

The spatial coding of the inhibition evoked by distractors

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Abstract

It is generally agreed that saccade deviations away from a distractor location represent inhibition in the oculomotor system. By systematically manipulating the location of a distractor we tested whether the inhibition of the distractor is coded coarsely or fine-grained. Results showed that the location of a distractor had an effect on the saccade trajectories, suggesting that the amount of inhibition observed depends on the location of the distractor. More specifically, the vertical distance of the distractor from fixation seems to be a determining factor. These findings have important implications for models that account for inhibition in the target selection process and the areas that could underlie inhibitory influences on the superior colliculus (SC), like the frontal eye fields (FEF) and the dorsolateral prefrontal cortex (dlPFC). Finally, the initial direction and the endpoint of a saccade were found to be strongly correlated, which contradicts recent models proposing that the initial saccade direction and saccade endpoint are unrelated.

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1. Introduction

In order to explore our environment, we continuously make fast eye movements called saccades. The decision on the exact target location of an eye movement involves resolution of the competition between the different elements in the visual scene. The competition between possible saccade goals is assumed to be resolved on a common motor map located in the intermediate layers of superior colliculus (SC) (Schall, 1991; Sparks & Hartwich-Young, 1989). This mid-brain area receives both visual (bottom-up) and task related (top-down) signals and integrates those signals on a motor map. Bottom-up visually evoked signals reach the SC from posterior cortical areas. For instance, cortical area V1 has fast projections to the intermediate layers of the SC (Schiller, Malpeli, & Schein, 1979). Top-down task related signals originate from areas in the frontal lobe, such as the dorsolateral prefrontal cortex (dlPFC) and the frontal eye fields (FEF). Responses in the dlPFC and the FEF are known to be responsive to task demands (Bichot & Schall, 2002; Pierrot-

Deseilligny, Milea, & Muri, 2004; Pierrot-Deseilligny, Muri, Nyffeler, & Milea, 2005) and both project to the SC (Goldman & Nauta, 1976; Graybiel & Ragsdale, 1979; Huerta, Krubitzer, & Kaas, 1986; Yeterian & Pandya, 1991).

It is thought that these top-down signals may involve both the activation of the appropriate target location and/or the inhibition of irrelevant ‘distractor’ locations (Godijn & Theeuwes, 2002; Tipper, Howard, & Jackson, 1997). Influence of the dlPFC seems to be primarily inhibitory (Lynch & Tian, 2006), while the FEF seems to select one location as the target by activating corresponding neural populations and by inhibiting neurons corresponding to distractor locations (Schlag-Rey, Schlag, & Dassonville, 1992).

A number of recent studies have addressed the spatial coding of inhibition (McSorley, Haggard, & Walker, 2004, 2005; Van der Stigchel & Theeuwes, 2005). These studies used saccade trajectory deviations as a measure to investigate the spatial coding of inhibition. Indeed, saccade trajectory deviations are assumed to reflect the competition between the different possible target locations in the SC (Godijn & Theeuwes, 2002; McPeck, Han, & Keller, 2003; McSorley et al., 2004; Trappenberg, Dorris, Munoz, & Klein, 2001) (for a recent review see,

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Van der Stigchel, Meeter, & Theeuwes, 2006). More specifically, saccades that deviate away from a location typically have been attributed to inhibitory processes (Godijn & Theeuwes, 2002; McSorley et al., 2004; Shelliga, Riggio, & Rizzolatti, 1994; Tipper et al., 1997; Van der Stigchel et al., 2006). Inhibition of a location causes the weighted eye movement vector to be shifted away from the inhibited location, leading to deviation away from that location. The amount of deviation away from a location is assumed to be a reflection of the amount of inhibition applied to that location: the stronger the inhibition, the greater the deviation away will be. For instance, in visual search experiments in humans, saccade trajectories have been found to deviate away from a distractor location (Godijn & Theeuwes, 2002; Walker, McSorley, & Haggard, 2006). However, this deviation away was stronger when the distractor was similar to the target compared to when they were dissimilar (Ludwig & Gilchrist, 2003). When a distractor was similar to the target, the distractor evoked stronger competition (Ludwig & Gilchrist, 2002) leading to stronger inhibition (Tipper et al., 1997).

Because saccade trajectories represent the strength of inhibition, they constitute an important tool that allows the investigation of the spatial coding of the inhibitory signal. If the inhibitory signal is sensitive to the distractor location ('fine grained'), there should be differences in saccade trajectories to a target for different spatial distractor locations. However, if the signal is not sensitive to the distractor location ('coarse'), there should be no differences between the trajectories across different distractor locations.

