When larger visual distractors become less disruptive: Behavioral evidence for lateral inhibition in saccade generation

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How neuronal activity is integrated over time may largely rely on excitatory and inhibitory mechanisms. Dynamic neural field models assume that local excitation and lateral inhibition (i.e., the "Mexican hat") shape the output of neural networks. Most models of saccade generation assume that such interactions in the superior colliculus play a key role in determining both the metrics and the latency of saccades. Here, we investigated the role of lateral inhibition in saccade metrics in humans. We used a saccade target task in which a visual distractor line was presented close to a peripheral visual target (i.e., a small circle). Models assuming lateral inhibition predict that beyond a critical size larger distractors induce less perturbation than smaller ones. To assess this prediction, we varied the length of the distractor. Results confirmed that a distractor presented along with the target deviated the saccade’s landing position away from the target. This perturbation increased with distractor length but only up to a critical size as the effect reversed for larger distractors, leading to a reduced perturbation on saccade metrics. These results suggest that larger distractors induce a neuronal activity pattern wide enough to involve lateral inhibition, thereby decreasing the distractor’s weight in the spatial integration of distractor and target locations. They are consistent with a critical role of lateral inhibition in the computation of saccade metrics.

Keywords: human, lateral inhibition, saccade metrics, saccadic eye movement, superior colliculus


Introduction

How neuronal activity is integrated over time may largely rely on excitatory and inhibitory mechanisms. Dynamic neural field models assume that local excitation and lateral inhibition (i.e., the “Mexican hat”) shape the output of neural networks (e.g., Amari, 1977). This is also a key assumption in the majority of models of saccade generation, which account for the metrics and/or the latency of saccadic eye movements based on lateral interactions within a “map” of the type found in the intermediate and the deeper layers of the superior colliculus or SC (Arai & Keller, 2004; Kopecz & Schöner, 1995; Meeter, Van der Stigchel, & Theeuwes, 2010; Trappenberg, Dorris, Munoz, & Klein, 2001; van Opstal & van Gisbergen, 1989; Wilimzig, Schneider, & Schöner, 2006; but see Findlay & Walker, 1999). These models rely on neurophysiological investigations suggesting that there are lateral interactions in the SC (e.g., McIlwain, 1982; Meredith & Ramoa, 1978; Munoz & Istvan, 1978; for a review, see Isa & Hall, 2009). Lateral interactions presumably operate across as well as within the colliculi, with intra-collicular connections conveying different signals depending on their extent; short-range connections spread excitation to neighboring sites while long-range connections inhibit remote locations. Such local excitatory and distant inhibitory interactions would reshape the neuronal activity profile that initially builds up as a result of visual stimulation. They would favor over time, in conjunction with endogenous influences, the emergence of a single peak of activity in the deeper layers of the SC, thereby determining where the eyes move.

Lateral interactions provide a privileged framework to account for saccadic behavior when several stimuli are simultaneously displayed in the visual field and, hence, when several sites in the collicular map are initially active. First, as originally shown by Van Opstal and Van...
Gisbergen (1989), lateral interactions can account for saccade averaging (see also Arai & Keller, 2004; Kopecz & Schöner, 1995; Wilimzig, Schneider, & Schöner, 2006). This phenomenon, also referred to as the global effect, reflects the tendency for the eyes to execute a saccade of an average amplitude and direction when two sites in the deeper layers of the SC are electrically stimulated (Robinson, 1972) or two (or more) visual elements are simultaneously displayed at nearby locations in space (Coren & Hoenig, 1972). As the eyes move closer to the largest or the brightest stimulus of a pair, one commonly describes the effect as a tendency to land near the center of gravity of the visual configuration formed by the stimuli (Deubel, Wolf, & Hauske, 1984; Findlay, 1982; Findlay, Brogan, & Wenban-Smith, 1993). Due to the interplay between short-range excitatory and long-range inhibitory interactions, the initially two active peaks would merge into a single, more or less central peak of activity that would trigger in turn the execution of a saccade to an intermediate location in space.

