On the effect of remote and proximal distractors on saccadic behavior: A challenge to neural-field models

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Two proposals have been made to account for the generation of saccadic eye movements. The first assumes that when the eyes move is under the control of a fixation gating system. The second attributes the decisions of both when and where the eyes move to the interplay between short-range excitatory and long-range inhibitory interactions within the motor map of the superior colliculus (SC). To distinguish both views, three behavioral experiments conducted on human participants tested the respective contributions of stimulus eccentricity and interstimulus distance on the effects of remote and proximal distractors on the latency and accuracy of saccades. Experiment 1 showed that the saccade-latency increase that results from the presentation of a remote distractor in the contralateral, nontarget hemifield varies with the ratio of distractor-to-target eccentricity, but not the interstimulus distance in visual or collicular space, thus indicating that the effect is not due to long-range inhibition. Experiments 2a and 2b showed that short-range excitation does not underlie the effect of proximal, ipsilateral distractors. Proximal distractors do not systematically shorten saccade latency, but rather show a range of effects (from a latency increase to no effect and then facilitation) as the ratio of distractor-to-target eccentricity increases, while deviating the eyes to gradually larger extents. The present findings strongly challenge the neural-field account, while suggesting that when a saccade is initiated depends mainly on the activity of a fixation gating system.

Keywords: saccade latency, remote distractor effect, lateral interactions, fixation system, saccade metrics, global effect


Introduction

Saccades are relatively accurate movements of the eyes that bring an isolated peripheral target object into the central, foveal part of the retina, with an average latency of about 150–175 ms. However, when only one additional visual stimulus is displayed simultaneously with the saccade target, saccadic performance is greatly reduced. As reported by Walker, Deubel, Schneider, and Findlay (1997), a distractor displayed in the vicinity of the target that is within \( \pm 20^\circ \) of the ipsilateral target axis greatly affects saccade accuracy by pulling the eyes towards an intermediate location between the two stimuli (i.e., the global effect; Findlay, 1982; see also Coren & Hoenig, 1972). In contrast, a remote distractor displayed anywhere outside the \( \pm 20^\circ \) window, in the ipsilateral or contralateral hemifield or at the center of the fovea, delays saccade onset up to about 40–60 ms (i.e., the remote distractor effect; see also Lévy-Schoen, 1969; L. E. Ross & Ross, 1980; S. M. Ross & Ross, 1981). The global effect is generally attributed to distributed spatial coding in the superior colliculus (SC), a brainstem region involved in saccade generation. Since neurons in the retinotopically organized sensory and motor maps of the superficial and deeper layers of the SC have large and overlapping receptive/movement fields, the simultaneous presentation of spatially proximal stimuli generates overlapping peaks of neuronal activity; these merge into a single central peak and trigger in turn the execution of a saccade to an intermediate location in space (e.g., Findlay & Walker, 1999; van Opstal & van Gisbergen, 1989). For the effect of remote distractors on saccade latency, the underlying mechanisms remain, however, debated.

Two main hypotheses have been proposed to account for when the eyes move in complex visual displays. The first, proposed by Walker et al. (1997) and further developed by Findlay and Walker (1999), is in terms of competitive interactions between a fixation system, whose function is to keep the eyes still, and a move system, whose reciprocal activity leads the eyes to move towards the periphery. This hypothesis assumes that saccades are held until the activity of the fixation system falls down below a certain threshold and that saccade onset delay in remote distractor conditions...
results from enhanced fixation activity. The fixation system shares properties with so-called fixation neurons, which have been found in the rostral pole of the SC (or the region receiving input from the 2° foveal area) and which presumably discharge, contrary to more caudal, saccade-related neurons, only during intersaccadic intervals (Munoz & Wurtz, 1993a, 1993b). However, the fixation system is most likely located downstream of the SC, in the brainstem omnipause region. One main reason is that neurons in the rostral pole of the SC may not be functionally different from saccade-related neurons; rather, they would be part of one single population of collicular neurons exhibiting a rostral-to-caudal continuum of discharge characteristics (Krauzlis, Basso, & Wurtz, 1997; see also Anderson, Keller, Gandhi, & Das, 1998) and selectivity to saccade amplitude (Hafed, Goffart, & Krauzlis, 2009; Hafed & Krauzlis, 2012). Omnipause neurons (OPNs), on the contrary, exhibit tonic discharge during visual fixation and pause during saccades. They receive excitatory projections from neurons in the rostral pole of the SC (Paré & Guittion, 1994), but also, though gradually less, from neurons located more caudally and coding for eccentricities as large as 10° (Bittner-Ennever, Horn, Henn, & Cohen, 1999) or even beyond (Gandhi & Keller, 1997). For this reason, they are assumed, in Findlay and Walker’s (1999) model, to form an extended fixation system, whose activity is increased by foveal as well as peripheral stimulation. When a distractor falls in either of those regions, it would therefore enhance fixation activity, compared to when the target is displayed with no distractor. However, whether or not this in turn delays saccade onset would first depend on the proximity of the distractor to the target since this determines, due to distributed spatial coding in the SC, how much, comparatively, the distractor increases saccade-related activity in the target area. It should also depend on the proximity of the distractor to the fovea given the rostro-caudal gradient of collicular projections to the omnipause region. A remote, compared to a proximal, distractor would thus be more likely to shift the balance towards fixation and hence delay saccade onset. However, a distractor, whether distal or proximal, should be more prone to increase saccade latency as it is presented closer to the fovea and closer to the fovea than the target, thus suggesting that the critical variable is the relative eccentricity of the stimuli.

The second main account of saccade generation, proposed in neural-field models, makes no recourse to a fixation gating system, but relies instead on lateral interactions within and across the colliculi (Godijn & Theeuwes, 2002; Meeter, Van der Stigchel, & Theeuwes, 2010; Trappenberg, Dorris, Munoz, & Klein, 2001; Wilimzig, Schneider, & Schoner, 2006). It assumes that when as well as where the eyes move results from competitive and cooperative mechanisms in the motor map of the intermediate layers of the SC, where exogenous and endogenous signals are integrated. This hypothesis relies on evidence for horizontal connections within and across the respective layers of the two colliculi and the more debated finding (see Isa & Hall, 2009; Lee & Hall, 2006) that these may have different properties depending on their extent. Intracollicular projections would be either short-range and excitatory or long-range and inhibitory, thus either spreading excitation locally (~1.5 mm in cats, McIlwain, 1982; ~1 mm in ferrets, Meredith & Ramoa, 1998) or inhibiting remote sites in the sensory/motor map (≥2 mm in monkeys, Munoz & Istvan, 1998; see also Mize, Jeon, Hamada, & Spencer, 1991); note that in the cat at least, the majority would still be short-range connections (1–2 mm, Behan & Kime, 1996). Intercollicular projections would be mainly inhibitory, except for those shorter, rostro-rostral excitatory connections (Infante & Leiva, 1986; Munoz & Istvan, 1998; Wurtz, Richmond & Judge, 1980; see also Olivier, Porter & May, 1998). When two (or more) stimuli are simultaneously displayed, the interplay of local excitation and long-range inhibition would presumably reshape the initial pattern of neuronal activity in the motor map, thereby determining when and where a maximal peak of activity emerges, and hence when and where the eyes move. In instances where a distractor appears at a remote location from the saccade target, saccade onset would be delayed as a result of long-range inhibition attenuating saccade-related activity at the target location. In contrast, due to the local spread of excitatory activity, a distractor displayed in the vicinity of the saccade target should quickly favor the buildup of activity at an intermediate location in the motor map, which should in turn hasten the execution of an averaging saccade. Interstimulus distance would thus exclusively determine where and when the eyes move.

It has not been unambiguously determined so far whether the critical variable in accounting for the effect of remote and proximal distractors on saccade latency is the distance between the stimuli as predicted by the lateral-interaction account, or the relative eccentricity of the stimuli as predicted by the fixation-system hypothesis. For the case of remote distractors, Walker et al. (1997) found an inverse relationship between the magnitude of the effect (or the saccade-latency increase in distractor compared to no-distractor trials) and the ratio of distractor-to-target eccentricity, which may support the fixation-system hypothesis. The distractor effect was greatest when the distractor was displayed at the center of the fovea, and then gradually reduced as the distractor was presented more peripherally and its eccentricity more closely matched the eccentricity of the
target (see also Griffiths, Whittle, & Buckley, 2006). However, since this result relied on manipulation of the eccentricity of the distractor for only two possible target eccentricities, it may have been in part an effect of the angular distance between the stimuli. Furthermore, given the nonhomogeneity of visual afferent mapping in the SC or foveal magnification (Ottes, Van Gisbergen, & Eggermont, 1986), the possibility remains that the greater impact of less eccentric distractors came from their distance to the target in collicular space being greater than the distance between more peripheral stimuli.

In accordance with this interpretation, Dorris, Olivier, and Munoz (2007) showed that irrespective of the eccentricity of the saccade target (1.5°–30°), a visual distractor displayed near the target greatly increased neuronal activity at the target, recorded site, and often favored the execution of erroneous saccades towards the distractor location; in contrast, a distant distractor in the ipsilateral or the contralateral hemifield inhibited activity at the target location. Importantly, the level of inhibition was no different for a distractor presented at the center of the fovea and beyond 10° in the periphery, at least as long as its distance to the target in collicular space was comparable, thus suggesting that distractor eccentricity is not the critical variable that determines the level of target-related activity. Still, there was no related saccade-latency increase, while this would be expected under a lateral-inhibition account of the remote distractor effect. This might have been specific to the use of a 200-ms gap paradigm combined with the presentation of the target at a fixed, predictable location; this favored preparatory activity at the expected target location (see also Dorris, Paré, & Munoz, 1997), and made that the distractor, displayed 100 ms before the target, modulated the level of preparatory activity, but not the visual signal associated with target onset. However, it may also be the case that long-range inhibition simply does not influence when a saccade is initiated. Along these lines, Watanabe, Kobayashi, Inoue, and Isa (2005) reported that nicotine injection in the intermediate layers of the SC increased the activity of both excitatory and GABAergic, inhibitory neurons. However, the injection failed to delay the onset of saccades directed to a location in space that was remote from the stimulation site, while still facilitating the occurrence of saccades to nearby locations. These results shed doubts on a lateral-inhibition account of the remote distractor effect. However, it still remains to be determined whether, as predicted by the fixation-system hypothesis, stimulus location more than interstimulus distance accounts for the effect of remote distractors on saccade latency.