To investigate the spatial coding of distractor related inhibition, McSorley et al. (2004) systematically varied the distractor-to-target and distractor-to-fixation spatial separation. They found no clear relation between saccade deviations and the distractor location. Although distractors presented in the same hemifield as the target evoked more deviation away than distractors in the opposite hemifield, finer-grained influences of the distractor location were not observed. On the basis of this finding, they concluded that distractor related inhibition is not highly spatially specific. This issue was further explored in a subsequent experiment with a small number of participants performing a large number of trials (McSorley, Haggard, & Walker, 2005). This set-up made it possible to examine individual differences in the spatial coding of the inhibition signal. Although for some subjects saccade deviation away did decrease with increasing distractor distance from the target, this effect was reversed for other observers. Similar to the previous study, they observed no modulatory effect of the distractor location on the saccade trajectory. Again, these results seemed to indicate that there is no general spatially specific distractor related inhibition.

In contrast to McSorley et al. (2004, 2005), we recently showed that the location of a distractor can have a modulatory effect on the saccade trajectory (Van der Stigchel & Theeuwes, 2005). Our paradigm had two possible distractor

locations. One was positioned close the target and the other was located close to fixation. Results showed that saccade trajectories tended to deviate towards the distractor location when this distractor was presented close to the target, whereas trajectories deviated away from distractor when presented close to fixation. So, in contrary to findings of McSorley et al. (2004, 2005) we did observe differences in saccade trajectories for different distractor locations. Specifically, we showed that presenting a distractor close to the target resulted in a relative lack of inhibition. For these saccades, a 'global effect' was observed in that the saccade landed in between the target and distractor location (Coren & Hoenig, 1972; Findlay, 1982). Such an 'averaging' saccade indicates the relative absence of inhibition, because the competition between the target and the distractor is not resolved, resulting in a movement that is an average of the two movement vectors.¹

There are a number of possible ways to explain these differences in modulator inhibition effects. Contrary to the experiments of McSorley and colleagues (2004, 2005), in the study that did find a modulatory effect on saccade trajectories, participants knew the exact location of the upcoming target in advance (Van der Stigchel & Theeuwes, 2005). The purpose of this manipulation was to make inhibitory mechanisms more pronounced in the target selection process. Recent studies have indicated that if the target location is known in advance, top-down inhibitory processes are more pronounced (Van der Stigchel et al., 2006; Walker et al., 2006), which might result in finer-grained inhibition.

In addition in our study both target and distractor were presented with an abrupt onset (Van der Stigchel & Theeuwes, 2005). This was not the case in the study of McSorley et al. (2004), in which only the distractor was presented with abrupt onset. This difference could account for their lack of a global effect for distractors presented close to the target location. Because the global effect has been attributed to the merging of two peaks in the SC (Glimcher & Sparks, 1993; Van Opstal & Van Gisbergen, 1990), it is possible that the global effect is only observed when target and distractor are presented simultaneously.

Besides these differences in experimental set-up, it is possible that the findings of McSorley et al. (2004) and of Van der Stigchel and Theeuwes (2005) are in fact consistent. It may be that Van der Stigchel and Theeuwes (2005) showed that the location of a distractor modulates the mere presence of inhibition and not its strength, as for only one of the two distractors locations inhibitory components were present (as reflected by trajectory deviations away from the distractor location). In that case, their results did not give an answer about the spatial nature of the inhibition evoked by distractors. The present study was designed to answer this question.

¹ It should be noted that averaging saccades are no direct evidence for the complete lack of inhibition. It might be that the inhibition is present but overwhelmed by excitation, resulting in averaging saccades.

In order to investigate the spatial coding of inhibition, the distractor was presented at one of six possible positions. All six locations were positioned outside the 20° zone in which averaging saccades are normally observed (Walker, Deubel, Schneider, & Findlay, 1997). As explained above, averaging saccades are caused by a relative absence of inhibitory components. Because our goal was to investigate inhibition, averaging saccades were not of interest in the current study. The target location was indicated in advance and both target and distractor were presented with abrupt onset.

Three measures of saccade trajectories were used: initial direction, peak deviation, and saccade endpoint. By doing this, we were able to explore on what part of the saccade trajectory the influence of the distractor location might be observed. It also enabled us to investigate the recent claim that initial saccade direction and saccade endpoint are unrelated and controlled by separate mechanisms (McSorley et al., 2004; Quaia, Optican, & Goldberg, 1998). These studies proposed that initial saccade direction is controlled by the SC, whereas the cerebellum corrects possible deviations from the target direction. If these two processes are indeed distinct, initial saccade direction and saccade endpoint should be unrelated.

2. Methods

2.1. Participants

Twelve students of the Vrije Universiteit, aged between 18 and 35 years old, served as paid volunteers. Five participants were male. All reported having normal or corrected-to-normal vision and could discriminate the colors used in the experiment. They were naïve as to the purpose of the experiment. All persons gave their informed consent prior to their inclusion in the study.

