Differences in distractor-induced deviation between horizontal and vertical saccade trajectories

Stefan Van der Stigchel[a] and Jan Theeuwes[b]

[a]Utrecht University, Utrecht and [b]Vrije Universiteit, Amsterdam, The Netherlands

Correspondence to Dr Stefan Van der Stigchel, Department of Experimental Psychology, Helmholtz Institute, Utrecht University, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands
Tel: + 31 30 253 3356; fax: + 31 30 253 4511; e-mail: S.VanderStigchel@uu.nl

The present study systematically investigated the influence of a distractor on horizontal and vertical eye movements. Results showed that both horizontal and vertical eye movements deviated away from the distractor but these deviations were stronger for vertical than for horizontal movements. As trajectory deviations away from a distractor are generally attributed to inhibition applied to the distractor, this suggests that this deviation is not only due to differences in activity between the two collicular motor maps, but can also be evoked by local application of inhibitory processes in the same map as the target. Nonetheless, deviations were more dominant for vertical movements which suggests that for these movements more inhibition is applied than for horizontal movements. *NeuroReport* 19:251–254 © 2008 Wolters Kluwer Health | Lippincott Williams & Wilkins.

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Introduction

Owing to our eyes which can only fixate one location at a time, there is a continuous competition for gaze between the various elements in our visual field. Therefore, at least part of successful goal-directed behaviour depends on the correct selection of relevant information (often labelled as the 'target') and the inhibition of irrelevant information (or so-called 'distractors'). Previous studies have indicated that the competition between target and distractor can be investigated by examining eye movement trajectories which are found to deviate in the presence of a distractor [1]. For instance, in situations in which there is little search necessary to find the target, the inhibition of a distractor is accompanied by a saccade trajectory to the target that deviates away from the location of the distractor (i.e. [2,3–8]).

The competition between possible saccade goals is assumed to be resolved in the intermediate layers of superior colliculus (SC) [9,10]. This mid-brain area receives both visual (bottom-up) and task-related (top-down) signals and integrates those signals on a motor map. Saccade trajectory deviations are assumed to reflect the competition between the different possible target locations in the SC [2,11]. The role of the SC in saccade trajectories was revealed by McPeek and colleagues [12], 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. Deviation *away* as frequently observed in human observers, however, has so far not been found in monkeys (without pharmacological deactivation). Deviation away from a location is typically attributed to inhibitory processes [2,13–15], but as neurophysiological evidence is still missing, the exact behavioural underpinnings of this oculomotor inhibition are still unknown.

In this study, the behavioural underpinnings of saccade deviations were further investigated by comparing horizontal and vertical movements. Almost all studies that have examined the effects of an irrelevant distractor have looked exclusively at vertical saccades and have found significant deviations away from the distractor (i.e. [2,3–8]). Horizontal and vertical saccades, however, are very differently represented in the brain and, in particular, in the SC. The SC is divided into two separate retinotopic neuronal maps and each colliculus encodes information corresponding to the contralateral visual hemifield [16]. Therefore, vertical saccades depend on activations from both colliculi (either medially for upward saccades or laterally for downward saccades), whereas horizontal saccades are represented by one colliculus. The goal of the present study was to investigate whether an analogous deviation would occur for horizontal as for vertical saccades.

One possibility is that the deviation away for vertical saccades is due to differences in activation between the two motor maps. In this explanation, the presence of a distractor in one motor map leads to a relatively stronger activation of the other motor map which results in a deviation away from the motor map in which the distractor is located. If true, deviations away will be only observed for vertical movements. If the representation of oculomotor inhibition is, however, more locally coded and does not operate on the level of the whole motor map, a distractor in the same motor map as the target should also evoke deviation away. In that case, horizontal saccades should also show deviation away

because target and distractor are represented in the same motor map. In the present experiment, eye movements were executed in the presence of an irrelevant distractor which was located on the same location for horizontal and vertical eye movements. This allowed us to investigate whether differences in deviation can be observed between the different eye movement directions. Furthermore, this setup enabled us to investigate possible differences in the influence of different distractor locations on saccade trajectories, irrespective of the movement direction. Both target and distractor were presented with abrupt onset to evoke a strong competition between the two elements (see for example, [5]).