For proximal distractors, the majority of studies have revealed that they fail to affect saccade latency, although consistently deviating the eyes away from the target (Cohen & Ross, 1978; Deubel, Findlay, Jacobs, & Brogan, 1988, see experiment 2; Eggert, Sailer, Ditterich, & Straube, 2002; McSorley & Findlay, 2003, see experiments 1 through 4; Ottes, Van Gisbergen, & Eggermont, 1985, see experiment 1; Sailer, Eggert, & Straube, 2002, see experiments 2 and 3; Walker et al., 1997, see experiments 1a and 3; see also Bompas & Sumner, 2011). Only a few studies reported a reduction of saccade latency together with saccade averaging (Godijn & Theeuwes, 2002, see experiment 1; see also Edelman & Xu, 2009), or an increase of saccade latency with still a global effect (Sailer et al., 2002, see experiments 1 and 4; see also Chou, Sommer, & Schiller, 1999). This is opposite to the prediction of the lateral-interaction hypothesis that a distractor displayed in the vicinity of the saccade target should not only favor a global effect, but also systematically reduce saccade latency. The lack of a systematic effect of proximal distractors on saccade latency may, however, be reconciled with the fixation-system hypothesis, at least under the assumption that the range of tested distractor and target eccentricities was most often inappropriate to make the balance of activity shift preferentially towards fixation or movement. Indeed, due to distributed spatial coding in the SC, a proximal distractor also enhances saccade-related activity in the vicinity of the target. Thus, it would be only when it increases the level of activity of the fixation system comparatively more, such as when it is displayed near the fovea, that it would succeed in delaying saccade onset. Conversely, a distractor would become more likely to facilitate saccade onset as it is presented more peripherally and closer to the target.

In accordance with this prediction, it appears that across all the above-mentioned studies, proximal distractors displayed at an eccentricity of 5° or more either had no effect or only a slight facilitating influence on saccade latency, while distractors displayed at smaller eccentricities, and closer to the fovea than the target, either delayed saccade onset or had no effect. Weber and Fischer (1994) also reported inhibitory effects of a proximal distractor in a gap task, showing a gradual reduction of the proportion of express saccades as the distractor moved from an eccentricity of 8.5° to 0.5° (see also Griffiths et al., 2006). However, this is only weak evidence for the fixation-system hypothesis since neither the angular nor the collicular separation between distractor and target stimuli was controlled for.

Here, we thus re-investigated the effect of remote (and contralateral; Experiment 1) and proximal (and ipsilateral) distractors (Experiments 2a and 2b) on saccadic behavior, but with a slightly different experimental design in order to isolate the respective contributions of stimulus eccentricity and interstimulus
distance. The distance was manipulated in degrees of visual angle, but to more optimally test the predictions of the lateral-interaction hypothesis, a-posteriori analyses were conducted after converting the angular separation between the stimuli in millimeters of collicular space. This was done using Ottes et al.’s (1986) logarithmic mapping function of the SC in monkeys, thus assuming that foveal magnification is of the same order in humans. On the other hand, proximal distractors were displayed in the fovea versus the near periphery in order to test the specific prediction of the fixation-system hypothesis—that depending on the balance of activity between fixation and move systems, a distractor may show a range of effects on saccade latency, from a latency increase to no effect and then facilitation.

**General methods**

In all three experiments, a single saccade-target stimulus was displayed either on its own (control condition) or simultaneously with a distractor on the horizontal target axis (experimental condition). Both the eccentricity of the distractor and the angular separation between distractor and target (referred to as D-T distance) were manipulated; the eccentricity of the target in both the experimental and the control conditions was derived from the combination of these two variables. In Experiment 1, the distractor was displayed at the center of the fovea (0°) or at eccentricities ranging between 0.5° and 3° in the contralateral nontarget hemifield; these were referred to as −0.5° and −3°. In Experiments 2a and 2b, the distractor was presented in the same hemifield as the target, at eccentricities ranging between 0.5° and 3°, being always less eccentric than the target; in two additional conditions, it appeared either at the center of the fovea (0°) or at an eccentricity of 0.5° in the opposite hemifield (−0.5°). The range of angular D-T distances in Experiments 1 (4°–6°) and 2a and 2b (1°–3°) corresponded to angular separations that were previously found to yield remote distractor and global effects respectively (see Casteau & Vitu, 2009; Walker et al., 1997). According to Ottes et al.’s (1986) model of monkeys’ SC (see below), these also corresponded to collicular distances that were respectively greater and smaller than the presumed extent of short-range excitation in monkeys (1 mm; Trappenberg et al., 2001). The resulting eccentricity of the target ranged between 1° and 6° in Experiment 1 and 0.5° and 6° in Experiments 2a and 2b.

The target was displayed either to the left or to the right of fixation, but target side was held constant in a given block of trials. This was done to minimize the uncertainty of target direction and hence to reduce the possible contribution of decisional and strategy-based processes to the distractor effect, particularly given that contralateral-distractor conditions were included in all blocks (see Walker et al., 1997). The fact that ipsilateral distractors in Experiment 2a and 2b were always less eccentric than the target also reduced the uncertainty of target location, and hence the contribution of decisional processes. Still, given that distractor eccentricity and D-T distance were manipulated within blocks of trials, the target appeared at variable eccentricities within a block. This likely reduced the probability of anticipatory saccades which could be encouraged by the predictability of target direction, although anticipatory saccades are most often observed in nonzero gap conditions (e.g., Rolfs & Vitu, 2007). Experimental and control trials were also randomly mixed within blocks.

**Stimulus material**

In Experiments 1 and 2a, single, lower-case letters were used as target and distractor stimuli; the target was either an ‘h’ or a ‘k’, and the distractor was an ‘o’. Each letter subtended about 0.27° of visual angle at a distance of 1,075 mm. In Experiment 2b, stimuli were presented at a distance of 850 mm. They were geometric forms; the target was an isosceles triangle (basis: 0.26°, side: 0.23°), which was oriented either upwards or downwards, and the distractor was a circle (diameter: 0.20°). The stimuli, displayed in white on a black background, had a luminance of 9 cd/m².

**Procedure**

The experiments lasted about 1.5 to 3 hrs. They were performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki, and individuals gave their informed consent prior to their participation in the study.

The room was dark except for a dim indirect light source. The participant was seated in an adjustable chair in front of a computer screen. A dental print was made in order to minimize his or her head movements. Each block of trials started after setting up the eye tracker and running a calibration phase. Calibration was made using 15 points presented successively on the entire screen: five points on both diagonal axes and five points around the central horizontal axis of the screen. Participants were asked to press a button when they were fixating very precisely at the dot location. If the correlation between the actual and the estimated eye location was satisfactory (more than 0.99), the block of trials began. Otherwise another calibration phase was initiated.
Each trial started with the presentation of two vertically-aligned bars (length \(0.5^\circ\) and width \(0.03^\circ\) in Experiments 1 and 2a, and length \(0.3^\circ\) and width \(0.03^\circ\) in Experiment 2b) at the center of the screen (see Figure 1). The participant was asked to fixate the gap in between the two bars; the gap subtended \(0.3^\circ\) and \(0.5^\circ\) in Experiments 1–2a, and \(2b\), respectively, which was greater than the angular size of the stimuli (see above), and hence reduced the likelihood that central distractors would be subject to visual masking. When the computer detected a fixation within a vertically-oriented rectangular region \((0.3^\circ \times 1^\circ)\) from the center of the fixation bars, these were removed and the stimuli (the target and the distractor in the experimental condition, and only the target in the control condition) were displayed (0-ms gap). On average, the removal of the fixation bars (and the onset of the stimuli) occurred 41, 52, and 37 ms after fixation onset in Experiments 1, 2a, and 2b, respectively; this was much shorter than in previous studies (\(\geq 500\) ms), but allowed the entire fixation period (or the total time between the start of the fixation and saccade onset) to be relatively similar to fixation durations in natural perceptual tasks (210–360 ms on average).

Participants were instructed to move their eyes as quickly and as accurately as possible to the target, while ignoring the distractor, and then to perform a discrimination task on the target; this task was aimed at reinforcing the execution of accurate saccades. Participants pressed the right- or the left-hand button depending on whether the letter was an ‘h’ or a ‘k’ in Experiments 1 and 2a, or an upward- or downward-oriented triangle in Experiment 2b. To further encourage participants to move their eyes precisely to the target, button press was effective only after their eyes had crossed an invisible boundary placed \(1^\circ\) in front of the target, but exclusively for targets displayed at an eccentricity greater than \(1^\circ\). Following button press, the stimuli were removed; thus, the presentation time of the target as well as the distractor was self-paced. Simultaneously, two symbols (a number and a letter, ‘C’ or ‘F’) were displayed for 1 s in the lower part of the screen; these indicated respectively the trial number and whether the participant’s response was correct or false. This latter, intervening phase was aimed at preventing participants to adopt some scanning rhythm, and possibly further reduced the likelihood of anticipatory saccades. Following this latter phase, a new trial began. Eye-movement data were stored from the beginning of a trial (display of the initial fixation bars) until button press.

**Apparatus**

Eye movements were recorded using a Dual-Purkinje-Image Eye-Tracker (Ward Electro-Optics, Inc., Gallatin, MO), which samples the right eye position every millisecond with an accuracy of 10 min of arc. The eye tracker was connected with a 486 IBM-PC compatible computer, which recorded and analyzed online both the eye-movement signal and button press. Eye-movement data were continuously sent from the first computer to a second 486 IBM-PC compatible computer.
computer which controlled the visual presentation of the stimuli, thus allowing eye-movement contingent stimulus presentation. Eye movements were analyzed online and reprocessed offline, using the software developed at the Catholic University of Leuven (Belgium) by Van Rensbergen and de Troy (1993). Stimuli were displayed on a 17” CRT monitor with 60-Hz refresh rate. Vision was binocular.

Data selection and analysis

The characteristics (latency and accuracy) of the first saccade initiated after target onset as well as the position of the initial fixation (relative to the center of the initial fixation bars) were analyzed in the different conditions. Trials were selected for analysis using the following criteria: (a) the stimuli (target or target and distractor) were displayed during a fixation and not during a saccade, (b) there was no artifact or signal irregularity in the trial, (c) there was no blink before or after the initial saccade, (d) a saccade was indeed launched after stimulus presentation, (e) the average eye position before saccade onset (as measured offline) was within less than 0.5° to the left or to the right of the fixation bars, and less than 1.2° above or below the center of the bars, (f) the latency of the initial saccade was longer than 80 ms in order to discard anticipatory eye movements, and (g) the saccade moved the eyes in the direction of the target.