2.2. Apparatus

A Pentium IV computer with a processor speed of 2.3 GHz controlled the timing of the events and recorded response times. Displays were presented on an Iiyama 21" SVGA monitor with a resolution of 1024×768 pixels and an 85-Hz refresh rate. A second computer controlled the registration of eye movements' data on-line. Eye movements were registered by means of a video-based eye tracker (SR Research Ltd, Canada). The Eyelink2 system has a 500 Hz temporal resolution and a spatial reso-

lution of 0.01° . The system used an infrared video-based tracking technology to compute the pupil center and pupil size of both eyes. An infrared head mounting tracking system tracked head motion. Both eyes were monitored, but only data from the left eye was analyzed. An eye movement was considered a saccade either when the movement velocity exceeded $35^\circ/\text{s}$ or when the movement acceleration exceeded $9500^\circ/\text{s}^2$. Although the system compensates for head movements, the participant's head was stabilized using a chin rest. The distance between monitor and chin rest was 75 cm. Participants performed the experiment in a sound-attenuated and dimly lit room.

2.3. Stimuli

See Fig. 1 for an illustration of the display sequence. All figures were presented in light gray (CIE x,y chromaticity coordinates of .291/.314; 26.4 cd/m^2) on a black background (0.0 cd/m^2). Each trial started with the presentation of a 'star' character ($0.27^\circ \times 0.27^\circ$) in the center of the screen that functioned as the fixation stimulus. After 600 ms a line segment ($0.14^\circ \times 0.83^\circ$) appeared directly above or below the fixation position ('cue'). A delay of 800–1300 ms then occurred followed by the onset of the target (a light gray filled circle with a diameter of 0.56°). The target location was related to the direction of the cue: if the cue was positioned above fixation, the circle was presented 7.19° above the fixation point. If the cue was positioned below fixation, the circle was presented 7.19° below fixation point. Simultaneously with the target onset, a light gray diamond shape distractor ($0.83^\circ \times 0.83^\circ$) appeared. The distractor was always positioned on the same upper or lower hemifield as the target, either to the left or to the right from the target onset. For each target location, there were 12 possible distractor locations: six locations on the left side and six on the right. Distractor locations on the left had the same distance from fixation as the corresponding locations on the right. The six conditions are listed in Fig. 2. For each site, the vertical distance of the 'Close Vertical' distractor locations was 2.78° from fixation and 4.42° from the target location. For the 'Far Vertical' distractor locations, the vertical distance was 5.56° from fixation and 1.64° from the target location. The horizontal distance from fixation was 4.17° ('Close Horizontal'), 5.56° ('Middle Horizontal') or 6.94° ('Far Horizontal'). The sequence of trials was randomized for each participant.

2.4. Procedure and design

Participants first received oral instructions. They were instructed to fixate the center fixation point until target onset and to then move their eyes to the target location. It was stressed that one had to make a single accurate saccade towards the target element. The experiment consisted of a training session of 24 trials and an experimental session of 600 trials. Each session started with a nine-point grid calibration procedure. Participants were required to saccade towards nine fixation points sequentially appearing at random in a 3×3 grid. In addition, simultaneously fixating the center fixation point and pressing the space bar recalibrated the system by zeroing the

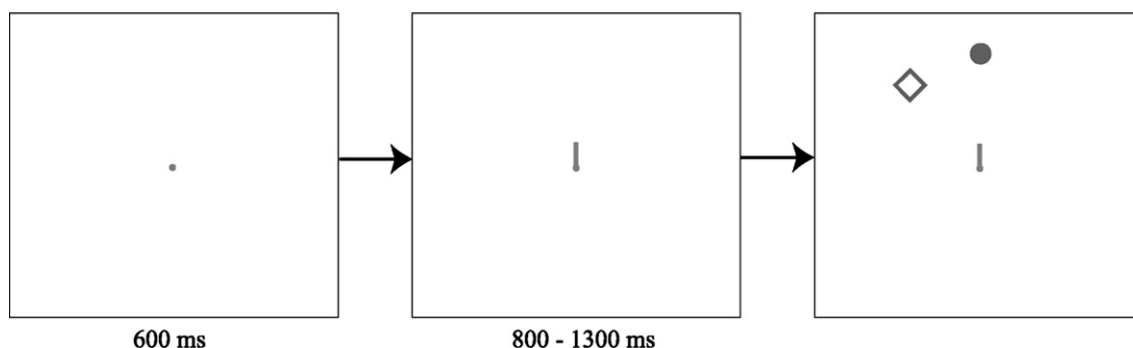


Fig. 1. Example of the display sequence. The central line segment indicated the target location. After a variable delay, the target ('filled circle') and the distractor ('diamond shape') were presented simultaneously and observers were required to make a fast eye movement to the target.

