RESEARCH ARTICLE

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Our eyes deviate away from a location where a distractor is expected to appear

Abstract Previous research has shown that in order to make an accurate saccade to a target object, nearby distractor objects need to be inhibited. The extent to which saccade trajectories deviate away from a distractor is often considered to be an index of the strength of inhibition. The present study shows that the mere expectation that a distractor will appear at a specific location is enough to generate saccade deviations away from this location. This suggests that higher-order cognitive processes such as top-down expectancy interact with low-level structures involved in eye movement control. The results will be discussed in the light of current theories of target selection and possible neurophysiological correlates.

Keywords Saccades · Trajectory · Inhibition · Superior colliculus

Introduction

Fast saccadic eye movements typically show a curved trajectory (e.g., Erkelens and Sloot 1995; Minken et al. 1993; Viviani et al. 1977). Even though the saccade curvature as a phenomenon may be interesting, the extent to which saccadic curvature is modulated by events that occur in the environment is more important, because it can inform our understanding of processes involved in saccade target selection. For example, in the so-called double-step task (Becker and Juergens 1979; Levy-Schoen 1969) in which a second onset target appears after the first onset target, the eyes deviate in the direction of the second onset.

Saccade deviations away from an attended location were described by Sheliga et al. (1994, 1995). These

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studies were executed to provide support for the premotor theory (Rizzolatti et al. 1987, 1994). According to this theory the mechanisms involved in saccade programming are basically the same as those involved in directing spatial attention. In their experiments, it was examined whether directing attention to a spatial location influences the trajectory of a predetermined saccade. Results revealed that the trajectory of an eye movement deviated away from the location to which attention was endogenously directed (also see Van der Stigchel and Theeuwes 2005). The results provided strong evidence for the premotor theory because they indicated that directing spatial attention leads to activation within the oculomotor system.

Subsequent studies showed that the eyes not only deviate away from locations to which attention is directed in a voluntary fashion like that found in the Sheliga et al. studies, but also deviated away from a task-irrelevant stimulus onset (Doyle and Walker 2001). This finding indicated that the prior voluntary allocation of covert attention is not responsible for trajectory deviations. Instead it appears that modifications of the saccade trajectory are the result of competitive interactions operating between saccade programs (McPeek et al. 2003). Furthermore, saccade deviations were not only observed for voluntary eye movements but also for reflexive saccades (Doyle and Walker 2001) which show that the modification of saccade trajectories is not solely a consequence of voluntary control, but can also be observed as a result of reflexive behavior. Similar results were obtained with the oculomotor capture paradigm (Theeuwes et al. 1998) in which dependending on the condition, eye movement trajectories to the target location either deviated toward or away from the onset distractor (Godijn and Theeuwes 2002b).

Saccade deviations can be explained by the so-called vector theory which is assumed to account for the initial direction of both hand and eye movements (e.g., Sheliga et al. 1994; Tipper et al. 1997). According to this theory a possible target location is represented by a large population of neurons that encode the target vector.

The value of such a vector is related to the salience of the corresponding object. When two objects are positioned in close proximity, the vectors are combined to one mean vector, which will point to an intermediate position. In order to facilitate the correct responding, competition between the two active responses has to be resolved by inhibiting one of them. Inhibitory selection of one target over the other may shift the vector in such a way that it affects the final response to the target. The amount of deviation is related to the inhibition applied to the cancelled vector: the stronger the inhibition, the greater the deviation away will be.

The source of target selection is supposed to be achieved by two inhibitory mechanisms (Tipper et al. 1997). The first mechanism makes use of lateral inhibition between direction-coding cells within the motor map (Georgopoulos 1995). Direction coding-cells are grouped in such a fashion that they are positioned near cells coding the same direction. Since each cell has excitatory connections to cells that are near and inhibitory connections to more distant cells (Munoz and Istvan 1998), activated target cells can inhibit distractors (Tipper et al. 2000). If distractor activity is too high, this mechanism is not sufficient to resolve response conflict. In this situation, a second mechanism can suppress the distractor activity by 'reactive feedback' (Houghton and Tipper 1994). The level of inhibition is related to the amount of activity of the distractor and can lead trajectories to deviate away from the distractors.

In the described theories of Tipper et al. and Sheliga et al. inhibitory mechanisms play an important role. There are not many behavioral eye movement studies that address the nature of the inhibitory mechanisms. The exact location of a distractor has only shown to have a weak effect on the amount of inhibition in eye movement studies (McSorley et al. 2004; Sheliga et al. 1994). There is, however, an influence of target similarity in those objects that share features with the target element receive larger inhibition than objects that are different from the target (Ludwig and Gilchrist 2003).