The position of the initial fixation relative to the initial fixation stimulus was analyzed in both the horizontal and the vertical directions in order to have a precise estimate of the actual location of distractor and target stimuli before saccade onset. This corresponded to the mean of all sampled eye positions from the onset of the fixation on the gap between the two vertically aligned fixation bars and the onset of the initial saccade. Saccade latency corresponded to the delay between the onset of the stimuli and the onset of the saccade. Saccade accuracy, also referred to as landing position error, was estimated by measuring the difference between the initial horizontal landing position and the eccentricity of the target, separately in each experimental and control condition. Two additional indexes were used in order to estimate the impact of the distractor on saccadic behavior. The saccade latency difference measured the difference between the mean latency of saccades in a given experimental condition and its corresponding target-control condition, where the target was displayed with no distractor, at the same location as the target on experimental trials. The Global Effect Percentage (or GEP; Findlay, Brogan, & Wenban-Smith, 1993) provided a standardized measure of the eye deviation induced by the distractor that was independent of the angular separation between distractor and target stimuli. It was calculated using the following formula:

$$GEP = 100\% \left( \frac{L_x - L_{dc}}{L_{tc} - L_{dc}} \right)$$

(1)

where $L_x$ was the mean landing position in a given experimental condition, $L_{tc}$ was the mean landing position in the target-control condition, where the target was displayed with no distractor, at the same location as the target in the experimental condition, and $L_{dc}$ corresponded to the mean landing position in the distractor-control condition, where the target was displayed with no distractor, at the same location as the distractor in the experimental condition. A GEP of 50% indicated that the eyes’ landing position was exactly midway between the landing positions in distractor- and target-control trials respectively. A GEP of 0% indicated that the eyes landed on average at the same location as with a single target was displayed at the distractor location, and a GEP of 100% indicated that the eyes landed on average at the same location as with a single target at the target location. Note that this analysis excluded the foveal-distractor condition since a target was never displayed at an eccentricity of 0°.

In all analyses, means and proportions were calculated for each participant. An analysis of variance was run on the mean for each participant in each condition. For post-hoc comparisons, Newman-Keuls were used. Distributions were also reported. Distributions of initial fixation positions grouped fixation positions into 0.2° bins and distributions of initial landing positions grouped landing positions into 0.5° bins; they corresponded to the means of the distributions for each individual. Distributions of saccade latencies were plotted across participants using 4-ms bins; a 9-point moving-window-average smoothing function was then applied to the obtained distributions. Preference for a small binning of saccade latencies was motivated by previous findings suggesting that a visual transient, and in particular a remote distractor, can induce a marked reduction of the frequency of saccades over a tiny time interval (see Buonocore & McIntosh, 2008; Reingold & Stampe, 2002). This phenomenon, referred to as saccadic inhibition, gives rise to a characteristic notched dip in the distributions of saccade latencies in distractor compared with no-distractor trials. Note that individual distributions, when computed with the same procedure, were noisier, but showed overall patterns that were similar to those reported here.

All dependent variables were analyzed as a function of the manipulated factors. Two additional independent variables were defined a-posteriori. The first was the ratio of distractor to target eccentricity, which was calculated by dividing the (absolute value of the) eccentricity of the distractor by the (absolute value of
the eccentricity of the target; a ratio of zero indicated that the distractor was displayed at an eccentricity of 0°, and a ratio of one indicated that target and distractor were presented at the same eccentricity, but possibly in different directions. The second, a-posteriori defined variable was the estimated collicular distance between distractor and target. This was calculated by converting the angular distance between distractor and target in millimeters of collicular space, using Ottes et al.’s (1986) logarithmic mapping function of the SC in monkeys. For a stimulus presented at an eccentricity, R, and at a meridional angle (or direction), ϕ, the collicular coordinate, u, as expressed from the rostral pole of the SC along the axis representing the horizontal was obtained with the following formula,

\[ u = B_u \ln \left( \sqrt{R^2 + A^2 + 2AR \cos \phi} \right) - B_u \ln A \]  

where B_u and A were constants, set at values of 1.4 and 3, respectively. For the particular case of contralateral distractors, which were displayed exclusively on the horizontal meridian (Experiment 1), we simply summed the estimated u coordinates of the distractor and target stimuli, which should be a reasonable approximation of the interstimulus, collicular distance given that intercollicular connections cross the collicular commissure at the level of the horizontal meridian.

**Experiment 1: The effect of remote distractors**

The first experiment was an attempt to replicate the remote distractor effect with contralateral distractor stimuli and to determine whether it is mainly a function of stimulus eccentricity as predicted by the fixation-system hypothesis, or the interstimulus distance as predicted by the lateral-interaction account.

**Methods**

**Observers**

Eight university students, aged between 18 and 23 years, participated in the experiment. All reported having normal vision and were unaware of the purpose of the experiment.

**Design**

All participants ran all conditions. Their data in the experimental and the control conditions were analyzed separately, using two repeated-measure designs with three and two independent variables respectively: (1) distractor eccentricity with five levels (–3°, –2°, –1°, –0.5°, and 0°); (2) D-T distance with three levels (4°, 5°, or 6°); and (3) target side with two levels (left vs. right) in the experimental condition; and (1) target eccentricity with nine levels (1°, 2°, 3°, 3.5°, 4°, 4.5°, 5°, 5.5°, and 6°), and (2) target side with two levels (left vs. right) in the control condition. There were 20 repetitions per combination of each factor level, which resulted in a total of 960 trials (600 experimental trials and 360 control trials). These were divided into 10 blocks of 96 trials, five blocks where the target appeared to the right of the initial fixation stimulus and five blocks where the target appeared to the left. Each block randomly mixed 60 experimental trials and 36 control trials, and all presentation conditions in similar proportions. Half the participants started with right-target blocks, and the other half started with left-target blocks. A practice block of 24 trials was run before left- and right-target blocks respectively.

**Results**

Data were excluded if they did not meet the above criteria (see General methods). Rejected trials represented 19.7% of the total number of trials across participants. This was in accordance with rejection rates obtained with a similar task and setup (see Vitu, Lancelin, Jean, & Farioli, 2006) and was mainly due to button press occurring before stimulus presentation or stimuli being displayed during a saccade and not during a fixation (8.6%) as well signal artifacts and blinks (5.8%). Other rejected trials were trials where no saccade was being made (1.4%), the saccade was anticipatory (3.7%), the saccade was in wrong direction (2%), or the initial fixation was not within the fixation window around the bars (0.8%).

**Initial fixation position**

Since the experiment involved the presentation of distractor stimuli at very small eccentricities (0.5° and 1°), it was important to first check the position of the initial fixation relative to the initial fixation bars. As shown in the upper panels of Figure 2, the eyes were most often perfectly aligned with the center of the bars, in both the horizontal and the vertical directions, and when there was a deviation, this remained rather small. Horizontal deviations, on average of –0.039° and 0.006° for left- and right-target presentation sides, respectively (mean of absolute deviation: 0.137°), ranged for the most between –0.3° and 0.3°. Vertical deviations, on average of 0.027° (mean of absolute deviation: 0.253°), ranged between –0.7° and 0.7°. A distractor displayed at a theoretical eccentricity of 0.5° on the horizontal axis thus remained in the central, 1° foveal region until the initial saccade was triggered. Its...
Figure 2. Distributions of initial fixation positions in the horizontal direction for left and right target-presentation sides (a-b, d-e, g-h) and in the vertical direction (c, f, i), in Experiments 1 (upper panels), 2a (middle panels), and 2b (lower panels). Fixation positions were grouped into 0.2° bins. For horizontal positions, negative and positive values corresponded to fixations located respectively to the left and to the right of the initial fixation stimulus. For vertical positions, negative and positive values corresponded to fixations located respectively above and below the center of the initial fixation bars.
actual location varied at the most between 0.2° and 0.8° in the horizontal direction and −0.7° and 0.7° in the vertical direction. Furthermore, as revealed in further analyses, the initial eye deviation did not differ between the different display conditions; only the effect of distractor eccentricity on the horizontal fixation position in the experimental condition. \(F(4, 28) = 5.13, p < 0.005\); other \(Fs \leq 3.21\), and the effect of target eccentricity in the control condition, \(F(8, 56) = 2.15, p < 0.05\); other \(Fs \leq 2.45\), were significant, but these did not reveal any consistent pattern.

**Saccade latency**

In the *control condition* where the target stimulus was presented with no distractor, the mean latency of saccades did not vary depending on whether the target appeared to the left or to the right of the fixation stimulus; target side had no significant effect, \(F(1, 7) = 1.73\), and it did not interact with target eccentricity, \(F(8, 56) = 0.85\). As shown in Figure 3a where data were represented across the two presentation sides, saccade latency was relatively stable across the tested range of eccentricities, being on average of about 175 ms (range: 173–182 ms) except when the target was presented near fixation (eccentricity of 1°). In that case, saccade latency was on average 20 ms longer. The effect of target eccentricity was significant, \(F(8, 56) = 4.77, p < 0.0001\), and as confirmed by post-hoc tests, only the 1° eccentricity condition differed significantly from other eccentricities (\(p < 0.005\)).

In the *experimental condition* where the target was displayed simultaneously with a contralateral or foveal distractor, saccade latency was on average longer than in the control condition with no distractor (199 ms). It showed again no main effect of target side, \(F(1, 7) = 2.34\), and no interaction of target side with the other manipulated variables (all \(Fs \leq 1.39\)). More importantly, latency did not vary with D-T distance, \(F(2, 14) = 1.74\). As can be seen in Figure 3b, saccade latency was mainly a function of distractor eccentricity, being gradually shorter as the distractor became more peripheral, \(F(4, 28) = 3.55, p < 0.01\). The interaction between distractor eccentricity and distance was significant, \(F(8, 56) = 2.65, p < 0.01\), and this was due to the much longer latency (212 ms) in the particular case where the distractor was presented at an eccentricity of 3° and the target, 4° away, appeared at an eccentricity of 1° in the opposite hemisphere; recall that a single target presented at an eccentricity of 1° also led to longer latencies (see Figure 3a). When the 3° distractor eccentricity was removed from analysis, the interaction was not significant anymore, \(F(6, 42) = 0.12\). Furthermore, as revealed by post-hoc analyses, the difference between the shortest, 4° distance and 5° and 6° distances was significant only for a distractor eccentricity of 3° (\(p < 0.001\)).

To more directly test the impact of the distractor in the different conditions, we calculated the *mean saccade latency difference* between the experimental and the target-control conditions (see General methods) for the different stimulus configurations. A three-factor analysis of variance was then conducted using the saccade-lateness difference as a dependent variable. Again, target side had no significant effect and did not interact with the other variables (all \(Fs \leq 1.34\), and this time neither the effect of distance nor the interaction between distance and distractor eccentricity was significant, \(F(2, 14) = 0.43\), \(F(8, 56) = 0.49\). The only variable that had a significant influence was the eccentricity of the distractor, \(F(4, 28) = 4.75, p < 0.005\). As illustrated in Figure 3c, the distractor delayed saccade onset irrespective of its location, but the time cost was greater for distractor eccentricities of 1° and less, being maximal when the distractor was presented at the center of the fovea. Paired-sample t-tests confirmed that 29 of the 30 experimental conditions differed significantly from their corresponding target-control condition at least at the 0.05 level (all \(rs \geq 2.55\)).