The reciprocal of the global effect is the remote distractor effect (Walker, Deubel, Schneider, & Findlay, 1997; see also Lévy-Schoen, 1969). It reveals that saccade latency is inflated, but saccade accuracy remains unaffected, when the saccade target is presented simultaneously with a distractor stimulus appearing outside a ±20° region around the saccade target axis. As first suggested by Olivier, Dorris, and Munoz (1999) and later implemented by Trappenberg, Dorris, Munoz, and Klein (2001; see also Meeter et al., 2010; Wilimzig et al., 2006), lateral interactions could also account for this phenomenon. Neuronal activity at the distractor location would generate inhibition at the distant, target location (see also Dorris, Olivier, & Munoz, 2007) and vice versa, thus delaying the onset of the saccade until the conflict is resolved.

The assumption that lateral interactions determine saccadic performance in two-stimulus visual displays still remains a matter of debate and the characteristics of lateral interactions at the neural level are subject to controversies. Several studies point against a clear dissociation in the extent of excitatory and inhibitory monosynaptic connections within the intermediate layers of the SC (Lee & Hall, 2006). Other recent in vitro experiments show that multisynaptic local excitation and long-range inhibition with a “Mexican hat” profile can be observed in the superficial layers but not in the intermediate layers of the SC (Phongphanhanee et al., 2009; for a review, see Isa & Hall, 2009). On the other hand, at the behavioral level, it is not established without ambiguity that the remote distractor effect reflects lateral inhibition within the SC. There is evidence that the lengthening of saccade latency in remote distractor conditions comes from suppression of early triggered saccades, as reflected by a dip in the distributions of saccade latencies, which is time-locked to distractor onset and intervenes on average some 93 ms after stimulus appearance (Buonomore & McIntosh, 2008; see also Reingold & Stampe, 2002). As recently shown by Bompas and Sumner (2011), this suppression pattern, classically referred to as saccadic inhibition, is best captured by neural field models that involve a non-linear rise of saccade-related activity, thus consistent with a role of mutual inhibition between competing signals associated with distractor and target. At the same time, the fact that distractors displayed near the saccade target do not yield a reduction of saccade latency compared to when the target is presented with no distractor (Bompas & Sumner, 2011; Walker et al., 1997) sheds some doubts on the notion that short-range excitation contributes to determine saccade latency.

Furthermore, the possibility remains that the remote distractor effect is unrelated to lateral inhibition in the SC and purely reflects competition between fixation and saccade-related activities (Walker et al., 1997; see also Findlay & Walker, 1999). Given that inter-collicular inhibition is weaker than intra-collicular inhibition (e.g., Munoz & Itsvan, 1978), the effect of a distractor displayed in the hemifield contralateral to the target should be smaller compared to the effect of an ipsilateral, though remote distractor. To the contrary, the original data of Walker et al. (1997) revealed that remote distractors displayed in the opposite or the same hemifield as the target were equally disruptive, their impact on saccade latency being mainly a function of their proximity to the fovea and their eccentricity as compared to that of the saccade target. As “fixation” neurons are more densely distributed in the rostral pole region of the SC than in more caudal parts (Munoz & Wurtz, 1993a, 1993b; see also Gandhi & Keller, 1997), Walker et al. proposed that the distractor effect comes from enhanced fixation activity and/or a greater mobilization of omnipause neurons in the brainstem reticular formation. Still, note that “fixation” neurons in the SC were found to be no functionally different from saccade-related neurons (Krauzlis, Basso, & Wurtz, 1997).

On the other hand, it is not clear yet whether lateral inhibition is necessary to account for saccade metrics. The model proposed by van Opstal and van Gisbergen (1989) predicts saccade averaging based on the interplay between short-range excitation and long-range inhibition, but this does not necessarily imply that lateral inhibitory interactions are obligatory for a global effect to occur. As suggested by several authors, the global effect may arise from distributed coding in the SC and the fact that neurons in the superficial and deeper layers of the SC have large and overlapping receptive or movement fields (see Deubel et al., 1984; Findlay, 1982; Findlay & Walker, 1999; Lee, Rohrer, & Sparks, 1988). Stimuli displayed at nearby locations in the visual field would activate overlapping population of neurons, thus with some neurons responding to different stimuli. The weighted average of saccade-related discharges of the whole active population would determine the end point of the saccade and hence promote saccade averaging. Such an overlapping mechanism,
which could possibly involve short-range excitatory interactions (see McIlwain, 1975, 1982), may thus be sufficient to account for saccade averaging, that is, in the absence of long-range inhibitory interactions.