The main goal of the present study was to investigate systematically the role of top-down (endogenous) factors on saccade trajectories. More specifically, we addressed the question whether the mere expectation that a distractor could appear at a specific location would influence the saccade trajectories. Furthermore, we wanted to determine whether a location at which no physical object is present could nonetheless be inhibited. To study the effect of expectancy, the design of the two experiments was such that it was likely that a distractor would be present in a known location. In both experiments a saccade target was presented. In 80% of the trials a distractor was presented (the distractor present condition). In the remaining 20% of the trials no distractor was presented (distractor absent condition). Observers were instructed to make a fast eye movement toward the target and ignore the distractor. The locations of the target and the distractor were known to the observer in advance. In Experiment 1 the location of this distractor was always the same, in Experiment 2 this location was cued by an endogenous, central cue. Eye movements were monitored and saccade deviation was computed by subtracting the amount of deviation in the distractor present and absent conditions with a baseline condition in which only a target was present. In this baseline condition, a distractor was never present, producing a condition in which observers never expected a distractor.

One may distinguish three possible outcomes: (1) if there is no deviation away in the condition in which the distractor is expected but not presented (the distractor absent condition), it would indicate that the mere endogenous expectancy of the appearance of a potential distractor is not reflected in eye movement trajectories. (2) If, however, in this condition deviation away from the distractor location is observed, it would imply that inhibition could be applied to a location at which no actual object is present. This would indicate that inhibition could be applied to locations that do not contain an actual object. (3) If there is deviation away in the condition in which a distractor is expected (the distractor absent condition), but the deviation away in the condition in which a distractor that is present is larger, this would indicate that both endogenous and exogenous activities are reflected in saccade trajectories and these effects summate. The endogenous inhibition is then applied because of the expectancy of an upcoming distractor, while exogenous inhibition is driven by the presentation of the distractor onset.

Experiment 1

In the first experiment, participants were instructed to make a fast eye movement toward an onset target. The target location was cued by a central arrow that appeared prior to target presentation. In 80% of the trials a distractor appeared simultaneously with the target. For each observer, this location was fixed across the whole experiment and participants were instructed in advance where the distractor, if it would be present, would appear. In the remaining 20% no distractor was present. To examine the influence on the saccade trajectory and to determine the standard trajectory of the participant's eye movement, a baseline condition was included in which there was no distractor during the whole session.

Method

Participants

Ten students of the Vrije Universiteit, aged between 18 and 35 years, served as paid volunteers. Three of the participants were male. All of them reported to have normal or corrected-to-normal vision and were able to discriminate the colors used in the experiment. They were naïve as to the purpose of the experiment.

340

All persons gave their informed consent prior to their inclusion in the study. The study was approved by the appropriate Ethics Committee and was therefore performed in accordance with the ethical standards laid down in the Declaration of Helsinki.

Apparatus

A Pentium II computer with a processor speed of 450 MHz controlled the timing of the events and recorded response times. Displays were presented on a Philips 21 in. SVGA monitor with a resolution of 1,024×768 pixels and an 85-Hz refresh rate. A second computer controlled the registration of the eye movements' data on-line. Eye movements were registered by means of an Eyelink tracker (SensoMotoric Instruments GmbH, Teltow, Germany). The system computes the pupil size and pupil center of both eyes using an infrared video-based tracking technology. The Eyelink system has a 250-Hz temporal resolution and an accuracy probability of 0.5°. Both eyes were monitored, but only the data from the left eye were analyzed. An eye movement was considered a saccade either when the movement velocity exceeded 35°/s or when the movement acceleration exceeded 9,500°/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.

Stimuli

See Fig. 1a 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 (0.27×0.27°) in the center of the screen which functioned as the fixation stimulus. After 600 ms an arrow (0.81×1.08°) appeared at fixation position pointing up or down. A delay of 800–1,300 ms then occurred followed by the onset of a light gray filled circle with a diameter of 0.54°. The onset location was related to the direction of the pointing arrow: if the arrow was pointing upward, the circle was presented 6.76° above the fixation point. If the arrow was pointing downward, the onset was presented 6.76° under the fixation point. In 80% of the trials, a diamond-shaped distractor (0.81×0.81°) appeared simultaneously with the target positioned 4.82° to the left (if the target was on the top of the screen) or to the right (if the target was on the bottom of the screen) of the target. This element was placed $x = \pm 3.81°$, $y = \pm 3.81°$ from the fixation point. This was counterbalanced across subjects. Figure 1b shows the possible target and distractor locations. The sequence of trials was randomly assigned to each participant.

Procedure and design

Participants received oral instructions before starting the experiment. They were instructed to fixate the center fixation point and the arrow well until they detected an onset and to move their eyes to the target element. It was stressed that one had to make a single accurate saccade toward the target element and that the distractor, if present, was always presented on the same location. This location was revealed to the observers prior to the experimental session. Participants heard a short tone when the saccade latency was higher than 600 ms. 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 toward 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 offset of the measuring device at the start of each trial.

Furthermore, to determine the baseline eye movement, participants performed the same task as in the experimental condition except that there was never a distractor present. This baseline condition consisted of 24 practice and 96 experimental trials. Baseline and experimental blocks were counterbalanced across participants.