Previous studies have shown that the shortening of saccade latency in remote distractor cases comes from suppression of saccades triggered early on, within approximately 67–120 ms from stimulus onset (Buonocore & McIntosh, 2008; see also Bompas & Sumner, 2011; Reingold & Stampe, 2002). We checked whether a similar pattern of saccadic inhibition was also present in our data. To this aim, we first plotted the *distributions of saccade latencies* in the no-distractor, control conditions, and then examined how the distribution in each experimental condition departed from its corresponding target-control distribution. Figure 4 shows that all distributions in the control condition were unimodal. They all peaked at latencies of about 160–170 ms, except for the distribution associated with a single target displayed at an eccentricity of 1°, which was overall shifted towards longer latencies and peaked at about 180 ms.

As can be seen in Figure 5, the distributions in the experimental distractor conditions (red) were shifted to the right of their corresponding target-control distribution (blue). However, the distributions associated with central, 0°, and to some extent 0.5°, distractors were more largely spread, and showed a tendency for bi- or even tri-modality. The first, smaller peak resembled the transient dip, characteristic of saccadic inhibition; it suggested that a large proportion of the saccades initiated roughly between 120 and 160 ms from stimulus onset was suppressed. Suppression then gradually reduced, between 160 ms and 180–200 ms, as indicated by the ascending part of the second peak, while early-suppressed saccades likely occurred later, contributing to form the right tail (or additional mode) of the experimental distributions. As distractor ecen-
tricity increased, there was gradually less evidence for a dip, as well as a right, longer tail in the experimental distributions. For 2° and 3° distractors, the almost-perfect rightward shift of the distributions relative to their controls indicated that the likelihood of a saccade was reduced to the same extent over the entire interval running from about 100–120 ms until about 160–200 ms from stimulus onset.

It is unclear whether the shift of the distributions for eccentric distractors could also be attributed to saccadic inhibition. However, the lack of a clear dip and the fact that the experimental distributions departed from their control slightly earlier than with central distractors, irrespective of D-T distance, seems to argue against systematic, transient saccadic inhibition that is time-locked to stimulus onset. Furthermore, since the 1° target-control distribution was shifted relative to the other control distributions in a similar manner and starting at about the same time (i.e., 100–120 ms; see Figure 4), it appears that similar latency profiles can be obtained with or without a distractor.

**Saccade metrics**

The landing position error (see General methods) was measured in the different conditions. As shown in Table 1a and b, saccades were relatively accurate in both the control and the experimental conditions; they undershot the center of the target by only 1/4° on average (0.26° and 0.24° respectively). In the control condition, the undershoot tendency gradually increased with target eccentricity, \( F(8, 56) = 10.76, p < 0.0005 \), going from 1/10° for targets presented at 1° to 1/3° for targets displayed further than 4.5°; it remained unaffected by target side, \( F(1, 7) = 0.09 \). In the experimental condition, the undershoot tendency slightly increased with both the eccentricity of the distractor, \( F(4, 28) = 4.05, p < 0.01 \), and the distance between distractor and target, \( F(2, 14) = 3.71, p < 0.05 \). A closer look at the data, however, revealed that this trend was slightly more pronounced for targets presented in the left hemifield, which tended to be overall less accurate (error range: ±0.1° to ±0.5° and ±0.1° to ±0.3° in left and right conditions, respectively). The effect of target side was only marginally significant, \( F(1, 7) = 4.74, p < \)
but the interactions between target side and distance and target side and distractor eccentricity were significant, $F(2, 14) = 6.93, p < 0.01; F(4, 28) = 4.32, p < 0.001$, respectively, as well as the three-way interaction, $F(8, 56) = 2.40, p < 0.05$.

Comparison of the mean initial landing position between each experimental condition and its corresponding control revealed no clear impact of the presence of a distractor on saccade accuracy. On average, differences ranged between $0.08$ and $0.28$ and as revealed by paired-sample $t$-tests, only 2 of the 30 experimental conditions differed from their control and by only $0.28$: $t(7) = 2.85, p < 0.05$ and $t(7) = 3.66, p < 0.01$; other $ts \leq 1.85$. Thus, as expected, there was no indication of a global effect in the distractor condition.

Discussion

In line with previous reports of the remote distractor effect, the present experiment showed that a distractor displayed at the center of the fovea or in the hemifield contralateral to the saccade target increased saccade latency compared to a condition with no distractor. Furthermore, it revealed that the latency increase in distractor conditions was a function of the eccentricity of the stimuli, but not the angular separation between them. Saccade onset delay was greatest with a distractor at the center of the fovea, and then gradually decreased as the distractor was presented more peripherally, irrespective of how distant distractor and target were. Thus, the angular separation between the stimuli affected neither the magnitude of the distractor effect nor the relationship between the distractor effect and distractor eccentricity.

Walker et al. (1997) previously showed that the relative eccentricity of distractor and target is critical in determining the onset time of a saccade in distractor conditions (see also Griffiths et al., 2006). However, their result relied on manipulation of distractor and target eccentricities only, thus with no control of the distance between the stimuli. Here, we disentangled the effects of the two variables and confirmed in line with the authors’ initial interpretation that the critical variable is indeed the eccentricity of the stimuli, but not their angular separation. The distance between distractor and target in collicular space, that is when foveal magnification was taken into account, did not contribute either. In Figure 6a, we replotted the latency difference (between experimental and target-control trials) but as a function of the estimated collicular distance between distractor and target stimuli (see General methods). In contrast with the prediction of the lateral-interaction hypothesis, the distractor effect did not increase, but decreased as the interstimulus distance became greater, and this was observed only...
Figure 5. Distributions of saccade latencies (in ms) in the experimental (red) versus the target-control trials (blue) of Experiment 1 as a function of distractor eccentricity (rows) and angular separation between distractor and target (columns). Data were represented across left and right target-presentation sides and participants (see General methods).
across distractor-eccentricity conditions; taken separately, the data points corresponding to each distractor eccentricity revealed no consistent variation with collicular distance. Furthermore, the distractor effect decreased in a curvilinear manner with the ratio of distractor to target eccentricity (see Figure 6b), thus replicating Walker et al.’s (1997) previous findings.

These findings are inconsistent with the lateral-interaction hypothesis, at least in its current form (Meeter et al., 2010; Trappenberg et al., 2001; Wilimzig et al., 2006). They cannot assert that the inhibitory influence of contralateral and foveal distractors on saccade latency is not conveyed respectively by cross-collicular and rostro-caudal inhibitory connections. However, they clearly indicate that it is not the extent of the connections that mediates the differential latency increase in different stimulus configurations. It was recently shown in line with the lateral-interaction hypothesis that the remote distractor effect involves the suppression of early saccades (see Buonocore & McIntosh, 2008), and that this so-called saccadic-inhibition phenomenon can only be accounted for by a nonlinear increase of saccade-related activity that results from mutual inhibition of competing signals (Bompas & Sumner, 2011). Here, however, we found only partial evidence for saccadic inhibition; the only conditions that yielded the typical transient dip in the distributions of saccade latencies were those involving a central, 0°- or 0.5° distractor. Furthermore, the onset time of the distractor effect was not time-locked to stimulus onset. It intervened slightly earlier with noncentral than with central distractors, and still 40–60 ms later on average than in previous studies; it also showed no consistent variation with the distance between distractor and target.

The fixation-system hypothesis remains a better candidate to account for the present findings (Findlay & Walker, 1999; Walker et al., 1997). As stimuli became less eccentric and the distractor was presented closer to the fovea than the saccade target, we may assume that a larger population of collicular neurons projecting onto the brainstem, omnipause region was recruited. This raised activity of the fixation system above the level of activity of the move system and shifted the balance towards fixation, thus putting saccadic behavior on hold. The fixation-system hypothesis presents another advantage, that of accounting also for saccade latencies in no-distractor control trials, with exactly the same basic mechanism. The fact that saccade latency was on average 20 ms longer when the target was displayed at an eccentricity of 1° compared to when it was more eccentric (see also Fendrich, Demirel, & Danziger, 1999; Kalesnykas & Hallett, 1994; Weber, Aiple, Fischer, & Latanov, 1992) likely came from the target more greatly eliciting fixation in opposition with saccade-related activity.

### Experiments 2a and 2b: The effect of proximal distractors

As a further test of lateral-interaction and fixation-system hypotheses, the present experiments investigated the effect on saccadic performance of a distractor displayed in the vicinity of an ipsilateral saccade target, as a function of its eccentricity and its distance to the target. The distractor was always displayed within the range of angular distances that typically yield a global

<table>
<thead>
<tr>
<th>Target eccentricity (°)</th>
<th>Left</th>
<th>Right</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
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<td>0.17</td>
</tr>
<tr>
<td>2</td>
<td>0.24</td>
<td>0.28</td>
<td>0.26</td>
</tr>
<tr>
<td>3</td>
<td>0.33</td>
<td>0.32</td>
<td>0.32</td>
</tr>
<tr>
<td>3.5</td>
<td>0.23</td>
<td>0.31</td>
<td>0.28</td>
</tr>
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<td>4</td>
<td>0.31</td>
<td>0.34</td>
<td>0.32</td>
</tr>
<tr>
<td>4.5</td>
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<td>0.36</td>
<td>0.34</td>
</tr>
<tr>
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<td>0.41</td>
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<tr>
<td>5.5</td>
<td>0.31</td>
<td>0.31</td>
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</tbody>
</table>

Table 1a. Mean landing position error (in degrees) in the control conditions of Experiment 1. A value of zero indicated maximal accuracy, positive values indicated that the eyes overshot the target, and negative values corresponded to target undershoot.

### Experiments 2a and 2b: The effect of proximal distractors

<table>
<thead>
<tr>
<th>D-T Distance (°)</th>
<th>Left</th>
<th>Right</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
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<td>0.11</td>
<td>0.10</td>
</tr>
<tr>
<td>2</td>
<td>0.19</td>
<td>0.18</td>
<td>0.19</td>
</tr>
<tr>
<td>3</td>
<td>0.34</td>
<td>0.24</td>
<td>0.29</td>
</tr>
</tbody>
</table>

Table 1b. Mean landing position error (in degrees) in the experimental conditions of Experiment 1. A value of zero indicated maximal accuracy, positive values indicated that the eyes overshot the target, and negative values corresponded to target undershoot.
effect (see Walker et al., 1997), and theoretically also within the presumed range of local excitation, at least in monkeys (i.e., less than 1 mm of collicular space; see Trappenberg et al., 2001). Thus, under the lateral-interaction hypothesis, the distractor was expected to favor saccade averaging and reduce saccade latency in all conditions, though to greater extents for smaller D-T distances. In contrast, the fixation-system hypothesis predicted that a proximal distractor would show a range of effects on saccade latency, from a latency increase to no effect and then possibly facilitation as its eccentricity increased and its distance to the target decreased.

The main difference between Experiments 2a and 2b was with respect to the tested range of distractor eccentricities and D-T distances. Other differences were only minor; they were related to the type of stimulus being used and the distance of the screen on which they were displayed (see General methods). Thus, the two experiments are reported jointly.