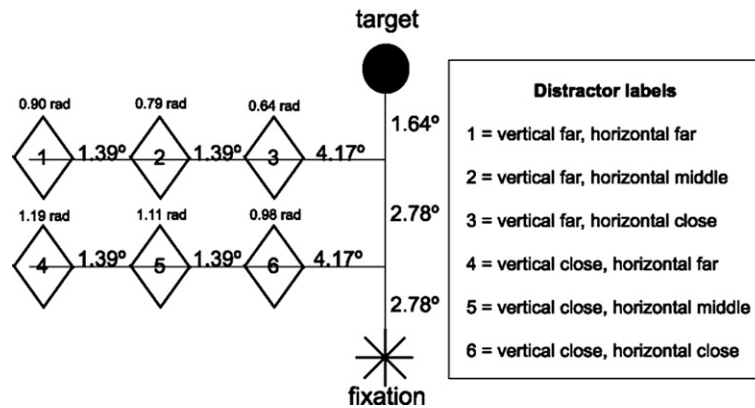


Fig. 2. The possible distractor positions. In this figure, the locations are only shown for the left side of fixation, but a distractor could also appear at mirrored locations on the right side of fixation. For each possible distractor location, the angle between the straight saccade and the location of the distractor is given in radians.

offset of the measuring device at the start of each trial. Participants heard a short tone when the saccade latency was higher than 600 ms. Each target and distractor location were equally probable. The sequence of trials was counterbalanced and randomized for each participant.

2.5. Data analysis

Saccade latency was defined as the interval between target onset and the initiation of a saccadic eye movement. If saccade latency was lower than 80 ms, higher than 600 ms, or further than two and a half standard deviations away from the mean latency the trial was removed from the analysis. Moreover, trials were excluded from analysis in which no saccade or a too small first saccade ($<3^\circ$) was made. If the endpoint of the first saccade had an angular deviation of more than 22.5° from the center of the target, the saccade was classified as an error and also not analyzed. Furthermore, the initial saccade starting position had to be within 1° from the center fixation point.

To examine the influence of the different conditions on saccade trajectories, we used three different measures: peak deviation, saccade endpoint and initial direction. This enabled us to explore on what part of the saccade distractor location might have an influence: for the beginning of the trajectory (initial direction), the maximum deviation in between beginning and endpoint (peak deviation), or for the endpoint of the saccade (saccade endpoint) (for an overview of all different measures and how to compute them, see, Van der Stigchel et al., 2006):

- Initial direction was defined as the difference between the angle of the saccade 10 ms after saccade initiation and a straight line between the saccade starting position and the target location (e.g. Van der Stigchel & Theeuwes, 2005; Van Gisbergen, Van Opstal, & Roebroek, 1987).
- Peak deviation was defined as the largest perpendicular deviation from the straight line connecting the saccade starting position and saccade endpoint divided by the amplitude of the movement (e.g. Doyle & Walker, 2001; Doyle & Walker, 2002; Smit & Van Gisbergen, 1990).
- Saccade endpoint was defined as the angular difference between a straight line from the saccade starting position to saccade endpoint and a straight line from fixation to the target location (e.g. Frens, Van Opstal, & Van der Willigen, 1995; McSorley et al., 2004).

Since it is known that natural directional biases exist in saccade trajectories (e.g. Erkelens & Sloot, 1995; Minken, Van Opstal, & Van Gisbergen, 1993; Viviani, Berthoz, & Tracey, 1977), the effect of a distractor on saccade trajectories is often compared to a baseline condition in which no distractor is present. Even though using a baseline condition is appropriate, it should be noted that there are also potential problems

when comparing a condition with a distractor to a baseline condition in which there is no distractor. For example, eye movements in the presence of distractors are different than those in the absence of distractors in terms of latency, amplitude, and speed (Walker et al., 1997). Our method uses the fact that distractor locations were mirrored to cancel out any natural bias in trajectories. Our method for calculating deviation assumes that the influence of inhibition is similar for both visual fields: the same amount of inhibition is evoked by a distractor in the left visual field as a distractor in the right visual field. This seems to be a fair assumption because no studies have reported saccade deviation differences between the two visual fields. Moreover, in the study by McSorley et al. (2004), a condition was included in which two distractors were presented simultaneously at mirrored locations. If inhibition were stronger in one field than in the other, net deviation one way or the other should have resulted in this condition. Instead, results showed that the trajectory was straightened by this manipulation. This finding indeed seems to indicate that similar influences can be found for both visual fields.