Studies on the trajectories of saccades do not seem to provide further evidence for lateral inhibition. They have revealed differences between distractor and no distractor conditions, namely, showing that saccades curve toward and away from the distractor (for a review, see van der Stigchel, Meeter, & Theeuwes, 2006). Deviations toward have been shown to be causally related to competitive activity within the deeper layers of the SC, but this does not seem to involve lateral inhibition (McPeek, Han, & Keller, 2003). The mechanisms underlying deviations away are less clear and possibly involve the frontal eye fields (FEFs) as a source of top-down inhibition (van der Stigchel et al., 2006). As recently shown with transcranial magnetic stimulation, the FEF may modulate the distractor-related deviation of saccade trajectory (Walker, Techawachirakul, & Haggard, 2009). In sum, it remains unclear whether intra-collicular inhibition contributes to determine where as well when the eyes move.

In the present study, we reexamined the role of lateral inhibition in saccade metrics. To this aim, we tested one strong prediction of neural field models in a global effect paradigm, namely, that larger distractor stimuli, at least beyond a critical size, should induce smaller deviations of the eyes from the saccade target. This prediction directly derives from the presumed “Mexican hat” type of neuronal activity profile and previous electrophysiological findings showing that neurons in the superficial layers of the monkey’s SC are inhibited when the visual stimulation exceeds the extent of their receptive fields (Goldberg & Wurtz, 1972). Thus, as stimuli become greater in size, their initially wider neuronal activity profile shrinks due to lateral inhibition. Saccade-related activity at the stimulus location is in turn reduced and should be less likely to shift the saccade end point. To our knowledge, there is at present no behavioral evidence for this prediction. Only a few studies investigated the influence of stimulus size on the accuracy of saccades in two-stimulus visual displays and results were exactly opposite to the prediction as they revealed greater eye deviations toward the largest stimulus of a pair (Findlay, 1982; Findlay et al., 1993). However, in these studies, the manipulations of stimulus size were rather small, as the angular extent of the stimuli ranged from 0.2° to 0.4° for the smallest and largest tested stimuli, respectively. Furthermore, since the stimuli were 2-dimensional, square stimuli, they extended further toward and away from the other target element, and the observed effect of stimulus size was merely an effect of the location of the stimulus boundaries (see Findlay et al., 1993). Here, we controlled for this potential confound while testing a larger range of stimulus sizes.

A saccade target task was used, in which participants were presented with a to-be-looked-at peripheral target at variable locations on the horizontal meridian, with or without a less eccentric distractor. As the distance between the distractor and the target affects spatial averaging (e.g., Ottes, van Gisbergen, & Eggermont, 1985), the size of the distractor was varied only in its vertical dimension while the horizontal distance between distractor and target was held constant. The distractor was expected to deviate the participants’ eyes away from the target, but the question was whether the deviation would decrease with increasing distractor size. Under the assumption that lateral inhibition contributes to saccade averaging, larger distractors were expected to be less disruptive than smaller ones, while the absence of lateral inhibition predicts that distractors would more largely deviate the eyes as they would become greater in size. Our data showed a smaller deviation for larger distractors beyond a critical size, consistent with the involvement of lateral inhibition in the computation of saccade metrics.

### Methods

#### Participants

Participants were eight volunteers (two males and six females, aged 23–30 years, mean: 26 ± 1) who reported having normal vision. They were naive with regard to the purpose of the experiment. They were paid for their participation. Informed consent was obtained according to the Declaration of Helsinki.