Methods
Observers
Eight individuals responding to the same criteria as in Experiment 1 participated in each experiment. In Experiment 2a, all participants, except for the two authors, were unaware of the purpose of the experiment; two had participated in Experiment 1. In Experiment 2b, none but one (the first author) had participated in Experiment 1.

The main difference between Experiments 2a and 2b was with respect to the tested range of distractor eccentricities and D-T distances. Other differences were only minor; they were related to the type of stimulus being used and the distance of the screen on which they were displayed (see General methods). Thus, the two experiments are reported jointly.

Figure 6. Mean saccade latency difference (in ms) as a function of the distance between distractor and target expressed in millimeters of collicular space (a) and as a function of the ratio of distractor to target eccentricity (b) for the different distractor eccentricities in Experiment 1. The collicular distance between the stimuli was estimated based on Ottes et al.'s (1986) logarithmic mapping function of monkeys' SC (see General methods).

Methods
Observers
Eight individuals responding to the same criteria as in Experiment 1 participated in each experiment. In Experiment 2a, all participants, except for the two authors, were unaware of the purpose of the experiment; two had participated in Experiment 1. In Experiment 2b, none but one (the first author) had participated in Experiment 2a.

Design
In both experiments, participants saw all conditions. Their data were analyzed using a repeated-measure design in the experimental and the control conditions respectively. In Experiment 2a, distractor eccentricity had six levels (−0.5°, 0°, 0.5°, 1°, 2°, and 3°), D-T distance had three levels (1°, 2°, or 3°), and target side
had two levels (left vs. right). The target thus appeared at 1 of 10 possible eccentricities (0.5°, 1°, 1.5°, 2°, 2.5°, 3°, 3.5°, 4°, 5°, and 6°) in the right or the left hemifield in both the experimental and the control conditions. Given that there were 20 repetitions of each condition, this resulted in a total number of 1,120 trials (720 experimental trials and 400 control trials), divided into 10 blocks of 112 trials, five with a target to the left and five with a target to the right.

In Experiment 2b, distractor eccentricity had seven levels (−0.5°, 0°, 0.5°, 1°, 1.5°, 2°, or 3°), D-T distance had four levels (1°, 1.5°, 2°, or 3°), and target side had two levels (left vs. right); the target thus appeared in both the experimental and the control conditions at 1 of 11 possible eccentricities (0.5°, 1°, 1.5°, 2°, 2.5°, 3°, 3.5°, 4°, 4.5°, 5°, and 6°) in the right or the left hemifield. There was a total of 1,560 trials (1,120 experimental trials and 440 control trials) that were divided into 20 blocks of 78 trials (10 with a right target and 10 with a left target). In both experiments, the order of the left- and right-target blocks was counterbalanced across participants, and the order of the conditions in each block was randomized. A practice block of 28 and 20 trials in Experiments 2a and 2b, respectively, preceded left- and right-target blocks.

**Results**

Excluded trials (see General methods) corresponded to 16.6% and 17.3% of the total number of trials across participants in Experiments 2a and 2b, respectively. Rejected trials were, for the most part, due to button press before stimulus onset or stimulus onset occurring during a saccade and not during a fixation (4.9% and 6.9% in Experiments 2a and 2b, respectively). Other rejected trials were due to signal artifacts and blinks (4.0% and 3.8%), anticipatory saccades (3.8% and 2.9%), trials with no saccades (2.6% and 2.5%), saccades in the wrong direction (1.8% and 1.4%), and the initial fixation location being outside the fixation window (1.7% and 1.8% respectively). The results of the two experiments were very similar. In the next sections, F values are reported systematically for both experiments, with those obtained in Experiment 2a always first.

**Initial fixation position**

As shown in the middle and lower panels of Figure 2, the position of the eyes during the initial fixation was, as in Experiment 1, quite near the center of the fixation stimulus. In Experiment 2a, the horizontal eye deviation ranged again between −0.3° and 0.3° for both left- and right-target presentation sides (mean: −0.043° and 0.035° respectively; mean of absolute deviation: 0.135°). In Experiment 2b, the horizontal eye deviation was slightly greater, ranging between −0.5° and 0.3°, and it was more radically biased towards the target’s presentation side, though remaining rather small (mean: −0.092° and 0.003° for left- and right-target sides, respectively; mean of absolute deviation: 0.179°). In both experiments, only target side had a significant effect: experimental condition: \( F(1, 7) = 11.32, p < 0.01 \) and \( F(1, 7) = 12.32, p < 0.01 \), respectively; control condition: \( F(1, 7) = 14.03, p < 0.01 \) and \( F(1, 7) = 13.49, p < 0.01 \). For the vertical eye deviation, it ranged between −0.7° and 0.7° in both experiments (mean: 0.085° and −0.049°, respectively; mean of absolute deviation: 0.260° and 0.242°, respectively); none of the effects were significant (all Fs ≤ 1.91 and 1.80).

**Saccade latency**

In the control condition, saccade latency was on average of about 180 and 185 ms in Experiments 2a and 2b, respectively, but it dramatically increased when the target was presented near the center of the fovea; for target eccentricities of 0.5° and 1°, the mean latency was respectively 60 and 20 ms longer (in both experiments) than for larger eccentricities (see Figure 7a, d). Analyses of variance showed no main effect of target side, \( F(1, 7) = 0.40, F(1, 7) = 0.24 \), and no interaction between target side and target eccentricity. \( F(9, 63) = 1.92, F(10, 70) = 0.79 \), but a significant effect of target eccentricity, \( F(9, 63) = 13.55, p < 0.0005 \), \( F(10, 70) = 20.61, p < 0.0005 \). When the two smallest eccentricities were removed from the analysis, the latter effect became nonsignificant, \( F(7, 49) = 1.07, F(8, 56) = 1.49 \). Furthermore, post-hoc tests indicated that in both experiments, the 0.5° eccentricity differed significantly from all other eccentricities (\( p < 0.0005 \)); for the 1° eccentricity, it differed from all, but the 1.5° eccentricity in Experiment 2b (\( p < 0.05 \)).

In the experimental condition, as shown in Figure 7b and e, the mean latency of saccades was longer when the distractor was displayed centrally (at the center of the fovea or at an eccentricity of 0.5° in the opposite or the same hemifield as the target) than when it was more eccentric. In addition, within the range of central distractor locations, saccade latency gradually decreased as the distractor moved from the contralateral, −0.5° location to the ipsilateral 0.5° location. This trend was more pronounced for the smaller angular separations between distractor and target (1° and 1.5°), thus meaning that saccade latency was longer when both the distractor and the target fell in the center of the foveal region. In the most extreme case, i.e., the distractor and the target were displayed at mirror 0.5° locations around the vertical meridian (distance of 1°), saccade latency was on average 100 and 70 ms longer in Experiments 2a and 2b, respectively, than when the distractor, at the same location, appeared with a more
Figure 7. Saccade latency for Experiments 2a and 2b (upper and lower panels respectively). Mean saccade latency (in ms) ± 1 SE in the control condition (a, d) as a function of target eccentricity and across left and right target-presentation sides. Mean saccade latency (in ms) in the experimental condition (b, e) and mean saccade latency difference (in ms; c, f) as a function of distractor eccentricity and D-T distance across left and right presentation sides.
distant target (2° or 3° away). In contrast, when the distractor was presented outside the central region at eccentricities ranging between 1.5° and 3°, saccade latency was mainly a function of D-T distance, being slightly longer for larger distances.

Both the effects of distractor eccentricity and distance were significant. Experiment 2a: \( F(5, 35) = 58.34, \ p < 0.0005 \) and \( F(2, 14) = 13.73, \ p < 0.0005 \), respectively; Experiment 2b: \( F(6, 42) = 46.87, \ p < 0.0005 \) and \( F(3, 21) = 3.61, \ p < 0.05 \), respectively, as well as their interaction, \( F(10, 70) = 25.09, \ p < 0.0005 \), \( F(18, 126) = 20.16, \ p < 0.0005 \), while there was again no main effect of target side, \( F(1, 7) = 0.44, \ F(1, 7) = 0.02 \), and no interaction between target side and the other variables (all \( F_s \leq 1.57 \)). As confirmed by post-hoc tests, the conditions in which a contralateral or foveal distractor was displayed near the target (1°) differed from all other conditions but one across the two experiments (\( p < 0.0005 \)). At the other extreme, the conditions in which a contralateral or foveal distractor appeared at a distance of 3° from the target differed only from the conditions involving a noncentral distractor, i.e., the eccentricity of the distractor was greater than 0.5° and 1°, respectively, in Experiment 2a (\( p < 0.05 \)) and greater than 0.5° in Experiment 2b (\( p < 0.01 \)). On the other hand, trials in which an ipsilateral distractor was displayed at an eccentricity of 0.5° were associated with significantly longer latencies (\( p < 0.05 \)) than most trials with a more peripheral distractor in Experiment 2b; this was true only for 0.5° distractors displayed within 1° from the saccade target in Experiment 2a.

Figure 7c and f presents the mean saccade latency difference between the experimental and the control conditions in the different stimulus configurations. These show that a distractor displayed centrally, from −0.5° to 0.5° locations, increased saccade latency as compared to the control condition with no distractor, with the time cost being greatest for contralateral and then foveal distractors displayed within 1°–1.5° from the target. All paired-sample t-tests contrasting each of the three central-distractor conditions with the corresponding control conditions were significant (Experiment 2a: \( t(8) \geq 3.07, \ p < 0.05 \); Experiment 2b: \( t(6) \geq 2.68, \ p < 0.05 \)). For ipsilateral distractors displayed outside the central region, their impact became progressively less as they appeared further towards the periphery and they were displayed closer to the target, except for the most eccentric, 3° distractors, which tended to facilitate saccade onset when they were presented near the target (1°). In Experiment 2a, only 1° distractors separated from the target by an angular distance of 2° significantly increased saccade latency, \( t(7) = 2.34, \ p < 0.05 \). In Experiment 2b, 1° distractors significantly increased saccade latency when they were displayed within 1°–2° from the target (\( t(8) \geq 2.34, \ p < 0.05 \)), while 1.5° and 2° distractors increased saccade latency only when they were separated from the target by a distance of 3° (\( t(8) \geq 2.46, \ p < 0.05 \)). In addition, 3° distractors when displayed near the target (1° distance) significantly shortened saccade latency, \( t(7) = 2.37, \ p < 0.05 \).