To compute the effect of the different distractor locations on saccade trajectories, differences between the trajectories evoked by distractors on the left and the right visual field were analyzed. We initially measured deviations in absolute space coordinates related to a similar reference point and therefore unrelated to the actual distractor position. The deviations for left and right distractors were computed on an arbitrary left-right scale for upward movements, and right-left scale for downward movements. Mean absolute space deviations for left and right visual field distractors were subsequently subtracted so that positive and negative values refer to measurements towards and away of the distractor location, respectively. For instance, if the mean deviation for a distractor location in the left visual field was -1.00 rad (relative to a reference point to the left of fixation; i.e., the eye movements deviated 1 rad to the right in absolute space), while the mean deviation for a distractor location in the right visual field was -0.75 rad (i.e. 0.75 rad to the right in absolute space), this would result in a difference of -1 to $(-0.75) = -0.25$ rad (a deviation away from the distractor location). For all measures, trials in which the outcome of that particular trajectory measure was two and a half standard deviations away from the mean outcome were removed from the analysis.

3. Results

The exclusion criteria led to a total loss of 11.4% of trials. Separate calculations were made for each distractor location ('Far Vertical, Far Horizontal,' 'Far Vertical, Middle Horizontal,' 'Far Vertical, Close Horizontal,' 'Close Vertical, Far Horizontal,' 'Close Vertical, Middle

Horizontal' and 'Close Vertical, Close Horizontal') and saccade direction ('upward' or 'downward').

3.1. Saccade latency

To determine whether the different conditions had an effect on saccade latency, an ANOVA with distractor location and saccade direction as factors was performed. There was only a main effect of direction ($F(1,11) = 7.34; p < 0.03$). Saccades upwards were faster (201 ms) than saccades downwards (208 ms). Distractor location had no systematic effect on saccade latency ($F(5,55) = 1.21; p > 0.30$).

3.2. Peak deviation

An analysis of variance (ANOVA) on mean peak deviation with distractor location and saccade direction as factors showed a main effect of location (see Fig. 3,

$F(5,55) = 2.91; p < 0.03$) and a significant interaction between distractor location and saccade direction ($F(5,55) = 4.11; p < 0.01$). There was no main effect of direction ($F(1,11) = 2.78; p > 0.10$).

We then determined whether the effect of distractor location could be explained by the horizontal or vertical distance of the distractor from fixation. With respect to the vertical distance we compared the three close vertical locations with the three far vertical locations. With respect to the horizontal distance from fixation, we compared the two far horizontal, the two middle horizontal and the two close horizontal locations. Neither factor had an effect (horizontal ($F < 1$), vertical ($F(1,11) = 3.27; p > 0.05$)). As can be seen in Fig. 3 the main effect of location in the original analysis was mainly due to the condition in which the distractor was presented at the closest distance from the target location ('Far Vertical, Close Horizontal') and the condition in which the distractor was presented at the closest distance