Data analysis

If saccade latency was lower than 80 ms or higher than 600 ms the trial was removed from the analysis. Saccade latency was defined as the interval between stimulus display onset and the initiation of a saccadic eye movement. Moreover, trials were excluded from further analysis in which no saccades, too early or small saccades (< 3°) were made. Also trials in which blinks during the saccade occurred were omitted. If the endpoint of the saccade had an angular deviation of less than 22.5° from the center of the target, the saccade was classified as correct and further 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 four different measures: saccade deviation, saccade curvature, initial direction, and overall direction:

Saccade deviations were examined by calculating the mean angle of the actual saccade path relative to the angle of a straight line between the starting position of the saccade and its target. The mean angle of the actual saccade path was calculated by averaging the angles of the straight lines between the saccade starting position and the different sample points (e.g. Godijn and Theeuwes 2002a, b; Theeuwes et al. 2005; Van der Stigchel and Theeuwes 2005).

Fig. 1 Sequence of frames on a given trial in Experiment 1. After 600 ms the central fixation point was replaced by an *arrow* pointing to the target location. After a variable period of 600–1,300 ms the target appeared. In 80 percent of the trials a distractor was presented simultaneously with the target at a fixed location. Participants had to make an eye movement to the onset target as soon as it was presented. **b** The possible target and distractor locations. The possible target locations are indicated by the *black circles*, the distractor locations by the *diamond shapes*. For half of the participants the situation was mirrored
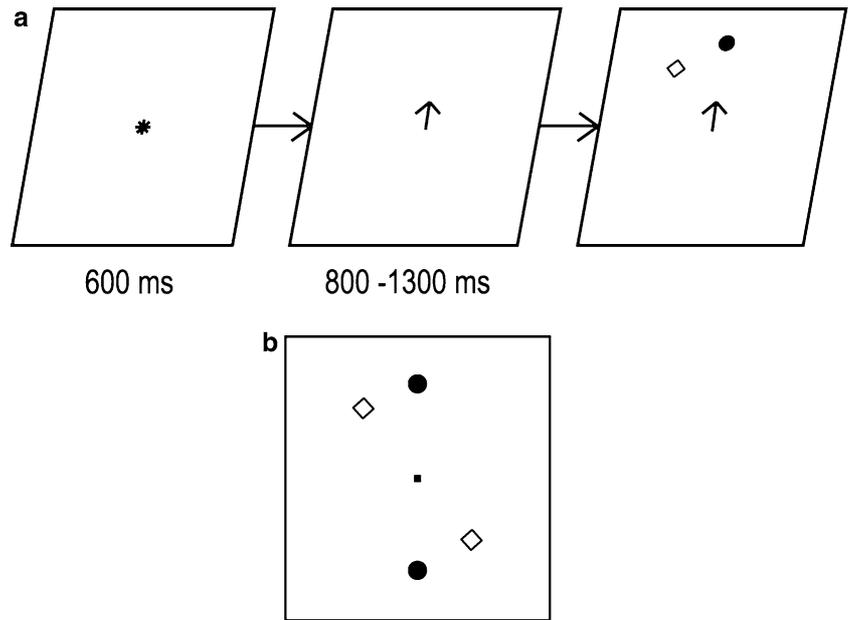
The overall direction was examined by calculating the difference between the angle of a straight line from fixation to saccade endpoint and the angle of a straight line from fixation to the target location (e.g. Frens et al. 1995; Van Gisbergen et al. 1987).

Initial direction was defined as the difference between the angle of the saccade at 20 ms after saccade initiation and the overall direction of the saccade (e.g. Findlay and Harris 1984; Van Gisbergen et al. 1987).

Saccade curvature was computed by the directional difference between the initial direction of a saccade and the overall direction (Van Gisbergen et al. 1987).

In previous studies we have used the deviation measure (Godijn and Theeuwes 2002a, b; Godijn and Theeuwes 2004; Theeuwes et al. 2005; Theeuwes and Godijn 2004; Van der Stigchel and Theeuwes 2005) because it takes both endpoint and initial direction into account and uses all the available data points. It computes in one measure the total *deviation* of the eye movement. It is however important to compare our measure to those that have been used before (for a detailed examination of different measures, see Ludwig and Gilchrist 2002).

For all measures, trials in which the angle of the overall direction was two times the standard deviation away from the mean angle were removed from the analysis. Positive and negative values refer to measurements toward and away of the distractor location, respectively. In the baseline and the no-distractor condition, saccades trajectories were measured with respect to the location where the distractor was presented in the distractor present condition.

To investigate the possible influence of the target location of the previous trial, we determined whether there was an effect of the target location of the previous trial on saccade trajectories on the current trial. When the saccade direction repeated, the target and the distractor location on the current trial were the same as on the previous trial. When, however, the direction switched, the target and distractor location on the current trial differed from the previous trial.

Results

The mentioned prerequisites led to a total loss of 20.7% of trials for the baseline condition and 18.2% for the experimental condition. Separate calculations were made for the experimental (distractor present or absent) and the baseline conditions.