#### Apparatus

The movements of the right eye were recorded with a 5th generation Dual-Purkinje Image Eye Tracker (Fourward Optical Technologies), which samples eye position at a frequency of 1000 Hz and with a spatial resolution of 10 min of arc (Cornsweet & Crane, 1973). The eye tracker was interfaced with two IBM-compatible microcomputers. The first computer recorded the eye movement parameters and analyzed them online, using the software developed by Van Rensbergen and de Troy (1993); this computer was interfaced with a response button. The second computer controlled the visual presentation of the stimuli. Eye movement parameters were continuously sent to the second computer, so that the visual display could be changed contingent on the position of the eyes. Visual stimuli were presented on a 17-in. CRT monitor with 60-Hz refresh rate. Vision was binocular.

#### Trial events and task

Figure 1 illustrates the displayed stimuli. Each trial started with the presentation of a fixation cross (0.4°,
Figure 1. Illustration of the stimuli for the condition with the longest distractor and target eccentricity of 6°. Here, the relative size (in degrees of visual angle) of fixation cross (Fix., 0.4°), distractor line (Distr., 4°), and target circle (Targ., 0.2°) was scaled as well as the relative distance between them; target eccentricity was 6° or 7.5° and the distance between distractor and target was 3°. The red vertical arrows indicate the various distractor lengths (0.3°, 0.8°, 1.9°, and 4°).

Figure 2, where the mean landing position of the initial saccade in distractor trials, expressed relative to no distractor trials, was plotted as a function of distractor length for the two target eccentricities. Here, we see that 0.8-degree distractors tended to deviate the eyes more greatly than 0.3-degree distractors, at least for the most eccentric targets. Importantly, for distractor lengths above 0.8°, the tendency reversed, such that longer distractors produced smaller eye deviations; this was the case irrespective of target eccentricity.

Statistical analysis confirmed this pattern. The effect of distractor length on the difference in landing positions between distractor and no distractor trials was significant ($F(3,21) = 5.68, p < 0.01$) as well as the effect of target eccentricity ($F(1,7) = 34.48, p < 0.01$) and the interaction between these factors ($F(3,21) = 5.47, p < 0.01$). Planned comparisons combining both eccentricities revealed that the deviation increased with increasing distractor length (for 0.3° to 0.8°, $F(1,7) = 6.69, p < 0.05$), but this effect then reversed with further increase of distractor length (for 0.8° to 1.9°, $F(1,7) = 9.16, p < 0.05$, and for 1.9° to 4°, $F(1,7) = 5.65, p < 0.05$). Post hoc tests performed for each eccentricity showed that this pattern tended to be less pronounced for the 6-degree eccentricity (see Figure 2), but not for the 7.5-degree eccentricity.

Results

Initial landing positions

In the no distractor (control) condition, saccades were relatively accurate, but in line with previous reports (for a review, see Becker, 1989), target undershoot remained prominent particularly with more eccentric targets (on average 0.2° for the 6-degree eccentricity and 0.8° for the 7.5-degree eccentricity). Still, the main question was whether, as predicted by the lateral inhibition hypothesis, longer distractors can be less disruptive than smaller distractors. The response is provided in Figure 2, where the mean landing position of the initial saccade in distractor trials, expressed relative to no distractor trials, was plotted as a function of distractor length for the two target eccentricities. Here, we see that 0.8-degree distractors tended to deviate the eyes more greatly than 0.3-degree distractors, at least for the most eccentric targets. Importantly, for distractor lengths above 0.8°, the tendency reversed, such that longer distractors produced smaller eye deviations; this was the case irrespective of target eccentricity.

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difference being significant only between 0.3- and 4-degree distractors ($p < 0.01$), as well as between 0.8- and both 1.9- and 4-degree distractors ($p = 0.03$ and $p < 0.01$, respectively). For the 7.5-degree eccentricity, the difference was significant between 0.3- and 0.8-degree distractors ($p < 0.01$), as well as between 0.8- and 1.9- ($p = 0.04$) and 1.9- and 4-degree distractors ($p = 0.01$).

As illustrated in Figure 3, both the conventional and the reverse distractor size effects were present in almost all participants. The critical distractor length at which the effect reversed still slightly varied across individuals.