Methods

Participants
Nine students, aged between 17 and 22 years, served as paid volunteers (four male). All reported having normal or corrected-to-normal vision. They were naïve as to the purpose of the experiment. All persons gave their informed consent prior to their inclusion in the study.

Apparatus
Eye movements were registered by means of a video-based eye tracker. The Eyelink2 system has a 500 Hz temporal resolution and a spatial resolution of 0.01°. Data were recorded from the left eye. 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.

Stimuli
See Fig. 1 for an illustration of the display sequence. All figures were presented in light grey (CIE x,y chromaticity coordinates of 0.291/0.314; 26.4 cd/m^2) on a black background. Each trial started with the presentation of a 'cross' character (0.83° × 0.83°) in the centre of the screen that functioned as the fixation stimulus. After 500 ms an arrow (0.21° × 0.97°) appeared directly above, below, to the right or to the left of the fixation position ('cue'). A delay of 800–1200 ms then occurred followed by the onset of the target (a light grey filled circle with a diameter of 1.11°). The target location was related to the direction of the cue: the circle was always presented 7.22° from the fixation point in the direction of the cue. Simultaneously with the target onset, a light grey diamond shape distractor (0.97° × 0.97°) appeared on two-thirds of trials. For vertical saccades, the distractor

was always positioned in the same upper or lower hemifield as the target, either to the left or to the right from the target. For horizontal saccades, the distractor was always positioned on the same left or right hemifield as the target, either above or below the target. For each target, the location of the distractor had the same horizontal and vertical distance from fixation (3.61°), such that the same distractor locations were used for horizontal and vertical saccades.

Procedure and design
Participants first received oral instructions. They were instructed to fixate the centre fixation point until target onset and 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 60 trials and an experimental session of 600 trials. Each session started with a nine-point grid calibration procedure. A drift correction was applied at the start of each trial. Participants heard a short tone when the saccade latency was higher than 600 ms or when the eyes moved more than 2° from fixation before target onset. Each target and distractor location was equally probable. The sequence of trials was counterbalanced and randomized for each participant.

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°) was made. If the endpoint of the first saccade had an angular deviation of more than 22.5° from the centre of the target, the saccade was classified as an error and not analyzed. The initial saccade starting position had to be within 1° from the fixation point.

Deviation was defined as the difference in mean angle of the observed saccade path and a straight line from the saccade starting position to the target location. The mean angle of the saccade path in a single trial was calculated by averaging the angles of a straight line from the saccade starting position and the different sample points (for a more detailed overview of saccade trajectory computation, see [1]). For each saccade in a trial with a distractor we compared its path angle to the mean path angle in trials without a distractor, to determine if the saccade deviated towards or away from the distractor. This then represented the distractor-induced deviation for that trial. Deviations were signed so that a positive value indicated deviation towards the distractor, and a negative value deviation away. Trials in which the deviation was two and a half standard deviations away from the mean outcome were removed from the analysis. The exclusion criteria led to a total loss of 15.5% of trials.
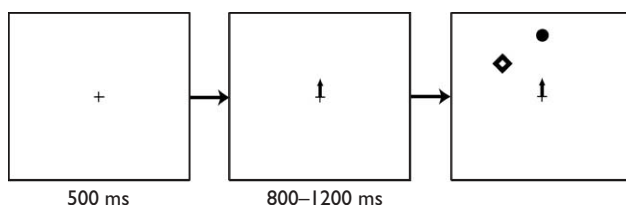