Figure 2 shows the main results of the present experiment. In Fig. 2a the results of the different saccade trajectory measures for the three conditions are represented. Positive values refer to deviations toward, while negative values refer to deviations away. The baseline condition was taken as the baseline measurement against which the experimental conditions were compared. For all four measures roughly the same effects can be observed. As the trajectory measures were lower in the no-distractor condition than in the baseline condition, it can be stated that saccades deviated away in the no-distractor condition compared to the baseline condition. When the distractor was expected and also presented, this deviation away was greater. Saccade latencies are represented in Fig. 2b. All reported *t* tests are two-tailed.

Saccade deviation

An analysis of variance (ANOVA) on mean overall direction with condition (baseline, distractor present or absent), direction (up or down) and repeated direction versus switched direction trial as factors showed a main effect of condition (see Fig. 2a, $F(2,18) = 10.62$; $P < 0.01$).

342

Fig. 2 The main results of
Experiment 1. **a** The results of
the different saccade trajectory
measures for the three different
conditions. *Error bars* represent
standard errors of the mean. In
the baseline and the no-
distractor condition, saccades
trajectories were measured with
respect to the location where
the distractor was presented in
the distractor present condition.
Positive values refer to
deviations toward this location,
while negative values refer to
deviations away. The different
measures show roughly the
same effects. In the baseline
condition, there was a tendency
for saccades to deviate with a
consistent rightward bias.
Saccade trajectories in the
conditions in which a distractor
was expected but not presented
deviated away compared to the
baseline condition. When the
distractor was expected and
also presented, this deviation
away was greater. **b** Saccade
latencies are represented. There
was no difference between the
different conditions. Saccades
were faster upward then
downward
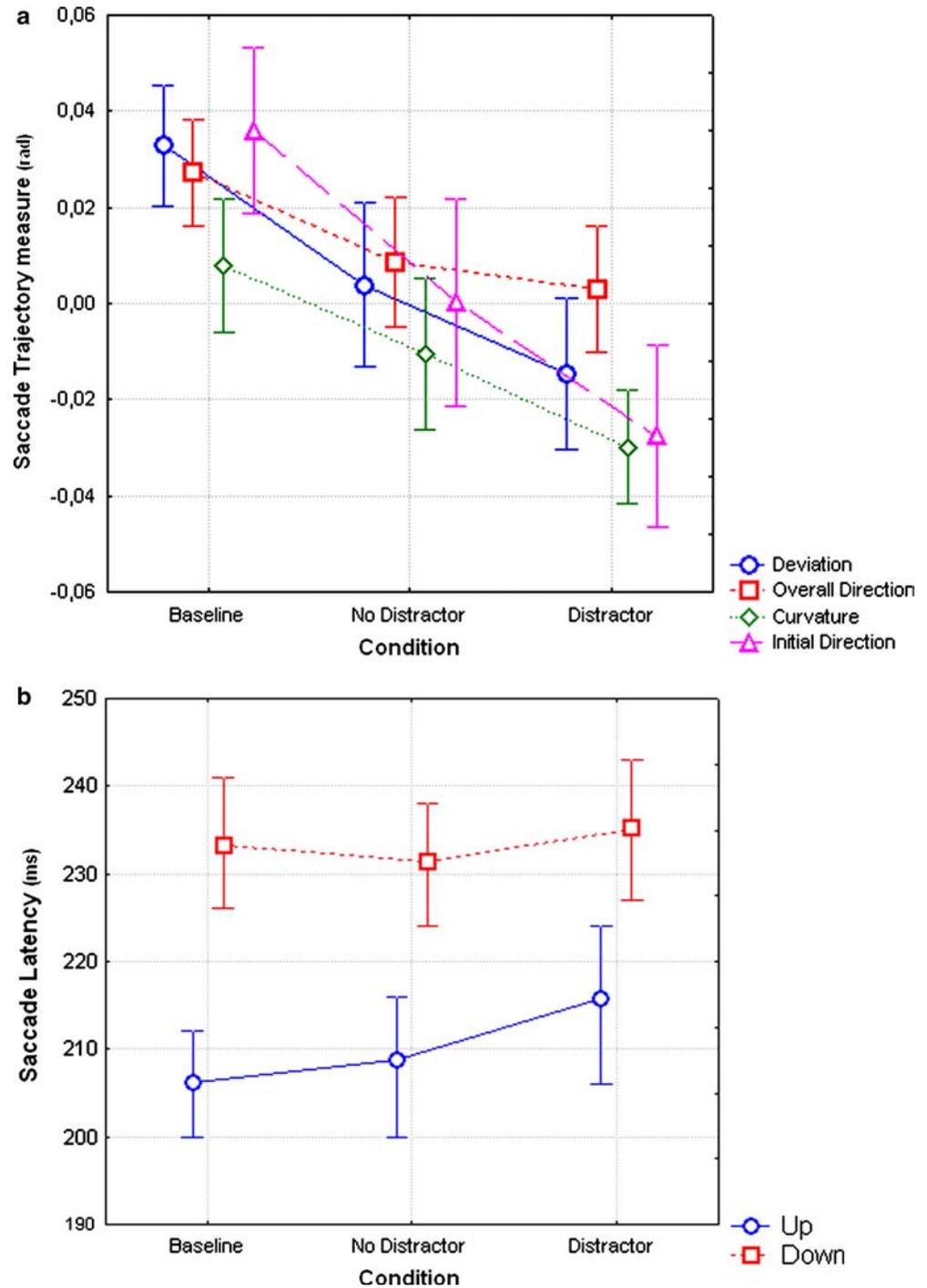
Note that direction ($F(1,9) = .21$; n.s.) and repeated
direction versus switched direction trials ($F(1,9) = 2.42$;
$P = 0.15$) were not reliable. Planned comparisons showed
that the baseline condition was significantly different
from the no-distractor condition ($t(9) = 5.51$; $P < 0.05$)
and the distractor condition ($t(9) = 15.95$; $P < 0.01$). Dis-
tractor and no-distractor conditions deviated away more
from the distractor location than the baseline condition.
The distractor condition deviated away more than the no-
distractor condition ($t(9) = 15.95$; $P < 0.01$).