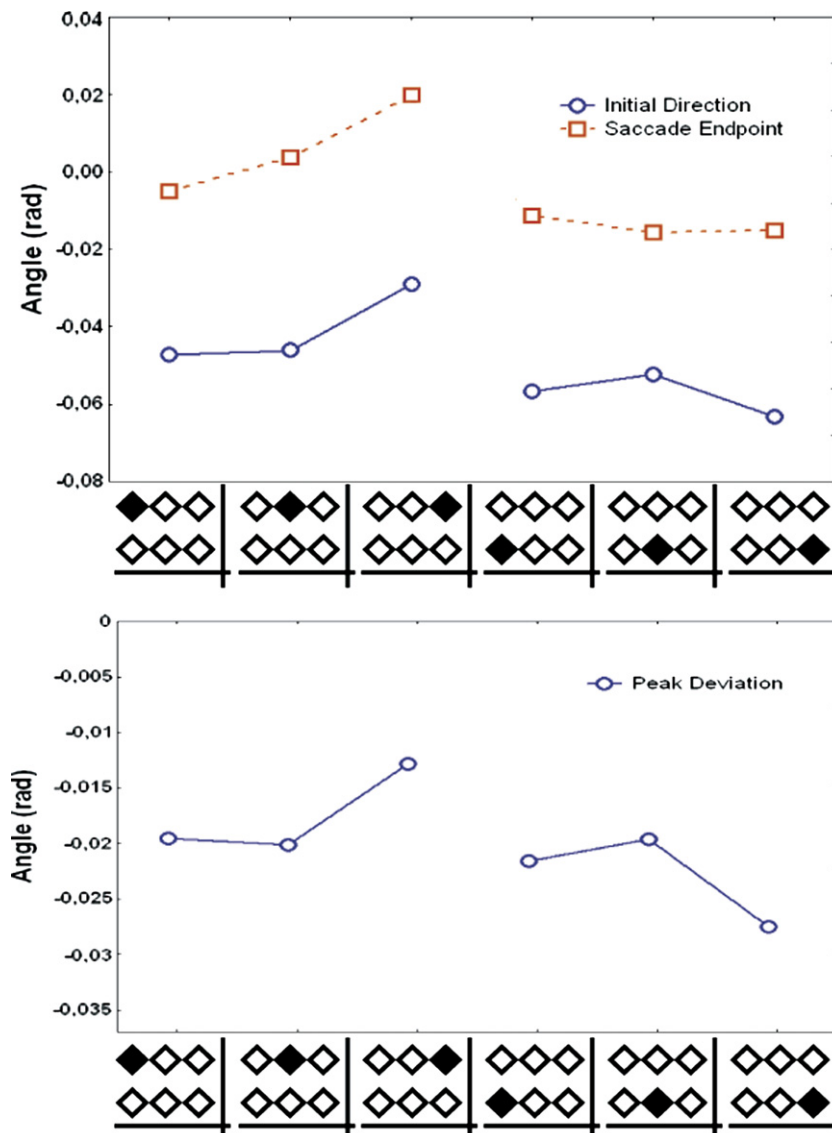


Fig. 3. Results of the six distractor locations for all three measures of saccade deviations. The graphical representations on x-axis refer to the distractor locations as described in Fig. 2. Negative values refer to deviations away. See text for further details.

from fixation ('Close Vertical, Close Horizontal'). Indeed, by Student–Newman–Keuls post hoc tests, these two locations were significantly different from each other ($p < 0.05$), with no other contrast being significant. These effects were stronger in saccades that were directed upward than for saccades that were directed downwards. This is reflected by the observed interaction between location and direction.

3.3. Saccade endpoint

An analysis of variance (ANOVA) on mean saccade endpoint with distractor location and saccade direction as factors showed a reliable effect of distractor location (see Fig. 3, $F(5,55) = 10.69$; $p < 0.001$), saccade direction ($F(1,11) = 20.14$; $p < 0.001$) and a significant interaction between distractor location and saccade direction ($F(5,55) = 4.02$; $p < 0.01$). Deviation was stronger for upward than for downward saccades.

With respect to vertical and horizontal distance from fixation, we now found an effect for vertical distance ($F(1,11) = 20.38$; $p < 0.001$), with deviation being larger for the lower distractor positions than for the upper distractor positions. There was no effect for horizontal distance ($F(2,22) = 2.77$; $p > 0.05$). Post hoc SNK showed that distractors at the location closest to the target ('Far Vertical, Close Horizontal') caused less deviation than at all other locations ($p < 0.05$). Furthermore, deviation at a neighboring location ('Far Vertical, Middle Horizontal') was also smaller than at all locations except one ('Far Vertical, Far Horizontal'; $p < 0.05$).

3.4. Initial direction

For initial direction, there was again a main effect of distractor location (see Fig. 3, $F(5,55) = 2.88$; $p < 0.03$). Both the main effect of saccade direction and the interaction between distractor location and saccade direction were not reliable ($F < 1$). We then investigated whether horizontal or vertical distance from fixation could account for the effect of distractor location. Again, only vertical distance from fixation showed an effect ($F(1,11) = 13.07$; $p < 0.01$): deviation was larger for the three lower positions than for the three higher positions. There was no effect for horizontal distance ($F(2,22) = 2.57$; $p > 0.05$). Post hoc SNK confirmed that deviation for the location closest to the target ('Far Vertical, Close Horizontal') was again significantly smaller than for the other locations ($p < 0.05$). Furthermore, in one other location ('Close Vertical, Close Horizontal') distractors caused significantly more deviation away than in all locations except two ('Close Vertical, Far Horizontal', 'Close Vertical, Middle Horizontal'; $p < 0.05$).

3.5. Relation between initial and saccade endpoint

Fig. 4 shows the development of deviation across the whole saccade trajectory. For each condition, the mean difference for each sample point was computed between

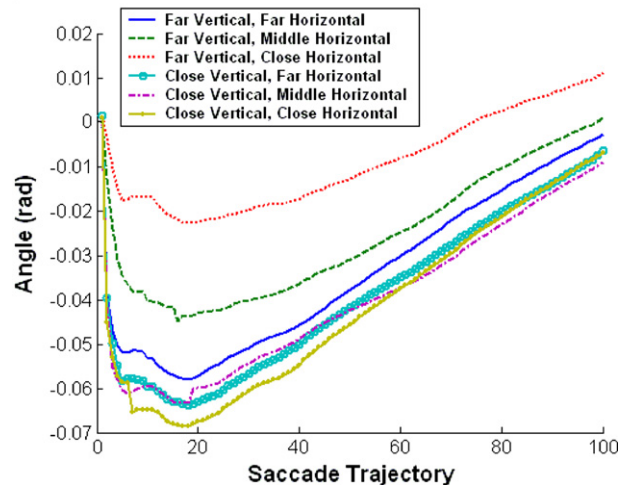


Fig. 4. The development of deviation across the whole saccade trajectory for the six distractor positions. Saccades are normalized so that the endpoint is always equal to 100. x- and y-axis are not on the same scale.

trajectories observed for left visual field distractors and right visual field distractors. Every saccade trajectory was stretched in such a way that every trajectory consisted of 100 sample points. It can easily be seen from Fig. 4 that the initial and saccade endpoint of the saccade trajectory are positively related, in that the more negative the initial deviation of a trajectory is, the more negative the saccade endpoint is.