**Saccade latencies**

Saccade latency on distractor and no distractor trials was, on average, 204 and 203 ms, respectively. As shown in Figure 4, saccade latency did not greatly vary between the different distractor conditions, except between 0.3- and 0.8-degree distractors; saccadic reaction times tended to be longer with 0.3-degree distractors and, to a greater extent, in the 7.5-degree eccentricity condition. The effect of distractor length on the latency difference between distractor and no distractor trials was significant ($F(3,21) = 15.87, p < 0.01$) as well as the interaction between
distractor length and eccentricity ($F(3,21) = 3.81, p = 0.03$), but there was no main effect of eccentricity ($F(1,7) = 1.76, p = 0.23$). Post hoc tests confirmed that the smallest distractors (0.3°) led to longer reaction times than longer distractors (0.8°, 1.9° and 4°) for both the 6- (6 ms on average, $p = 0.02, p < 0.01$, $p < 0.01$, respectively) and the 7.5-degree eccentricity (10 ms on average, $ps < 0.01$). In addition, they showed that saccade latencies were shorter for the 7.5- than for the 6-degree eccentricity for all distractor lengths (4 ms on average, $p < 0.01, p < 0.01, p = 0.04$, respectively) except the smallest one ($p = 0.29$), thus indicating that the decrease of saccade latency for distractor lengths above 0.3° was more pronounced in the far eccentricity condition.

Note that the reduction of saccade latencies for distractor lengths above 0.3° could potentially account for the greater eye deviation observed with 0.8- compared to 0.3-degree distractors, but it could not be at the origin of the reverse distractor size effect on initial landing positions (see Figure 2). Indeed, this effect, observed for distractors between 0.8° and 4° in length, was not associated with a modulation of saccadic reaction times, thus suggesting that it was not due to a speed–accuracy trade-off.

**Landing positions by saccade latency**

Further analyses were conducted to examine the contribution of saccade latency to both conventional and reverse distractor size effects but also to assess how this dual effect unfolds over time. Estimating when, following stimulus onset, the effect emerged is critical as it may provide further evidence for the lateral inhibition account. As lateral inhibition may be quickly effective (e.g., Munoz & Istvan, 1978), the reverse distractor size effect may already be present in the shortest latency saccades. In Figure 5, mean initial landing positions were plotted for the different conditions but separately for two saccade latency bins. The two bins were defined after splitting each individual’s distribution of saccade latencies at its median; this varied from 163 ms to 242 ms across individuals and was on average 199 ms (Figure 5A: the fastest saccadic reaction time (SRT) bin; Figure 5B: the slowest SRT bin). Note that, due to the above data selection criterion, the fastest SRT bin comprised latencies from 80 ms to the individual’s median. Data in both saccade latency bins replicated the overall pattern, namely, a greater eye deviation with 0.8- compared to 0.3-degree distractors and a reverse distractor size effect for distractor lengths above 0.8°; note that the two effects were more pronounced with more eccentric stimuli in both time intervals.

In the fastest SRT bin (Figure 5A), there was no main effect of distractor length ($F(3,21) = 1.63, p = 0.21$) but an interaction between distractor length and eccentricity ($F(3,21) = 4.97, p < 0.01$), as well as an effect of target eccentricity ($F(1,7) = 7.00, p = 0.03$). Post hoc tests revealed that for the 6-degree eccentricity, the deviation was less pronounced for the distractor of 4° than for the smaller distractors (0.3°, $p < 0.01$; 0.8°, $p < 0.01$; 1.9°, $p = 0.03$); for the 7.5-degree eccentricity, the difference was significant between 0.3- and 0.8-degree distractors ($p < 0.01$), as well as between 0.8- and 4-degree distractors ($p = 0.02$), and there was a trend for a difference between 1.9- and 4-degree distractors ($p = 0.06$).

In the slowest SRT bin (Figure 5B), both the effects of target eccentricity and distractor length were significant ($F(1,7) = 26.22, p < 0.01$ and $F(3,21) = 11.15, p < 0.01$, respectively), but the interaction failed to reach significance ($F(3,21) = 2.29, p = 0.11$). Post hoc tests revealed that: for the 6-degree eccentricity, the difference was significant between 0.8- and 1.9-degree distractors ($p = 0.03$), as well as between 0.8- and 4-degree distractors ($p = 0.01$) and 0.3- and 4-degree distractors ($p = 0.04$). For the 7.5-degree eccentricity, the difference was significant between 0.3- and 0.8-degree distractors ($p = 0.04$), 1.9- and 4-degree distractors ($p = 0.01$), and 0.3- and 4-degree distractors ($p = 0.04$), and it was marginally significant between 0.8- and 1.9-degree distractors ($p = 0.08$).