Overall direction

An ANOVA on mean overall direction with condition,
direction and repeated direction versus switched direc-
tion trial as factors did not show a reliable effect of
condition ($F(2,18) = 3.46$; $P = 0.54$), direction ($F(1,9) = 0.12$; n.s.) and repeated direction versus switched direc-
tion trials (whether or not the target location on the
previous trial was the same as on the current trial)
($F(1,9) = 0.87$; n.s.).

Initial direction

There was a main effect of condition ($F(2,18) = 12.44$; $P < 0.001$). Other factors (direction and repeated vs. switched) were not reliable. Planned comparisons showed that the baseline condition was significantly different from the no-distractor condition ($t(9) = 6.40$; $P < 0.05$) and the distractor condition ($t(9) = 18.29$; $P < 0.01$). The initial direction in the distractor and no-distractor conditions showed greater deviation away from the distractor location than the baseline condition. The initial direction in the distractor condition showed greater deviation away than in the no-distractor condition ($t(9) = 11.21$; $P < 0.01$).

Saccade curvature

A reliable main effect of condition was observed ($F(2,18) = 5.356$; $P < 0.05$). The other factors were not reliable. Planned comparisons between the different conditions showed that the baseline condition was significantly different from the distractor condition ($t(9) = 8.95$; $P < 0.02$). The distractor condition curved away more from the distractor location than the baseline condition. The other comparisons were not statistically significant.

Order of presentation

To determine whether the order of presentation had an effect on the results, an additional ANOVA was run on saccade deviation with order (first experimental then baseline condition and vice versa) as a between-subject factor. Order of presentation had no effect ($F(1,8) = 0.17$, n.s.) suggesting that it did not matter whether participants first did the baseline condition and then the experimental condition or vice versa.

Saccade latency

To determine whether the different conditions had an effect on saccade latency, an ANOVA with condition and direction as factors was performed. There was only a main effect of direction ($F(1,9) = 29.70$; $P < 0.001$). Saccades upwards were faster (210 ms) than saccades downwards (233 ms). Condition had no systematic effect on saccade latency (see Fig. 2b, $F(2,18) = 2.03$; $P = 0.16$).

Discussion

In this experiment we examined the trajectory differences between eye movements to a target when a distractor was either absent or present. The experiment was designed in such a way that if inhibition (with the resulting saccade deviation) to an empty location would be possible, it would be revealed by a modulating effect on saccade trajectory. In each trial, it was very likely that a distractor would be presented, and if it would appear it was always at the same location.

Four different measures were used to investigate the influence of the different conditions on saccade trajectories: initial direction, overall direction, saccade curvature and saccade deviation. All measures show basically the same effect: compared to the baseline condition saccades deviate away in the distractor absent and present conditions. Only overall direction of the saccade failed to show a statistically reliable effect.

The strongest effects were observed for saccade deviation and initial direction. For these measures the eyes deviated away from an empty location where no actual physical object was present. As there is no exogenous stimulation at the distractor location, these results suggest that the expectation that a distractor may appear at a particular location is enough to generate an 'endogenous' effect on the saccade trajectory. Because it was highly likely that a distractor would be presented, participants may have already started to inhibit the distractor location during the preparation interval. Furthermore, in distractor present trials the deviation away was more than in the distractor absent condition. This additional inhibition reflects an exogenous component, which is applied in response to the onset of the object. In order to successfully fulfill the required task, the distractor needs to be ignored. This bottom-up inhibition seems to add up with the endogenous inhibition applied in the preparation of the upcoming distractor. Note that we do not claim that the effects of these two types of inhibition are completely additive because we do not have a measure of bottom-up inhibition in isolation.

One may argue that the observed deviation differences between distractor present and absent conditions have nothing to do with expectancy but with differences in saccade latencies between these conditions. There was however no effect of the different distractor conditions on saccade latencies suggesting that the presence or absence of a distractor did not alter the speed with which participants were able to respond.