A three-factor analysis of variance using the latency difference as a dependent variable showed again that target side had no significant effect and did not interact with the other variables, except distance in Experiment 2b, \( F(3, 21) = 3.39, \ p < 0.05 \), other \( F_s \leq 1.36 \); the distractor effect was a few milliseconds larger for left compared to right targets, except when distractor and target were separated by a distance of 3° (not shown here). Most importantly, there was a significant effect of distance in Experiment 2a only, \( F(2, 14) = 4.68, \ p < 0.025 \), \( F(3, 21) = 1.61 \), but a significant effect of distractor eccentricity, \( F(5, 35) = 39.68, \ p < 0.0005 \), and a significant interaction between distractor eccentricity and distance, \( F(10, 70) = 5.88, \ p < 0.0005 \), \( F(18, 126) = 2.89, \ p < 0.0005 \), in both experiments. Post-hoc tests indicated that contralateral- and foveal-distractor conditions differed from all conditions involving a distractor displayed outside the central region (eccentricity ≥1°) in both experiments (\( p > 0.0005 \)). They also indicated that 0.5° ipsilateral-distractor conditions differed from most conditions involving a distractor displayed at a large eccentricity (≥2° in Experiment 2b, \( p < 0.05 \); ≥3° in Experiment 2a, \( p > 0.01 \)) and separated from the target by a small distance (1° and 1°–2° in Experiments 2a and 2b, respectively). In addition, they differed from foveal distractor conditions only when these were combined with a small D-T distance (1°–1.5°; \( p < 0.05 \)), while foveal distractor conditions differed only from the condition in which a 0.5° contralateral distractor was displayed at a distance of 1° from the target in Experiment 2a (\( p > 0.0005 \)).

As can be seen in Figure 8, the saccade-latency distributions corresponding to the three central-distractor conditions all showed a rightward shift and a much larger spread compared to the distributions in the corresponding target-control conditions. Most of them tended to be bimodal and exhibited a tendency for a dip at shorter latencies and a longer right tail, suggestive again of saccadic inhibition. Saccadic suppression intervened roughly between 120 and 200 ms from stimulus onset, except when both distractor and target fell within the central 1° region. In those instances, it occurred later, probably simply as a result of the control distribution being shifted towards longer latencies. In the most extreme case, when distractor and target were displayed at mirror, 0.5° locations in opposite hemifields, saccadic inhibition intervened between about 160 and 240 ms from stimulus onset.

In contrast, there was no major distortion of the distributions associated with noncentral distractors. A
Figure 8. Distributions of saccade latencies (in ms) in the experimental (red) versus the target-control trials (blue) of Experiment 2b as a function of distractor eccentricity (rows) and angular separation between distractor and target (columns). Data were represented across left and right target-presentation sides and participants (see General methods). The data of Experiment 2a (not shown here) presented very similar patterns.
number of them were slightly shifted to the right of their target-control distributions from about 120 ms from stimulus onset, and for the distributions associated with 2° and 3° distractors displayed within 1°–1.5° from the target, they lay on top of target-control distributions. The only exception was for 3° distractors displayed at a distance of 1° from the target; in this particular case, the experimental distribution tended to be slightly shifted to the left of the control distribution, mainly as a result of a greater proportion of short-latency saccades initiated between 120 and 170 ms from stimulus onset, thus confirming facilitation.

In Figure 9, the distributions of saccade latencies in control no-distractor trials were replotted in order to re-examine the effect of target eccentricity. The distributions associated with 0.5° and, to a lesser extent, 1° targets were more largely spread and showed a drastic rightward shift relative to the other eccentricity distributions. This came from a great reduction of the proportion of saccades occurring between about 140 and 200 ms from stimulus onset. The great similarity of this pattern and that observed in distractor compared to no-distractor trials in the particular case where an eccentric target was displayed with an ipsilateral 0.5° distractor (Figure 8, Row 3) suggested that stimulation of the central foveal region sufficed to trigger so-called saccadic inhibition.

Saccade metrics

In the control condition, the mean landing position error was relatively small. As shown in Figure 10a and d, saccades towards nearby 0.5° targets were either perfectly accurate or slightly hypermetric (0.03° on average), while saccades towards more eccentric targets were only slightly hypometric even at the largest eccentricities; the error, which increased with target eccentricity, $F(9, 63) = 15.87, p < 0.0005, F(10, 70) = 13.08, p < 0.0005$, was of a maximum of $–0.55°$ and $–0.33°$ in Experiments 2a and 2b, respectively. There was no effect of target side ($F_s \leq 0.26$), but the interaction between target eccentricity and target side was significant, $F(9, 63) = 2.82, p < 0.01, F(10, 70) = 8.09, p < 0.0005$. Right- compared to left-directed saccades were slightly more hypometric at small eccentricities and slightly more accurate at large eccentricities, but the difference between rightward and leftward cases was never greater than 0.2° on average (not shown here).

In the experimental condition, the mean landing position error was larger; it ranged between 0° and $–1.7°$ or $–1.3°$ in Experiments 2a and 2b, respectively, thus indicating that saccades were overall hypometric (see Figure 10b, e). The error was minimal for contralateral and foveal distractors and then gradually increased as the distractor was displayed further towards the periphery in the ipsilateral target hemifield and as the angular separation between distractor and target increased. The effect of distractor eccentricity was significant, $F(5, 35) = 71.55, p < 0.0005, F(6, 42) = 65.69, p < 0.0005$, as well as the effect of D-T distance, $F(2, 14) = 20.85, p < 0.0005, F(3, 21) = 24.69, p < 0.0005$, and the interaction between distractor eccentricity and distance, $F(10, 70) = 11.41, p < 0.0005, F(18, 126) = 8.59, p < 0.0005$. Target side had no effect and did not interact with the other variables (all $F_s \leq 1.52$ and 0.93).

The pattern observed in the experimental condition, but with no comparison to the control condition, gave no clear indication of the distractor or global effect. An increase of the landing position error with the interstimulus distance may indeed simply reflect a shift of the center of gravity of the global visual configuration as a result of the distance between the two stimuli being larger, but without indicating a greater influence of the distractor. This is illustrated in Figure 11, where the distributions of initial landing positions in the different experimental conditions of Experiment 2a were plotted against the distributions in the corresponding distractor- and target-control conditions. In line with the above description, contralateral and foveal distractors clearly failed to produce a global effect; the landing-site distribution in the experimental condition largely overlapped with the target-control distribution and this irrespective of the distance between distractor and target stimuli. Ipsilateral distractors displayed at an eccentricity of 0.5° produced slightly greater eye deviations than the control condition, but generated a modest global effect exclusively when the distance separating distractor and target stimuli was minimal (1°). By contrast, ipsilateral distractors displayed at eccentricities of 2° and 3° yielded a clear global effect and across the whole range of tested D-T distances. At small angular separations, the distribution in the experimental condition formed a unique distribution in between distractor and target-control distributions. As the distance between distractor and target increased, the experimental distribution became larger and more irregular and shifted gradually closer to the target-control distribution, but it failed to perfectly match the target-control distribution even at the largest 3° angular separations. The pattern observed in the 1° distractor condition was intermediate; the global effect, present at the smallest 1° distance, was almost completely resolved at the maximal 3° distance.

A series of paired-sample $t$-tests compared the mean landing position error in each experimental condition with its corresponding target-control condition. All differences were significant at least at the 0.05 level, except for the case of $–0.5°$ and 0° distractors when displayed at a distance of 1° or 3° from the target in Experiment 2a ($t_s \leq 1.53$) and a distance of 1.5°–3° in
Experiment 2b ($t_s \leq 2.11$); the few significant differences for $-0.5^\circ$ and $0^\circ$ distractor cases were still very small in amplitude ($\leq 0.06^\circ$). In a second series of analyses, the GEP (see General methods) was calculated for the different stimulus configurations in order to determine where in between distractor and target stimuli the eyes exactly landed, and in turn better compare the likelihood of center-of-gravity tendencies for different angular separations between distractor and target. As expected, there was absolutely no global effect in the contralateral, $0.5^\circ$ distractor condition; all GEP values approached 100%, thus indicating that the eyes landed at about the same location as when there was no distractor (see Figure 10c, f). The impact of ipsilateral, $0.5^\circ$ distractors remained relatively small as indicated by GEP values of about 90% in most conditions; the only exception was when a small, $1^\circ$ angular distance separated the distractor and the target; in this case, the eyes were more clearly deviated towards the distractor (GEP values of 75% and 84% in Experiments 2a and 2b, respectively). The global effect still became clearer as the distractor was displayed more peripherally; in the most extreme cases, i.e., the distractor and the target were displayed at eccentricities of $3^\circ$ and $4^\circ$, respectively, GEP values approached 50%, thus indicating that on average, the eyes landed almost exactly midway between where they landed when a single stimulus was displayed at target and distractor locations respectively.

Both the effects of distractor eccentricity and D-T distance were significant, Experiment 2a: $F(4, 28) = 65.69, p < 0.0005$ and $F(2, 14) = 8.68, p < 0.005$, respectively; Experiment 2b: $F(5, 35) = 43.11, p < 0.0005$ and $F(3, 21) = 4.86, p < 0.01$, respectively; the interaction was also significant in Experiment 2a, $F(8, 56) = 2.15, p < 0.05$, but only marginally significant in Experiment 2b, $F(15, 105) = 1.66, p < 0.07$. Target side again had no effect ($F_s \leq 0.61$) and did not interact with the other variables (all $F_s \leq 2.04$ and 1.73). Post-hoc tests revealed that contralateral as well as ipsilateral $0.5^\circ$ distractor conditions differed from all conditions involving a more eccentric distractor ($p < 0.05; p < 0.0005$), except the $1^\circ$ distractor condition in Experiment 2a ($p > 0.06$), thus confirming the specificity of central distractors. Still, the two conditions differed from one another in most cases; seven of the nine comparisons in Experiment 2a and 9 of the 12 comparisons in Experiment 2b were significant at least at the 0.05 level.

**Discussion**

It was previously reported that when a distractor is displayed in the vicinity of an ipsilateral saccade target, the eyes are deviated towards an intermediate location between the two stimuli, while saccade latency remains unaffected (e.g., Walker et al., 1997). The present...
Figure 10. Saccade Metrics - Experiments 2a and 2b (upper and lower panels, respectively). Mean landing position error (in degrees) ± 1 SE in the control condition (a, d) as a function of target eccentricity across left and right target-presentation sides. Mean landing position error (in degrees) in the experimental condition (b, e) and GEP (c, f) as a function of distractor eccentricity and D-T distance across left and right target-presentation sides.
Figure 11. Distributions of initial landing positions (in degrees) in experimental (red) versus distractor- and target-control trials (gray and blue) of Experiment 2a, separately for the different distractor eccentricities (rows) and the different angular separations between distractor and target (columns), but across left and right target-presentation sides.
findings revealed that this is not a general rule. Proximal distractors showed a continuum of effects depending on their eccentricity, and to a lesser extent, their angular separation to the saccade target. A distractor appearing within 1° from the center of the fovea, but in the same hemifield as a more eccentric saccade target, significantly delayed saccade onset irrespective of its distance to the target. Its effect remained smaller compared to the effect of a foveal or contralateral distractor, particularly when this was presented with a near target that also fell in the central 1° region. It also contrasted with the effect of more eccentric ipsilateral distractors (1.5°–3°), which tended to delay the onset of saccades to distant targets, but less largely, and had no impact or even shortened the latency of saccades to nearby targets. Conversely, while an ipsilateral distractor displayed at an eccentricity of 0.5° only slightly deviated the eyes away from the target, even when it was separated from the target by a minimal distance of 1°, more eccentric distractors generated a clear global effect; this became gradually less likely as the angular separation between the stimuli increased.