**Discussion**

In the present study, we investigated the role of lateral inhibition in saccade generation. We used a saccade target task in which a peripheral target was, on some trials, simultaneously displayed with a less eccentric but spatially proximal distractor. This paradigm is known to yield a...
global effect (or saccade averaging) that is a deviation of the eyes toward an intermediate location between the stimuli. Models of saccade generation can account for saccade averaging based on local excitation and lateral inhibition within the SC (e.g., van Opstal & van Gisbergen, 1989; Wilimzig et al., 2006). Still, it remains undetermined whether lateral interactions are a necessary condition for the global effect to occur and, more generally, whether lateral interactions indeed underlie the computation of saccade metrics. We thus tested the prediction derived from neural field models that, due to lateral inhibition, larger distractors can be less disruptive than smaller ones; for this, the saccade target, a small circle, was presented with or without a thin distractor line of variable length. Our results confirmed the prediction of the models; they showed that as distractors became greater in size they first induced slightly greater eye deviations, but above a critical size they gradually produced less deviation. These findings are consistent with a critical role of lateral inhibition in the computation of saccade metrics. In the following, we first discuss the dual distractor size effect in relation with previously reported findings. We then detail how lateral inhibition likely shaped both the accuracy and the latency of saccades in our experimental setup and finally consider the possible role of top-down inhibition.

**Dual effect of distractor size**

Previous findings have shown that the tendency to move the eyes toward the center of gravity of the peripheral configuration is weighted by the size and the luminance contrast of the stimuli; the eyes are more largely deviated toward the largest or the brightest stimulus of a pair (Deubel et al., 1984; Findlay, 1982; Findlay et al., 1993). Here, we confirmed such a relationship between stimulus size and the eyes’ initial landing position for a range of rather small stimulus lengths (0.3–0.8°), comparable to the range of stimulus sizes tested in previous studies (0.2–0.4°; Findlay, 1982; Findlay et al., 1993).

This conventional, stimulus size effect is consistent with an account of the global effect in terms of lateral interactions within the SC. When two separate but neighboring sites in the collicular map are simultaneously activated, neuronal activity progressively builds up at an intermediate location due to the local spread of excitation. This pulls the eyes between the two visual stimuli but where exactly depends on the relative strength and width of the two initial peaks of neuronal activity. Stimulus size is one contributing factor; the boundaries of larger stimuli being further apart, the resulting peak of activity may be more widely spread and may in turn deviate the eyes further than in the case of smaller stimuli (e.g., Findlay et al., 1993). In our case, however, we cannot rule out that the greater eye deviation observed with 0.8° in opposition with 0.3-degree distractors was at least partly due to the eyes being launched more quickly when distractors were 0.8 degree long (Figure 4). Indeed, as reported in several previous studies, the global effect is quite pronounced for early triggered saccades but progressively reduces as saccade latency increases (e.g., Ottes et al., 1985; for a review, see Vitu, 2008).
The novel finding was the reverse distractor size effect observed for distractor lengths above 0.8°; larger distractors induced smaller eye deviations compared to smaller distractors. Speed–accuracy trade-offs could not account for the effect. First, the gradual reduction of the eye deviation as distractor length increased from 0.8° to 4° was not accompanied by an increase of saccade latency. Furthermore, an analysis of the eyes’ initial landing positions separately for short- and long-latency saccades revealed that the effect was already present in the first half of the distribution of saccadic reaction times. The present data thus extended previous findings by revealing that above the classically tested range of stimulus sizes, stimulus size has a reverse effect on saccade metrics.