One may further argue that the endogenous effect on saccade trajectories observed in our experiment is caused by some form of residual inhibition of the previous trial. This would imply a mechanism that is not necessarily under top-down control but represents something like residual automatic inhibition carry-over effects similar to 'negative priming' (Tipper 1985). The fact that inhibition is present on trials in which the distractor was absent might then be caused by the residual inhibition evoked by distractor presentation on the previous trial. Because of the low probability of distractor absence, there were not enough observations to directly test this idea. Instead, we determined whether there was an effect of the target location of the previous trial on saccade trajectories on the current trial. If the residual inhibition were indeed underlying the results, the inhibition would be larger when the target and the distractor locations on

the current trial are the same as on the previous trial. The analysis indicated no effect of the previous target location for all four measures on the saccade trajectory of the current trial.

To seek further evidence for the claim that the observed trajectory modulation can be attributed to the observers expecting a distractor at a particular location and not some residual bottom-up inter-trial effect, we conducted a second experiment in which we directly cued the distractor location with a central cue. This experiment aimed at investigating whether the preparatory inhibition can be applied to the distractor location on a trial-by-trial basis. In the previous experiment, the distractor location was fixed given the direction (up or down) of the saccade. In Experiment 2 four locations were assigned that could either be the target or the distractor location. Note that in this design a location could be a target location on one trial while being a distractor location on another. If endogenous inhibition is observed when a trial-by-trial cueing procedure is used, it would imply that the system is rather flexible in assigning inhibition to particular locations. We further wanted to investigate whether introducing more possible target and distractor locations would make it more difficult for the system to set up the spatial parameters for this inhibition.

Experiment 2

The second experiment was similar to the first experiment except there were four possible target locations and that not only the target location was cued, but also the distractor location was cued by a central, endogenous line segment. Again, a distractor was present in 80% of the trials. There was a low probability of repeating the same target location but then without a distractor, namely 4%. The four locations were assigned in such a way that target and distractor locations were positioned at 45° angular distance and that they were never presented in the same visual hemisphere.

Method

Participants

Twelve students of the Vrije Universiteit, aged between 17 and 31 years, served as paid volunteers. Two of the participants were male.

Stimuli, procedure, design and data analysis

See Fig. 3 for an illustration of the display sequence. Each trial started with the presentation of a 'star' character (0.27×0.27°) in the center of the screen, which functioned as the fixation stimulus. After 600 ms two lines of different length (0.81 and 0.54°) appeared at fixation position both pointing in one of the four possible directions: 1, 5, 7 or 11 o'clock. The two lines were always presented in pairs, pointing either up or down (in other words, the two possible combinations were 11 and 1 o'clock and 5 and 7 o'clock). A delay of 800–1,300 ms then occurred followed by the onset of the target. The onset location was related to the direction of the longer line: i.e., if the line was pointing to 1 o'clock, the target was presented at the corresponding location on an imaginary circle with radius 6.76°. In 80% of the trials, a diamond shape distractor (0.81×0.81°) appeared in the direction of the smaller line on an imaginary circle with radius 4.82°. The sequence of trials was randomly assigned.

The experiment consisted of a training session of 24 trials and an experimental session of 600 trials. The baseline condition was run before or after the experiment. After 24 training trials, participants had to perform the same task as in the experimental condition for 96 trials with the only difference that in this condition a distractor was never present. The order of the baseline and experimental blocks was counterbalanced across participants. For data analyses, the same prerequisites as in Experiment 1 were applied.

Results

These prerequisites led to a total loss of 17.1% of trials for the baseline condition and 17.5% for the experimental condition. Separate calculations were made according to whether the distractor was presented or not and for the baseline measurement.

The main results of the present experiment can be seen in Fig. 4. Figure 4a presents the results of the different saccade trajectory measures for the three conditions. For all four measures roughly the same effects can be observed as in Experiment 1. Compared to the baseline condition, saccades in the conditions in which a distractor was expected but not presented deviated away. When the distractor was expected and also presented, this deviation away was greater. All reported t tests are two-tailed.

Saccade deviation

An ANOVA on saccade deviation with condition (baseline, distractor present or absent) and target location (1, 5, 7, 11 o'clock) as factors showed a main effect of condition (see Fig. 4a, $F(2,22) = 14.59$; $P < 0.001$) and location ($F(3,33) = 3.94$; $P < 0.05$). Planned comparisons showed that the baseline condition was significantly different from the no-distractor ($t(11) = 12.52$; $P < 0.01$) and the distractor conditions ($t(11) = 16.75$; $P < 0.01$). Saccades in the distractor and no-distractor conditions deviated away more from the distractor location than saccades in the baseline condition. Saccades in distractor