To quantify the relation between the initial and saccade endpoint, we calculated for each participant the mean correlation between these two trajectory measures for the different distractor locations. To assure that the correlation value was not influenced by whether a saccade deviated away or towards a distractor, correlations were computed with deviations irrespectively of their direction (away or toward). It was computed whether the mean correlations were significantly different from zero. Analyses showed that all mean correlation values were significantly different from zero ('Vertical Far, Horizontal Far': $t(11) = 7.87$; $p < 0.001$; 'Vertical Far, Horizontal Middle': $t(11) = 9.27$; $p < 0.001$; 'Vertical Far, Horizontal Close': $t(11) = 8.17$; $p < 0.001$; 'Vertical Close, Horizontal Far': $t(11) = 9.30$; $p < 0.001$; 'Vertical Close, Horizontal Middle': $t(11) = 6.45$; $p < 0.001$; 'Vertical Close, Horizontal Close': $t(11) = 6.97$; $p < 0.001$). There were no statistical differences between the six conditions ($F(5,55) < 1$; $p > 0.9$). All mean six correlations were positive and their value varied between 0.52 and 0.56. Fig. 5 shows a scatter plot of all saccades.

4. Discussion

By manipulating the location of a distractor and measuring the trajectory deviations away from this location, we systematically investigated the spatial coding of the inhibition of distractor locations. We were able to determine whether the evoked inhibition is indeed coarsely coded and not sensitive to the distractor location, as has been found in

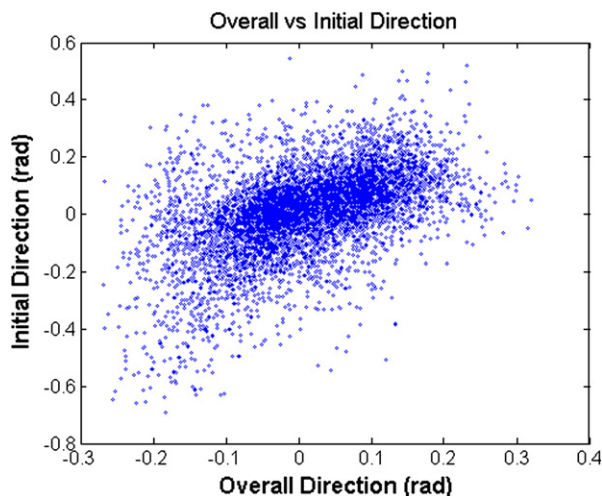


Fig. 5. Scatter plot of all saccades for their initial direction and saccade endpoint.

earlier studies (McSorley et al., 2004, 2005). Both target and distractors were presented with abrupt onset to evoke a large competition between the two elements. Furthermore, the location of the target was known in advance to allow inhibitory mechanisms time to develop.

Results showed differences in saccade trajectories between the various distractor locations in that for some locations saccade deviations away were stronger than for other locations. Because it is widely assumed that trajectory deviations away are a reflection of inhibition (Doyle & Walker, 2001; Godijn & Theeuwes, 2002; Sheliga et al., 1994; Tipper et al., 1997; Van der Stigchel et al., 2006), we conclude that the distractor location has a modulatory effect on the amount of inhibition evoked by the distractor. These findings were replicated for all three measurements of the saccade trajectory (initial direction, saccade endpoint and peak deviation).

Because three different measures were used, it was possible to investigate which part of the trajectory was affected by distractor location. As noted before, all measures showed a modulatory effect of distractor location. For two of our measures, saccade endpoint and initial direction, the observed differences in the evoked inhibition were best explained by the vertical distance of the distractor from fixation. For peak deviation, there was no clear factor that could explain the observed differences. However, it should be noted that two locations showed significantly different responses on the mean peak deviation. Again, these two locations only differed in terms of their vertical distance from fixation. Therefore, we conclude that vertical distance of the distractor from fixation is the most important factor that influences the evoked inhibition for all parts of the trajectory, with locations vertically closer to fixation causing more inhibition than locations further away from fixation. It is possible that this is only true for vertical saccades, as these were the only ones tested.