The observed modulations of the distractor effect with stimulus eccentricity and interstimulus distance were, for the most part, inconsistent with the lateral-interaction hypothesis. First, the finding that ipsilateral distractors most often delayed saccade onset or simply had no effect was opposite to the prediction that ipsilateral distractors presented within short and presumably excitatory ranges from the saccade target would speed up the execution of an averaging saccade. Second, the time penalty observed when the target was displayed with a distractor in the central 1° region was unlikely due to lateral inhibition. Indeed, the suppression of a proportion of relatively early saccades underlay not only this effect, but also the lengthening of saccade latency when a single target was displayed with no distractor in the central 1° region. Furthermore, as suggested by electrophysiological findings, rostro-rostral connections may be mainly excitatory (e.g., Munoz & Istvan, 1998). This may suggest that in the particular case where both the target and the distractor appeared in the central 1° region, the drastic latency increase was the effect of lateral, excitatory interactions that further enhanced the activity of a fixation gating system.

The possibility remains that the lack of systematic facilitation of saccade onset time with proximal distractors came from most distractor and target stimuli having rather small eccentricities and from their separation on the collicular map being too large due to foveal magnification. However, as shown in Figure 12a and b where the data of Experiment 2b were replotted as a function of the collicular distance between the stimuli, this was unlikely the case. As the collicular distance became larger, the distractor effect on saccade latency evolved from a modest shortening of saccade latency to a gradually greater latency increase (r = 0.55, p < 0.0025). Still, the relationship did not hold within distractor-eccentricity conditions, except the 3° eccentricity condition (r = 0.97, p < 0.05; other rs ≤ 0.88), thus suggesting that the overall trend was mainly a result of distractor eccentricity but not collicular distance. A similar pattern was observed for the likelihood of saccade averaging. The GEP showed an overall increase with collicular distance (r = 0.64, p < 0.0005), meaning therefore that saccade averaging became progressively less likely. However, GEP values exhibited little variation with collicular distance for a given distractor eccentricity (all rs ≤ 0.92, p > 0.08).

In contrast, as revealed in Figure 12c and d, both the latency difference and the GEP showed, in line with the fixation-system hypothesis, a clear relationship with the ratio of distractor to target eccentricity (r = −0.51, p < 0.005 and r = −0.40, p < 0.05, respectively). As the ratio increased, the distractor delayed saccade onset to gradually smaller extents, having no effect, and even a slight facilitating influence for ratio values of 0.6 and above. The very few marginal data points (in blue) corresponded to instances where both the distractor and the target fell within the central 1° region; ratios were of 1 and 0.5, but the time penalty was maximal. This likely came to fixation activity being more greatly enhanced in those particular instances (see above). Conversely, saccade averaging became gradually more likely as the ratio of distractor to target eccentricity increased. The only exception came from the contralateral 0.5° distractors, which yielded no global effect at all; this was due to saccade averaging being unlikely to occur between stimuli presented in contralateral hemifields (see Walker et al., 1997).

The reciprocal effect of proximal distractors on the latency and the accuracy of saccades is illustrated in Figure 13, where the mean saccade latency difference was plotted against the GEP. This shows that a reduction of the global effect (or an increase of GEP values within the range of 50%–100%) was associated with an increasingly disturbing influence of the distractor on saccade onset time (r = 0.96, p < 0.0005). In other words, as the eyes landed closer to the target, the likelihood the distractor increased saccade latency became gradually more likely. This was consistent with the hypothesis that fixation and move system compete in determining when the eyes move.

Given the reciprocal relationship between the distractor effect on saccade latency and saccade accuracy, the possibility remains that the reduced likelihood of a global effect with distractors displayed near the center of the fovea came from saccade latency being longer in those instances (or vice versa). This was
examined in Figure 14 where the landing position error in both the experimental and the control conditions of Experiment 2b were plotted as a function of saccade latency for the two smallest 1° and 1.5° angular separations between distractor and target and separately for different distractor eccentricities. As reported above, the global effect, which could be visualized by the shift of the red compared to the blue dots, was greater for more eccentric distractor and target stimuli. It also tended to be greater for shorter-latency saccades in the case of nonfoveal distractor and target stimuli; landing position errors were larger and more widely spread for early-triggered saccades compared to longer-latency saccades (e.g., McSorley & Findlay, 2003; for a review see Vitu, 2008). However, within a given time interval (e.g., 150–200 ms), the proportion of averaging responses was clearly less with distractors displayed within the central 1° region than with more peripheral distractors. Thus, reduction of the global effect with less eccentric stimuli could not entirely result from a speed-accuracy trade-off.

A more plausible explanation of the overall pattern of saccade latency is in terms of balance of activity between fixation and move systems. We may speculate that as ipsilateral distractor stimuli were presented closer to the fovea and/or further away from a more eccentric saccade target, the level of neuronal activity in the rostral pole of the SC and in the brainstem omnipause region gradually increased, which in turn further delayed saccade onset. This came with a reduction of the likelihood of a global effect probably because neurons in the rostral pole of the SC pause during the execution of a larger range of saccades compared to neurons located more caudally, with the most rostrally-located neurons reducing their discharge for saccades as small as 3° (Anderson et al., 1998).
Saccade averaging was thus less likely, and the eyes failed to land exactly midway between distractor and target stimuli.

**General discussion**

In the last two decades, two alternative hypotheses have been proposed to account for the generation of saccadic eye movements. The first predominant, neural-field view assumes that when, as well as where, the eyes move results from lateral, neuronal interactions within the intermediate layers of the SC, which integrate exogenous and endogenous inputs in a retinotopically-organized map (Godijn & Theeuwes, 2002; Trappenberg et al., 2001; Wilimzig et al., 2006; see also Arai, Keller, & Edelman, 1994; Kopecz & Schoner, 1995; Meeter et al., 2010; van Opstal & van Gisbergen, 1989). The second, fixation-system hypothesis proposes that a saccade is initiated only once the activity of a fixation gating system falls down below a given threshold (Findlay & Walker, 1999). As will be discussed below, the present findings provide a number of arguments against the former lateral-interaction account, while suggesting that fixation-type mechanisms intervene to determine when, and possibly also where, the eyes move.

**On the limited role of lateral interactions**

The hypothesis proposed in neural-field models that lateral interactions play a main role in saccade generation relies on presumed evidence for short-range, excitatory and long-range, inhibitory connections within the intermediate layers of the SC, and the additional assumption that these determine the onset time of saccades in complex visual displays. When the saccade target is displayed with a remote distractor, long-range inhibition of neuronal activity at the target location would delay saccade onset; conversely, when the target appears with a proximal distractor, the local spread of excitatory activity would facilitate the initiation of a saccade to an intermediate location in space. There was so far only weak evidence for this hypothesis and several neural findings previously challenged this view. First, long-range inhibition was revealed using electrical micro-stimulation, while this technique presents the disadvantage of activating fibers of passage from outside the SC. Furthermore, as suggested by in-vitro studies, there might not be long-range, monosynaptic inhibition in the SC (Lee & Hall, 2006), and multi-synaptic inhibition may be at work only in the superficial layers of the SC (see Isa & Hall, 2009). On the other hand, several studies failed to observe an increase of saccade latency as a result of long-range neuronal inhibition (Dorris et al., 2007; see Figure 13. Mean saccade latency difference (in ms) plotted as a function of the GEP across distractor eccentricities, D-T distances, and target side. Only the data of Experiment 2b are presented here, but the data of Experiment 2a showed the same pattern.
Figure 14. Landing position error (in degrees) in both the experimental (red) and the corresponding target-control conditions (blue) of Experiment 2b as a function of saccade latency (in ms) for the different distractor eccentricities and two sample D-T distances, 1° (upper panels) and 1.5° (lower panels). Each data point corresponded to the landing position error of a given individual on a given trial.
also Watanabe et al., 2005). Here, we did not record neuronal activity, but our behavioral findings were opposite to the predictions made by the lateral-interaction hypothesis for the effect of remote as well as proximal distractors.

First, in contradiction with the hypothesis that long-range inhibition underlies the effect of remote distractors, the saccade-latency increase that results from the presentation of a contralateral distractor was found to be a function of the relative eccentricity of distractor and target stimuli (see also Griffiths et al., 2006; Walker et al., 1997), but not their angular separation nor their distance in collicular space. Second, in contradiction with the hypothesis that short-range excitation determines both where and when the eyes move, an ipsilateral distractor displayed near the target failed to systematically shorten saccade latency, while still deviating the eyes from the target. As distractor eccentricity increased, and to a lesser extent as the distance between distractor and target decreased, the likelihood of a global effect became gradually greater, while a gradient of effects on saccade latency was observed from a latency increase to no effect and then facilitation. The tested angular separations between distractor and target were within the range of angular distances which typically yield a global effect (1°–3°; see Casteau & Vitu, 2009; Walker et al., 1997), but also within the presumed range of local excitation, when converted in millimeters of collicular space (<1 mm; e.g., Trappenberg et al., 2001). We still checked whether the (greater) latency-increase as well as the reduction of the global effect with central distractors did not result from the interstimulus distance in collicular space being greater than for more eccentric stimuli. However, as for remote distractors, the collicular distance was a much poorer predictor of the distractor effect than the ratio of distractor to target eccentricity.

One limitation of these and the above analyses is that they relied on conversion of angular distance in millimeters of collicular space, using Ottes et al.’s (1986) logarithmic mapping function of the SC in monkeys, while there is no evidence so far that the same mapping function describes the geometry of the SC in humans. It remains also unclear whether the presumed range of lateral excitation and inhibition is comparable between monkeys and humans. However, the great similarity of the properties of saccades in monkeys and humans (see Findlay & Walker, 1999), as well as the fact that the maximal separation angle for a global effect is comparable in humans (Ottes et al., 1985) and monkeys (Chou et al., 1999), suggests that similar principles may underlie saccadic behavior in both species.

On the other hand, one may still argue in the framework of neural-field models that the greater impact of remote distractors when they were displayed closer to the fovea came from the signal associated with the distractor being possibly stronger, due to foveal magnification, and the competition with the weaker signal of the more peripheral target being unfair (see also Tam, 1999), due to stronger lateral inhibition. However, controlling for the interstimulus distance in collicular space probably also allowed us to equate the strength of the signal associated with different distractor locations, and as we have seen, this did not neutralize the effect of distractor eccentricity. In addition, a similar assumption cannot be made for the case of proximal, ipsilateral distractors. Since in that case, cooperative, but not competitive, mechanisms were a priori involved, the presumably stronger signal associated with a less eccentric distractor should have further reduced saccade latency, and more greatly deviated the eyes from the saccade target. Our findings were exactly opposite to this prediction.

