dots) contained in these stimuli. This interpretation in terms of local features is in line with the notion that the number and the intensity of the elementary features that compose the stimuli first determine where the eyes move (McGowan et al., 1998). It is worth mentioning that this interpretation of our results is in contradiction with the findings reported by Findlay, Brogan, and Wenban-Smith (1993). This contradiction may be due to a difference in sharpness of the stimulus boundaries in the two studies. Indeed, one limitation of our study may be that larger stimuli were composed of more widely spread pixels, and thus, that their overall space-averaged luminance was lower. This may have reduced their influence on saccade metrics, and hence cancelled out the typical effect of stimulus size. We cannot, therefore, exclude that other factors related to the visual density of the stimuli such as their overall luminance or perceptual grouping contributed to some extent to reduce the effect of stimulus size in our display conditions. Nevertheless, it appears unlikely because the overall luminance of our distractor stimuli was similarly low in both conditions of stimulus size (< 0.1 cd/m²). Although we cannot completely rule out an effect of perceptual grouping, we also doubt that it played a main role. Indeed, the gap between the dots that composed the small distractors was only 0.05 degree less than in the case of large distractor stimuli (see Figure 1); this was likely below the resolution of the visual system in the periphery. Moreover, if overall luminance or perceptual grouping of the distractor stimuli compensated for the influence of stimulus size, there should have been no effect of stimulus size on both the mean and the variability of landing positions. In contrast, the landing-site distributions were more widely spread for larger distractor stimuli (Figure 2; see also Kowler & Blaser, 1995; McGowan et al., 1998; Ploner, Ostendorf, & Dick, 2004).

As described above, population coding in the SC very likely underlies the computation of saccade metrics to target stimuli presented in isolation or simultaneously with another visual stimulus. As neurons in the superficial and deeper layers of the SC have large and overlapping receptive fields (Goldberg & Wurtz, 1972), stimuli displayed at two separate but neighboring locations in the visual field would initially activate two overlapping populations of neurons. The weighted average of the activity of the recruited neuronal population would then determine the endpoint of the saccade (Findlay & Walker, 1999). In line with the local-feature hypothesis, we propose that the neuronal activity profile that builds up as a result of visual stimulation and serves as a basis for saccade averaging is determined by two kinds of properties of the elementary features that compose the stimulus pattern. As further detailed below, luminance contrast of elementary features as well as their number would contribute to determine both the height and the width of the pattern of neuronal activity, although the location of the elementary features within the integration area would influence only the width of the neuronal activity pattern. This assumption accounts for previously reported effects of stimulus intensity and stimulus size on both the mean and the variability of landing positions when larger stimuli are composed of a greater number of elementary features. It also accounts for the lack of an effect of stimulus size on the mean but not on the variability of landing positions when the number of elementary features is held constant as in the present study.

First, the level of activity of the neuronal population recruited by the visual stimulation would likely increase for brighter stimuli (e.g., Bell et al., 2006) as well as larger stimuli that are usually composed of a greater number of elementary features. Robinson (1972) indeed reported that electrically evoked saccade averaging in the SC was weighted by the relative intensity of the electrical current applied at two simultaneously stimulated sites in the deeper layers of the SC. A similar mechanism would likely account for the finding that the eyes are more greatly deviated when the visual target stimulus is displayed simultaneously with a brighter distractor stimulus, as in the present study (see also Deubel et al., 1984), or with a larger distractor stimulus composed of a greater number of elementary features, as in previous studies (Findlay, 1982; Findlay et al., 1993; Tandonnet et al., 2012). However, the level of neuronal activity would likely not increase as distractor stimuli become greater in size but the number of elementary visual features is held constant; this would contribute to the lack of an effect of distractor size on mean landing positions as in the present study.

Second, the width of the recruited neuronal populations would likely increase for brighter stimuli as well as for stimuli which extend over larger regions of the visual field and whose elementary visual features are located further away from one another. Indeed, brighter dots should be more likely to evoke neuronal activity even when falling near the edges of the neurons’ receptive fields, although the features of larger stimuli would fall within the receptive fields of a more widely spread neuronal population. This would account for the more widely spread landing—position distributions that we observed here when the saccade target was displayed simultaneously with a brighter or larger distractor and despite the number of elementary features being held constant (see also McGowan et al., 1998). This would also account for the greater variability of landing positions that was previously reported for larger distractor stimuli composed of a larger number of elementary features (e.g., Ploner et al., 2004).

The present assumption thus suggests that larger stimuli would trigger a higher level of neuronal activity only as long as they are composed of a greater number of elementary visual features. This raises the possibility that local features, more than global features, would be critical in shaping the amplitude and the width of the neuronal activity patterns associated with the visual stimulation, and hence in determining where the eyes move. Note that the present results involved effects of distractor rather than target properties, thus exemplifying the role of automatic processing of irrelevant local features in the peripheral visual field. It must still be noted that this scheme applies only to stimulus sizes within the range of influence of excitatory connections in the SC, and hence below the range of influence of lateral inhibition (Van Opstal & Van Gisbergen, 1989). Long-range inhibition may intervene when stimuli are particularly large, as supported by results showing that
larger distractors can be less disruptive than smaller ones on saccade metrics (Tandonnet et al., 2012).

In conclusion, the disruptive effect of larger distractor stimuli may become weaker when the number of elementary features that compose these stimuli is matched with that of smaller stimuli. Spatial integration of visual inputs into a single averaged oculomotor response seems to rely to a greater extent on the luminance contrast as well as the number and the location of the elementary features that compose the stimuli than on the spatial extent of the stimuli as indexed by the distance between their boundaries. Such a predominance of local over global features suggests that computing the landing position of visually triggered saccades does not necessarily require extraction of stimulus boundaries. These results are consistent with the notion that local features contribute to determine the neuronal activity patterns associated with the visual stimuli and hence their respective weight in the computation of saccade metrics.

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