Fig. 1 Example of the display sequence. The arrow indicated the target location. After a variable delay, the target ('filled circle') and the distractor ('diamond shape') were presented simultaneously and observers were required to make a fast eye movement to the target. The distractor was presented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

Results

Saccade latency
To determine whether the different conditions had an effect on saccade latency, an ANOVA with saccade direction (up, down, right, versus left) and distractor condition (present versus absent) as factors was performed. There was only a

trend for an effect of the distractor condition [F(1,8)=4.52; $P=0.07$] in that saccade latencies in the distractor present condition tended to be longer (211.4 ms) than in the distractor absent trials (205.4 ms). Saccade direction had no systematic effect on saccade latency [F(3,24)=1.24; $P>0.30$].

Saccade deviation

We determined whether trajectories of vertical and horizontal saccades deviated in the presence of a distractor. If the distractor has no effect on the saccade trajectory, a deviation of zero will be observed. Deviations of vertical saccades differed significantly from zero [mean=−0.024 rad; SD=0.013 rad; $t(8)=5.49$; $P<0.001$] showing that saccades deviated away from the distractor. This same effect was observed from horizontal movements [mean=−0.009 rad; SD=0.006 rad; $t(8)=4.92$; $P<0.002$]. The deviation was stronger for vertical than for horizontal movements [see Fig. 2, $t(8)=3.46$; $P<0.01$]. There was no difference between leftward and rightward saccades [$t(8)=1.20$; $P>0.20$] and upward and downward saccades [$t(8)=0.77$; $P>0.40$]. Figure 3 shows, as an example, the mean trajectories of one participant for leftward and upward movements for each condition.

This experiment also enabled us to investigate whether the different distractor locations evoked different levels of deviation. Therefore, the effect of each distractor location (top-left, top-right, bottom-left, versus bottom-right) were analyzed by collapsing the effect of each distractor on vertical and horizontal movements. Each distractor location evoked trajectories that significantly differed from zero ($P<0.02$). No difference, however, was there between the four locations ($F<1$).

Discussion

By manipulating the target location of the eye movement and measuring saccade trajectory deviations induced by a distractor, we systematically investigated the influence of distractors on horizontal and vertical eye movements. Both horizontal and vertical eye movements were found to deviate away from the distractor. The deviation was, however, stronger for vertical than for horizontal movements. No
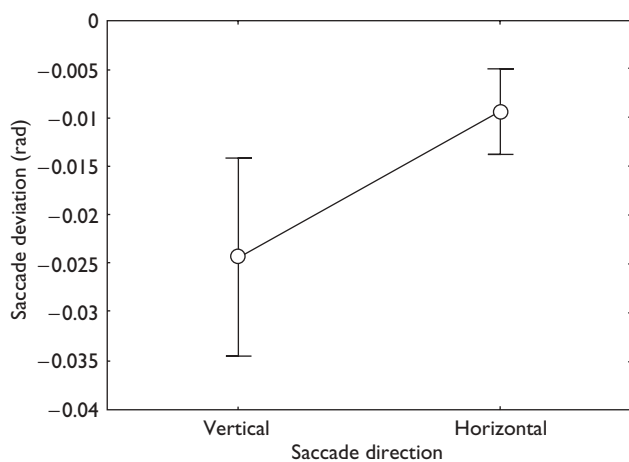
Fig. 3 Mean saccade trajectories for upward and leftward saccades for one observer. Both axes denote visual angle (deg).

difference was there between upward and downward saccades or left and right saccades. The results also showed that there were no differences in the influence of the different distractor locations on saccade trajectories, in that all distractor locations evoked similar amounts of deviation.