Fig. 3 a Sequence of frames on a given trial in Experiment 2. After 600 ms the central fixation point was replaced by two line segments. The long line segment indicated the target location and the small one the distractor location. After a period of 600–1,300 ms the target appeared. In 80% of the trials a distractor was presented at the distractor location. Participants had to make an eye movement to the onset target as soon as it was presented. **b** The possible target and distractor locations. The possible target locations (1, 5, 7, 11 o'clock) are indicated by the *black circles*, and the distractor locations by the *diamond shapes*
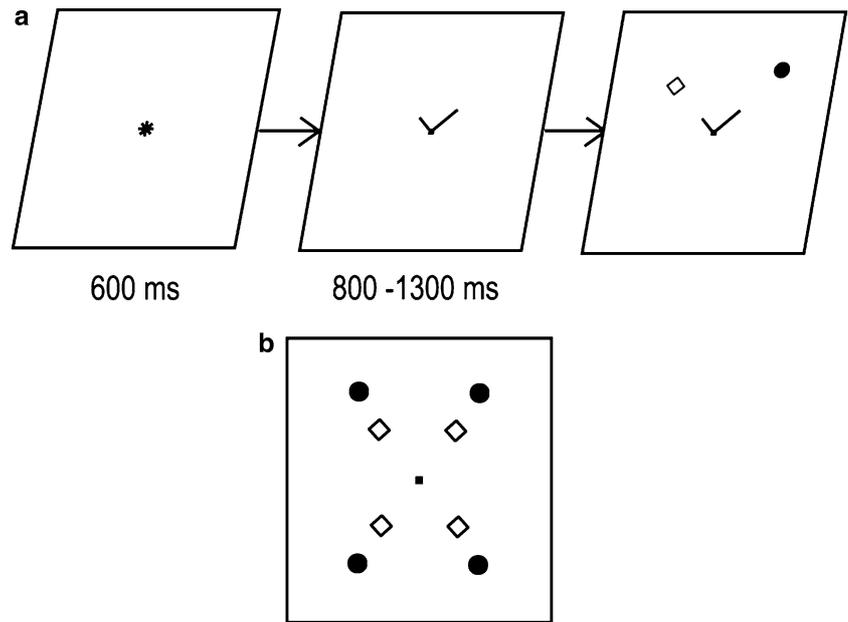
condition deviated away more than saccades in the no-distractor condition ($t(11) = 9.51$; $P < 0.02$).

A subsequent post-hoc test (Newman–Keuls) showed no systematic effect of location on saccade deviation. Again, there was no effect of the order of testing on saccade deviation ($F(1,11) = 0.32$; n.s.).

Overall direction

An ANOVA on the overall direction with condition and target location as factors showed no main effect of condition ($F(2,22) = 1.97$; $P = 0.16$). There was a main effect of location ($F(3,33) = 9.75$; $P < 0.01$).

Initial direction

There was a main effect of condition ($F(2,22) = 12.47$; $P < 0.001$) and location ($F(2,22) = 4.47$; $P < 0.02$) on the initial direction. Planned comparisons on the condition factor showed that the baseline condition was significantly different from the no-distractor ($t(11) = 10.89$; $P < 0.01$) and the distractor conditions ($t(11) = 13.94$; $P < 0.01$). The initial direction in the distractor and no-distractor conditions showed greater deviation away from the distractor location than the baseline condition. The initial direction of the distractor condition showed greater deviation away than in the no-distractor condition ($t(11) = 9.40$; $P < 0.02$).

Saccade curvature

A reliable main effect of condition ($F(2,22) = 7.26$; $P < 0.01$) and location ($F(2,22) = 5.95$; $P < 0.01$) was observed. Planned comparisons between the different

conditions showed that the baseline condition was significantly different from the no-distractor ($t(11) = 7.78$; $P < 0.02$) and the distractor conditions ($t(11) = 8.02$; $P < 0.02$). The distractor and the no-distractor conditions curved away more from the distractor location than the baseline condition. The comparison between the distractor and the no-distractor condition was not statistically significant ($t(11) = 2.84$; $P = 0.12$).

Saccade latency

It was further determined whether the different conditions had an effect on saccade latency. An ANOVA revealed that there was no difference in saccade latency between the baseline (229 ms) and the two conditions in the experimental set-up (230 ms for the no-distractor and 229 ms for the distractor conditions) (see Fig. 4b; $F(2,22) = 0.07$, n.s.).

Discussion

The results of this experiment confirm the most important conclusions derived from our first experiment. Compared to the baseline condition in which a distractor was never present, eye movement trajectories deviated away from a location at which participants expected that a distractor would appear. Since there was no object present at the inhibited location this inhibition must be endogenous in origin. However, when the distractor was present along with the target, the deviation away from the onset distractor was stronger than in experimental trials in which the distractor was absent. This greater inhibition is related to the suppression of the activity evoked by the onset of