**Lateral inhibition**

The assumption that there are short-range excitatory interactions within the SC has received strong empirical support (e.g., McIlwain, 1982; for a review, see Isa & Hall, 2009). These excitatory interactions are likely at work when two spatially proximal stimuli are simultaneously presented in the periphery. They can account for most previous reports of the global effect, although they may not be a necessary condition, as suggested by the alternative population-coding assumption (see Findlay & Walker, 1999; Lee et al., 1988). Lateral inhibitory connections within and across the SC have also been reported (McIlwain, 1982; Meredith & Ramoa, 1978; Munoz & Istvan, 1978; for a review, see Isa & Hall, 2009), but whether these contribute to determine both the metrics and the latency of saccadic eye movements, as assumed in neural field models, has not been unambiguously determined. As previously demonstrated by the model of van Opstal and van Gisbergen (1989), lateral inhibition could, in combination with local excitation, play a critical role in reshaping neuronal activity in two-stimulus cases and in producing in turn saccade averaging. However, to our knowledge, there is not yet similar behavioral evidence; previous investigations of the global effect in humans did not provide any evidence for a role of lateral inhibition. The finding that the global effect cancels out when stimuli are too far apart (e.g., Ottes et al., 1985; Walker et al., 1997) does not necessarily imply a role of lateral inhibition, as it may simply reflect the limited spatial extent of the spread of excitation. The same limitation would apply to our data if the distractor effect had remained unchanged for distractor sizes above a critical threshold. However, we found that for distractor lengths greater than about 0.8°, the eye deviation became gradually smaller as the length of the distractor increased. This clearly suggests, in line with the prediction of neural field models, that lateral inhibition was involved and contributed to determine saccade metrics.

We used vertical lines as distractor stimuli in order to hold the distance between the boundaries of distractor and target stimuli constant irrespective of distractor length. Still, as distractor lines became longer, their extremities were further apart from one another as well as further away from the target. Neurons coding for the extremities of long distractor lines were thus more likely to inhibit each other. They were also more likely to inhibit neural activity at the target location and reversely to receive inhibition from target-related neurons. Both intra-distractor inhibition and inter-stimulus inhibition potentially contributed to reduce the impact of longer distractor lines, although intra-distractor inhibition was probably more likely. Indeed, increased inhibition of target-related activity should have delayed saccade onset, thereby producing longer latencies with longer distractors. In contrast, saccade latencies were found to be comparable when distractors subtended 0.8° of visual angle or more. Moreover, our pattern of findings showed striking similarity with previously reported variations of neuronal activity in the superficial layers of the SC as a function of stimulus size (Goldberg & Wurtz, 1972). This suggested that the observed reduction of the global effect with increasing distractor size mapped a gradual reduction of neuronal activity as the distractor stimulus extended beyond the neurons’ receptive field and, hence, reflected intra-distractor inhibition. Since “Mexican hat” local excitation and long-range inhibition seem to operate in the superficial but not in the deeper layers of the SC (Isa & Hall, 2009), we may even speculate that the reverse effect of distractor size originated from lateral inhibition within the superficial layers of the SC.

Further evidence for an account in terms of intra-distractor inhibition comes from the critical angle at which our distractor stimuli yielded a reverse effect of size; this was in the range of previous estimations of maximal inter-stimulus angles for a global effect. The distance between the ends of 1.9-degree distractors displayed at eccentricities of 3° and 4.5° corresponded to windows of about 35° and 24° around the horizontal meridian. In Walker et al.’s (1997) study, the global effect cancelled out when the distractor was displayed outside a ±20-degree window around the horizontal target axis. In Ottes et al.’s (1985) study, the global effect greatly reduced for inter-stimulus angles above 30°. Thus, the present results suggest that the previously reported reduction of the global effect for angles greater than about 30° did not only reflect a reduced spread of excitation but also increased inhibition.