Differences in the amount of movement trajectory are generally explained by models of movement trajectory devi-

ations that state that possible target objects are represented by a large population of neurons encoding the movement towards each target object as a vector (Tipper, Howard, & Houghton, 2000; Tipper et al., 1997). When two possible targets are positioned in close proximity, the populations corresponding to these targets are combined to a mean population of which the vector will point to an intermediate location. Since participants are instructed to move their eyes to only one location, competition between the two active populations has to be resolved by inhibiting one of them. Because saccades are executed on the basis of this initial vector, inhibitory selection of one population over the other may shift the resulting movement vector in such a way that it affects the final response to the target.

One possible explanation for the observed findings might be that the saliency of a distractor for the oculomotor system is based on the decomposed distractor vector. Every distractor vector can be decomposed in a vertical and a horizontal component. On the basis of the present findings, we hypothesize that the distractor saliency is determined by the vertical component of the corresponding vector. More specifically, it seems to be that distractors with a small vertical distance from fixation have a higher saliency for the oculomotor system than distractors with a large vertical distance. They evoke more competition and inhibitory components are therefore more potent to resolve this competition. The present findings are reminiscent of a hand centered reaching effect which shows larger deviations for distractor presented near the hand (Tipper et al., 1997).

A second contributing factor which might play a role is the global effect (Coren & Hoenig, 1972; Findlay, 1982). Although we presented all distractors outside the zone in which this effect is generally observed, mean saccade endpoint might still have been affected by a subset of global effect trials. If true, this should hold for the distractors with a large vertical distance from fixation. Indeed, saccade endpoint in these conditions did not deviate away from the distractor. Therefore, a second explanation for the present findings is that distractors with a small vertical distance from the target are more subject to averaging saccades, resulting in less deviation away.²

Our findings have important implications for models that include inhibitory components in the target selection process (Godijn & Theeuwes, 2002; McSorley et al., 2004; Tipper et al., 1997; Trappenberg et al., 2001) and with respect to the influence of the areas that could underlie inhibitory influences on the SC, the FEF and the dIPFC (Lynch & Tian, 2006; Schlag-Rey et al., 1992). The present results indicate that the distractor related inhibition is not coarse, but modulated by the precise distractor location.

² We also investigated directly whether distance from fixation or distance from target could account for the inhibition differences. We used the average deviation in each of the six positions as input to a regression analysis. None of the two factors explained the deviation for all three measures ($\beta < \pm 0.80$).

The role of the SC in saccade trajectories was revealed by McPeck et al. (2003), who showed that when a trajectory deviated towards a distractor location in a visual search experiment, there was increased pre-saccadic activity at that location. Also, micro-stimulation of the SC below the threshold for saccade generation resulted in eye movements that deviated towards the stimulated location. The magnitude of this deviation was correlated with the induced activity at the stimulated location.

Saccade deviations away have been observed only in humans. In visual search experiments in monkeys, saccade trajectories to a target location have been shown to only deviate towards a distractor (McPeck & Keller, 2001; Port & Wurtz, 2003). Deviations away have been shown in monkeys after deactivating of a location by an injection of a GABA agonist, muscimol (Aizawa & Wurtz, 1998), but not without pharmacological deactivation. One possible explanation for this difference between humans and monkeys might be the different paradigms adopted. In a recent review of the literature, we have suggested that deviation away is observed in situations in which top-down preparation can influence the target selection process (Van der Stigchel et al., 2006). Studies that have looked at saccade trajectories in monkeys have done this in visual search paradigms, in which the precise location of the upcoming target is unknown. Previous studies in humans have shown that when observers know where to expect the target and have the time to prepare for the saccade, distractors will result in deviation away. However, if observers either do not have the knowledge or the time to prepare for the saccade, distractors will elicit deviation towards (Van der Stigchel et al., 2006; Walker et al., 2006). These findings suggest that deviations away might be seen in monkeys in paradigms where top-down preparation can influence the target selection process.

In the present study, there was a main effect of the distractor location for all measures, including the saccade endpoint and the initial direction. This suggests that the initial direction and the endpoint of a saccade are related, and contradicts recent models proposing that the initial saccade direction and saccade endpoint are unrelated and controlled by separate mechanisms (McSorley et al., 2004; Quaia et al., 1998). In these models, initial saccade direction is controlled by the SC, while the cerebellum corrects possible deviations from the target direction. The cerebellum monitors saccade progress and compensates for directional errors by adjusting the motor signal. So, when the initial direction of the saccade is programmed to a location that is not the target location, on-line cerebellum feedback takes care of the saccade the correct landing position. In the present study this hypothesis was tested by quantifying the relation between the initial direction and saccade endpoint. Indeed, the two measures were strongly correlated. Although in principle it is still possible that the initial direction and saccade endpoint is controlled by different mechanisms, the current findings

suggest that any influence on the initial deviation is also reflected in the saccade endpoint.

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