The deviations observed in the current study are generally attributed to inhibitory processes applied to the distractor location due to the top-down selection of the target [2,13–15]. These models of movement trajectory deviations assume that possible target objects are represented by a large population of neurons encoding the movement towards each target object as a vector. Owing to saccades being executed on the basis of the weighted average of these vectors, inhibitory selection of one population over the other shifts the weighted eye movement vector away from the inhibited location, leading to deviation away from that location. The present study shows that this inhibition is not due to differences in activation between two motor maps, but can be coded within the same motor map as the target. If the deviations away from a distractor were due to an imbalance between the two motor maps, these deviations should only be observed for vertical saccades, as they depend on activations from both motor maps. The fact that inhibitory deviations were also observed for horizontal movements shows that the

Fig. 2 Results for both saccade directions. Negative values refer to deviations away. Vertical saccades have stronger deviations away from a distractor than horizontal movements.
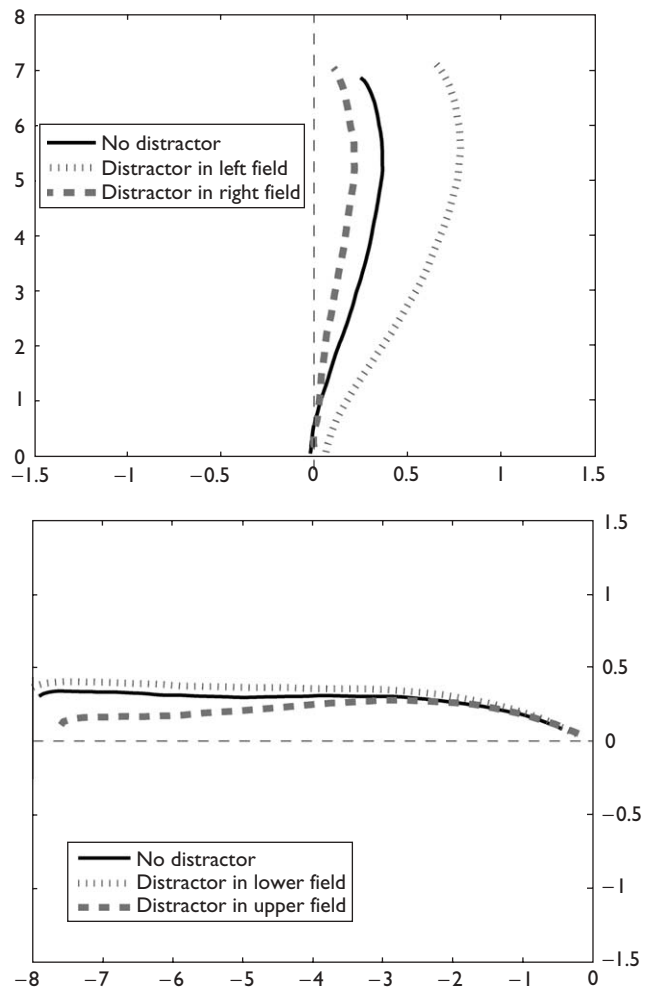
inhibition of the distractor can be applied in the same motor map as the target.

The results, however, also showed that the trajectory deviations were stronger for vertical movements than for horizontal movements. As the amount of deviation away from a location is assumed to be a reflection of the amount of inhibition applied to that location [4], this shows that applied inhibition is stronger for vertical movements. Possibly this could account for the observed differences between horizontal and vertical eye movements. For vertical movements, a complete motor map can be inhibited, whereas for horizontal movements a very strong inhibition potentially could result in an inability to execute a correct eye movement to the target. For this reason, inhibition of a distractor in the same motor map as the target might therefore be less strong than when the distractor is located in a different map like for vertical movements. As saccade deviations away have been observed only in humans, this remains speculation, however. It must be noted that deviations away have been shown in monkeys after deactivating of a location in the SC by an injection of a GABA agonist, muscimol [17], but not without pharmacological deactivation.

The present results are in line with findings of one study that also investigated the relation between horizontal and vertical deviations [18]. These deviations, however, were not induced by irrelevant distractors but by voluntary shifts of covert attention to peripheral locations. They also reported horizontal movements to show less deviation than vertical movements. The present findings therefore suggest that similar mechanisms underlie the inhibition of activity due to both irrelevant onsets and voluntary shifts of covert attention.