**Dissociating lateral and top-down inhibition**

As proposed in models of saccade generation, top-down or endogenous projections also influence the metrics of saccadic eye movements (Findlay & Walker, 1999; Meeter et al., 2010; Trappenberg et al., 2001). Top-down modulations were likely at work in our study as variations of distractor size inevitably modified the visual similarity between distractor and target. As the distractor line became longer, it was less and less similar to the target and, hence, easier to discriminate. Distractor-related activity could, in
turn, be more easily suppressed or target-related activity enhanced, thereby reducing the global effect. The remote distractor effect was found to be greater for physically congruent distractor and target stimuli (Born & Kerzel, 2009; 2011). The same could be true for the reciprocal, global effect. The dual distractor size effect in the present study may thus have resulted from the combination of the conventional relationship between distractor size and eye deviation and an opposite distractor–target similarity trend. We must acknowledge that we cannot rule out such a contribution of visual similarity and top-down processes associated with target selection.

However, we see two reasons why top-down inhibition might not explain our findings. First, if the gradually smaller eye deviation with increasing distractor size was due to a progressively easier target discrimination/selection process, then saccade latency should decrease accordingly, as observed in previous studies (e.g., Born & Kerzel, 2009), and it should be further reduced for more visible and hence less eccentric distractor and target stimuli. To the contrary, saccade latencies remained in the same range across distractor lines of 0.8° to 4°, and they were longer for less eccentric distractors and targets. Note that the same was not true in a study reported by White, Gegenfurtner, and Kerzel (2005) where the saccade target stimulus (a small Gabor patch) was presented simultaneously with a centrally displayed patch of pink noise; as the distractor patch became greater in size, saccade accuracy remained unaffected, but saccade latency gradually reduced, to become almost as short as that observed on no distractor trials. This pattern of data more likely reflected top-down inhibition of a progressively less salient, background-like distractor stimulus, although lateral inhibitory interactions remained a viable alternative.

The second reason why we think our data do not reflect top-down inhibition is related to the observed time course of the reverse distractor size effect. This emerged rather early on, being present in saccades with median latencies as short as 186 ms, and hence with a number of saccades being triggered much earlier than 186 ms. The relative earliness of the effect is consistent with the assumption made in neural field models that lateral inhibition, as a basic low-level mechanism, takes place relatively quickly following stimulus onset; it is also in agreement with electrophysiological studies suggesting monosynaptic inhibition (Munoz & Istvan, 1978). It appears however more difficult to reconcile with the relative slowness of target selection processes, as suggested by the persistence of the global effect with visually dissimilar distractor and target stimuli until about 250 ms following stimulus onset (e.g., McSorley & Findlay, 2003). Moreover, recent studies showed that humans can discriminate peripheral objects extremely rapidly, within 100–120 ms from stimulus onset. However, this applies mainly to a restricted set of very specific objects such as faces and, to a lesser extent, animals, when they are presented simultaneously with contralateral dissimilar visual stimuli (e.g., landscape scenes) but not to stimuli that are visually more complex or less ecologically relevant such as vehicles (Crouzet, Kirchner, & Thorpe, 2010; Kirchner & Thorpe, 2006). In the present study, non-ecological geometrical shapes (a vertical thin line for the distractor and a small circle for the target) were used; in addition, stimulus pairs were displayed in the same hemifield, which showed that they were more prone to lateral masking or crowding (Bouma, 1970). It thus appears unlikely that specific and rapid visual discrimination processes occurred and could account for the present pattern of results. If top-down inhibition associated with visual discrimination and target selection processes was involved at all, this probably accounted only for the reversed distractor size effect observed in saccade with relatively long latencies. Further research will still be necessary to precise the respective contributions of top-down processes and lateral inhibitory mechanisms.

Finally, given the resemblance of our findings with the electrophysiological data reported by Goldberg and Wurtz (1972) on the effect of stimulus size on collicular activity, we made the speculative assumption that our reverse distractor size effect operated as early as within the superficial layers of the SC. To our knowledge, there is no evidence that cortical projections to the superficial layers of the SC except from the visual cortex, while the intermediate and deeper layers do receive numerous cortical projections (for review, see Isa & Sparks, 2006). If our assumption appeared to be valid, then it would be evidence that top-down endogenous inhibitory influences did not contribute to the reverse effect of distractor size.

**Acknowledgments**

This research was supported by two French-German ANR-DFG Grants (ANR-07-FRAL-014 and ANR-10-FRAL-009-01).

Commercial relationships: none.
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