Finally, the recent finding that contralateral distractors induce suppression of early-triggered saccades (Buonocore & McIntosh, 2008), and the additional fact that so-called saccadic inhibition is best predicted based on a nonlinear rise of neuronal activity has recently been taken as evidence for a role of lateral interactions in saccade generation (Bompas & Sumner, 2011). Here, the effect of remote as well as proximal distractors displayed in the central 1° region came with marked changes in the distributions of saccade latency, namely a transient dip at early time intervals and a tail (or additional mode) towards longer latencies, which suggested early saccadic inhibition and later recovery. However, there was no clear evidence of transient saccadic inhibition for the case of peripheral distractors displayed remotely from the saccade target, while these overall delayed saccade onset. Furthermore, the onset time of the effect of remote and proximal distractors was not time-locked to stimulus onset as would be expected under monosynaptic inhibition, nor a function of the distance between distractor and target as could be predicted by multi-synaptic inhibition. Rather, the effect emerged at variable times depending on the eccentricity of the distractor; it intervened gradually later as the distractor (as well as the target) appeared later as the distractor (as well as the target) appeared closer to the fovea, and also as saccade latency in the corresponding, no-distractor control condition was overall longer. More importantly, the drastic latency increase observed when a single target was displayed at an eccentricity of 0.5°, but with no distractor, came with a distortion of the saccade-latency distribution, which was very similar to that observed with central distractors. Thus, saccadic inhibition again intervened, but this time in the absence, a priori, of a competing signal. This suggested that saccadic inhibition as revealed by saccade-latency distributions may not be diagnostic of competitive mechanisms relayed by
lateral inhibition, while confirming that lateral inhibition does not determine when the eyes move.

**Favoring a fixation-system hypothesis**

The hypothesis that a saccade is initiated only when the activity of a fixation gating system falls down below a certain threshold relies on the finding that neurons in the brainstem omnipause region exhibit tonic discharge during visual fixation, but remain silent during the execution of saccades (see Findlay & Walker, 1999; Walker et al., 1997). Neurons in the rostral-pole region of the SC were originally found to exhibit similar characteristics (Munoz & Wurtz, 1993a, 1993b). However, more recent findings suggested that these so-called fixation neurons may form, together with saccade-related neurons, only one single population exhibiting a rostral-to-caudal continuum of discharge characteristics (Anderson et al., 1998; Krauzlis et al., 1997) and selectivity to saccade amplitude (Hafed et al., 2009; Hafed & Krauzlis, 2012). The omnipause region maintains the eyes’ stillness by inhibiting the brainstem excitatory and inhibitory burst neurons, which directly project on motor neurons. It receives excitatory projections from regions of the SC encoding eccentricities up to about 10° (Büttner-Ennever et al., 1999) or even beyond (Gandhi & Keller, 1997), but the majority of the projections comes from the rostral pole (see also Paré & Guittton, 1994). This makes it a privileged system to account for the observed relationship between stimulus location and the effect of remote as well as proximal distractors on saccade latency. It also presents the advantage to account, with the same mechanisms, for the drastic saccade-latency increase observed when a single target is displayed in the central 1° region, compared to when it is displayed more peripherally.

We propose in line with Findlay and Walker’s (1999) model of saccade generation that when a saccade is generated results from competition between the omnipause fixation system and a move system. A visual stimulus, distractor, or target would first generate saccade-related activity in the motor map of the SC, and due to excitatory projections to the omnipause fixation system, would also generate fixation-type activity, but mainly when it appears within about 10° of eccentricity, and to gradually larger extents as it is presented closer to the fovea. The raise of activity in the fixation system would potentially delay saccade onset, all depending on the corresponding level of activity in the move system. When a single target is presented with no distractor, the balance would most often quickly shift towards movement, except when the target is displayed centrally and activity of the fixation system is in turn strongly enhanced. In this particular case, fixation would be favored and saccade onset would be delayed (see also Fendrich et al., 1999; Kalesnykas & Hallett, 1994; Weber et al., 1992). When an additional distractor stimulus is displayed at a remote location from the saccade target, fixation activity would also be enhanced, compared to a condition with no distractor, and gradually more as the distractor is displayed closer to the fovea, and closer to the fovea than the target. In turn, saccade onset would be delayed, and gradually more as the ratio of distractor to target eccentricity decreases (see also Griffiths et al., 2006; Walker et al., 1997). However, as shown here, the latency increase would be greatest when both distractor and target stimuli are displayed in the central 1° region (for related findings see Vitu, 2008; Vitu et al., 2006), possibly as a result of the slight overlap of the neurons’ receptive fields across the vertical midline (see Goldberg & Wurtz, 1972) and/or rostro-rostral excitatory connections (e.g., Munoz & Istvan, 1998). These would reinforce neuronal activity in the rostral pole of the SC, and in turn the brainstem omnipause region, but more greatly than when only the distractor falls in the central region.

The shift towards fixation or movement would, however, be more subtle when an ipsilateral distractor is displayed near the saccade target. Indeed, as a result of distributed spatial coding in the SC and possibly short-range excitation (e.g., McIlwain, 1975, 1982), saccade-related activity in the distractor/target area would be increased, though to slightly various extents depending on the exact distance between the stimuli as well as their location (see below), and it would in turn more largely compete with fixation activity. This would favor some equilibrium between fixation and move systems that would most often result in no saccade-latency change compared to a no-distractor control condition. The balance would more radically shift towards fixation only when activity in the omnipause region is optimally enhanced, such as when the distractor is displayed in the central 1° region or it is slightly more eccentric (1.5°–2°), but relatively distant to the target (3°), as suggested by the latency increase in these conditions. Reversely, the balance would shift towards movement, and saccade onset would be slightly facilitated when the distractor would be more radically peripheral and the inter-stimulus distance minimal (here, 3° × 1°).

Thus, the reason why most previous studies failed to reveal a proximal-distractor effect on saccade latency was probably simply due to the tested range of stimulus eccentricities and/or inter-stimulus distances, which did not allow the balance to shift towards fixation or movement. In addition, previous studies, unlike ours, used rather long fixation periods before distractor and target onset (i.e., ≥500 ms compared to 30–53 ms on average here). Under the additional assumption that the activity of the fixation system returns to a resting level after being active for too long, these long fixation
periods may have contributed to favor movement at the expense of fixation, and reduced in turn the likelihood that subtle changes in the level of fixation/move activity modulate saccade onset time. However, previous report of an inhibitory influence of proximal and remote distractors on saccade latency in a 200-ms gap task (Weber & Fischer, 1994), thus when fixation was likely disengaged at stimulus onset, seems to argue against this assumption. Furthermore, the effect of remote distractors in the present study was quite comparable to that previously reported by Walker et al. (1997), despite fixation periods varying between 500 and 1000 ms in their study. This suggests that the initial level of fixation activity may not be that critical in determining the impact distractors have on saccade onset time.

The remote distractor effect was replicated in a number of studies using different variants of Walker et al.’s (1997) original paradigm (e.g., Benson, 2008; Born & Kerzel, 2008; Honda, 2005; Ludwig, Gilchrist, & McSorley, 2005; Sumner, Adamjee, & Mollon, 2002; Walker, Mannan, Maurer, Pambakian, & Kennard, 2000; White, Gegenfurtner, & Kerzel, 2005). One particular study, reported by White et al. (2005), was interpreted most favorably in terms of visual saliency, but could be another manifestation of the fixation-move balance. This revealed that the effect on saccade latency of a foveally-centered distractor patch decreased as the patch became greater in size (but see Vitu et al., 2006). It may well be that as the extent of the distractor increased, the omnipause fixation system was being activated to gradually smaller extents in comparison with the move system, which in turn progressively reduced its potentially inhibitory influence on saccade initiation. On the other hand, the finding by the same authors, that a distractor displayed along the vertical meridian and remotely from the saccade target failed to delay saccade onset irrespective of distractor eccentricity, could also be interpreted in terms of balance between fixation and move systems. Since stimuli displayed on the vertical meridian project in both colliculi (Goldberg & Wurtz, 1972), it could well be that the distractor not only reinforced fixation, but also saccade-related activity in the target hemifield, thereby having little influence on saccade onset time. Thus, it appears that the fixation-system hypothesis can potentially account for a larger range of findings than previously thought.

Accounting for modulations of the global effect

The global effect is a very robust phenomenon that is classically interpreted in terms of distributed spatial coding in the SC (but see Edelman & Keller, 1998). Whether the interplay between short-range excitation and long-range inhibition within the SC is a necessary condition for the global effect remains an open question. Van Opstal and van Gisbergen (1989) showed that this may indeed be the case (for recent behavioral evidence, see Tandonnet, Massendari, & Vitu, 2012). However, the global effect may also simply arise from weighted averaging of the entire active population in the SC (see Findlay, 1982; Findlay & Walker, 1999; Lee, Rohrer, & Sparks, 1988; Meeter et al., 2010; Robinson, 1972). The present data did not distinguish between these alternative hypotheses, and the possibility remains that lateral interactions determine where, but not when, the eyes move. Still, the gradual reduction of the likelihood of a global effect that was observed as ipsilateral distractors were presented closer to the fovea may suggest that other mechanisms intervene.

We previously reported that a foveal distractor stimulus fails to deviate the eyes from a more eccentric ipsilaterial target when it extends within less than 1.25° from the center of the fovea, thus suggesting a foveal deadzone for the global effect (Vitu, 2008; Vitu et al., 2006). Here, we found a global effect with ipsilateral distractors in the central region, but this was greatly reduced as compared to the effect of more eccentric distractors. Importantly, neither the present findings nor previous data could be interpreted in terms of speed-accuracy trade-offs. Reduction of the global effect with central distractor stimuli was thus not a result of saccade onset being delayed in those instances. Rather, this likely reflected the fact reported by Anderson et al. (1998) that neurons in the rostral pole of the SC pause during the execution of a larger range of saccades and hence contribute less to saccade averaging. Whether this must be regarded as another manifestation of fixation-type mechanisms remains, however, an open question.

Conclusion

Not only remote, but also ipsilateral, distractors displayed in the vicinity of a saccade target can affect saccade latency. While remote distractors systematically delay saccade onset, proximal distractors show a range of effects from a latency increase to a latency decrease, as well as modulations of the likelihood of a global effect. The variable that accounts best for the whole range of remote and proximal distractor effects is the relative eccentricity of distractor and target stimuli, but not the distance between them. When the eyes move towards an eccentric target stimulus thus seems to be under the control of a fixation gating system, while lateral interactions within the collicular map may play only a minor role.
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