Conclusion

The present study shows that trajectories of both horizontal and vertical eye movements deviate away from an inhibited distractor location. This suggests that this deviation is not only due to differences in activity between the two motor maps, but can also be evoked by local application of inhibitory processes in the same map as the target. Deviations were more dominant for vertical movements which suggests that for these movements more inhibition is applied than for horizontal movements.

References

1. Van der Stigchel S, Meeter M, Theeuwes J. Eye movement trajectories and what they tell us. *Neuroscience & Biobehavioral Reviews* 2006; **30**:666–679.
2. McSorley E, Haggard P, Walker R. Distractor modulation of saccade trajectories: spatial separation and symmetry effects. *Experimental Brain Research* 2004; **155**:320–333.
3. McSorley E, Haggard P, Walker R. Spatial and temporal aspects of oculomotor inhibition as revealed by saccade trajectories. *Vision Research* 2005; **45**:2492–2499.
4. Ludwig CJH, Gilchrist ID. Target similarity affects saccade curvature away from irrelevant onsets. *Experimental Brain Research* 2003; **152**: 60–69.
5. Van der Stigchel S, Meeter M, Theeuwes J. The spatial coding of the inhibition evoked by distractors. *Vision Research* 2007; **47**:210–218.
6. Van der Stigchel S, Theeuwes J. Relation between saccade trajectories and spatial distractor locations. *Cognitive Brain Research* 2005; **25**:579–582.
7. Doyle MC, Walker R. Curved saccade trajectories: voluntary and reflexive saccades curve away from irrelevant distractors. *Experimental Brain Research* 2001; **139**:333–344.
8. Doyle MC, Walker R. Multisensory interactions in saccade target selection: curved saccade trajectories. *Experimental Brain Research* 2002; **142**:116–130.
9. Sparks DL, Hartwich-Young R. The deeper layers of the superior colliculus. In: Wurtz RH, Goldberg ME, editors. *The neurobiology of saccadic eye movements*. Amsterdam: Elsevier Science Publishers; 1989. pp. 213–255.
10. Schall JD. Neuronal basis of saccadic eye movements. In: Leventhal AG, editor. *Vision and visual dysfunction. The neural basis of visual function.* Vol. 4. London: Macmillan Press; 1991. pp. 388–442.
11. Trappenberg TP, Dorris MC, Munoz DP, Klein RM. A model of saccade initiation based on the competitive integration of exogenous and endogenous signals in the superior colliculus. *Journal of Cognitive Neuroscience* 2001; **13**:256–271.
12. McPeek RM, Han JH, Keller EL. Competition between saccade goals in the superior colliculus produces saccade curvature. *Journal of Neurophysiology* 2003; **89**:2577–2590.
13. Sheliga BM, Riggio L, Rizzolatti G. Orienting of attention and eye movements. *Experimental Brain Research* 1994; **98**:507–522.
14. Tipper SP, Howard LA, Jackson SR. Selective reaching to grasp: evidence for distractor interference effects. *Visual Cognition* 1997; **4**:1–38.
15. Godijn R, Theeuwes J. Programming of endogenous and exogenous saccades: evidence for a competitive integration model. *Journal of Experimental Psychology: Human Perception and Performance* 2002; **28**: 1039–1054.
16. Hall WC, Moschovakis AK, editors. *The superior colliculus: new approaches for studying sensorimotor integration*. Boca Raton: CRC Press; 2003.
17. Aizawa H, Wurtz RH. Reversible inactivation of monkey superior colliculus. I. curvature of saccadic trajectory. *Journal of Neurophysiology* 1998; **79**:2082–2096.
18. Sheliga BM, Riggio L, Craighero L, Rizzolatti G. Spatial attention-determined modifications in saccade trajectories. *Neuroreport* 1995; **6**: 585–588.