Fig. 4 The main results of Experiment 2. Figure 4a shows the results of the different saccade trajectory measures for the three different conditions. The different measures show roughly the same effects. Saccade trajectories in the conditions in which a distractor was expected but not presented deviated away compared to the baseline condition. When the distractor was expected and also presented, this deviation away was greater. In Fig. 4b saccade latencies are represented. There was no difference between the different conditions
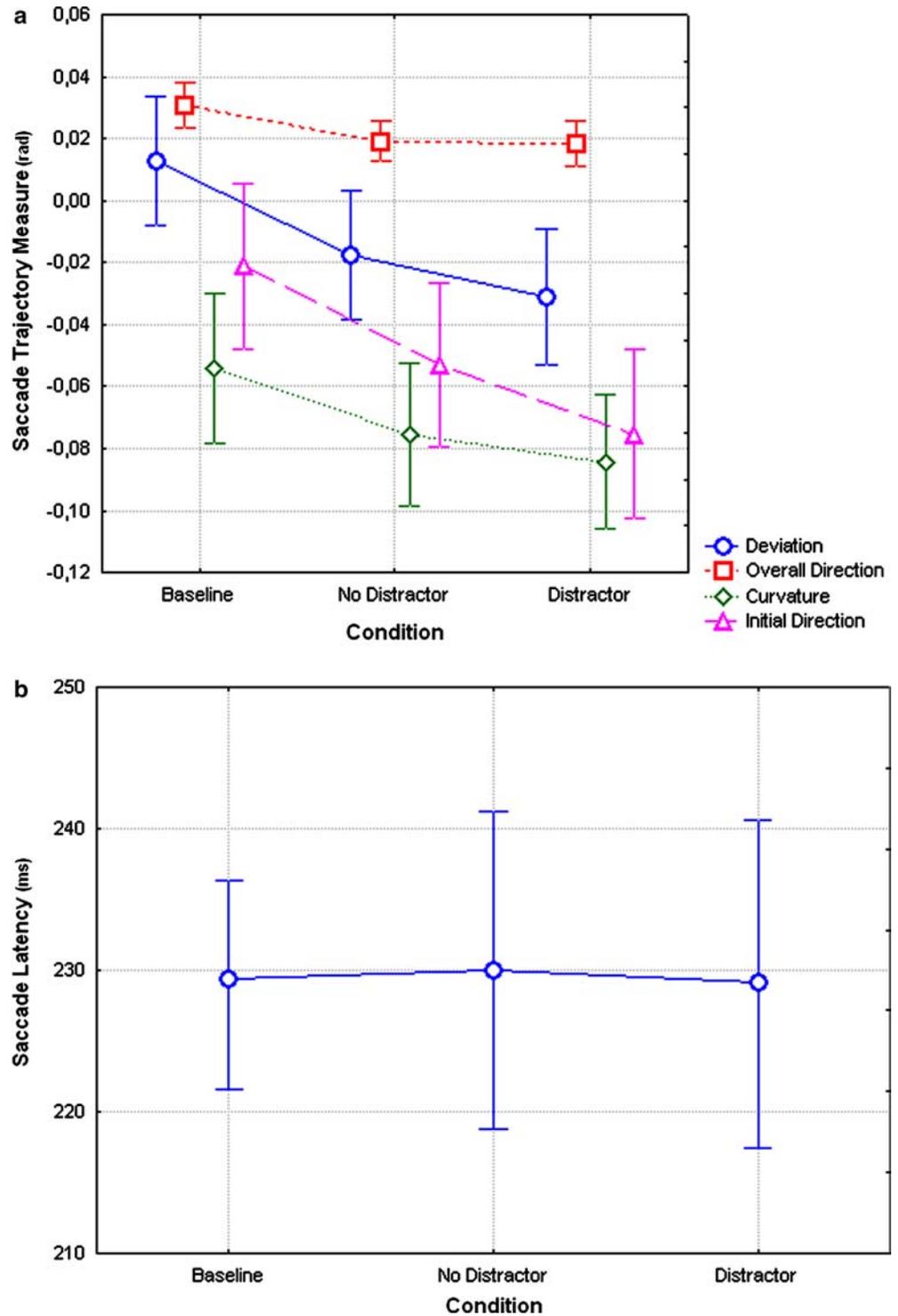
the distractor. These results were also observed for the initial direction of the saccade. There was no effect of the different conditions on the overall direction of the saccade. Again, there was no effect of the different distractor conditions on saccade latencies. Therefore, the findings with respect to the trajectory differences cannot be attributed to the variations in saccade latencies.

The present experiment provides further evidence for the idea that the preparatory inhibition could be applied to the distractor location on a trial-by-trial basis and is not caused by some form of residual inhibition of the previous trial. Compared to Experiment 1, there was a much lower probability of repeating the same target location without a distractor when on the previous trial a distractor was present. Yet, the magnitude of the

expectation effect on the saccade trajectory deviations was similar in both experiments[1].

General discussion

In order for the saccadic system to select the appropriate target location for an eye movement, other possible locations have to be deselected. Different authors have hypothesized that this selection is accomplished through inhibition (Sheliga et al. 1994; Tipper et al. 1997). The inhibition occurring in the oculomotor system can be determined by examining the saccade trajectory deviations. More deviation away from a distractor location indicates stronger inhibition at the distractor location. In two experiments we investigated whether the preparation for an upcoming distractor can result in saccade deviations.

With respect to the saccade deviation and the initial saccade direction, the most important finding of the present study is that the mere *expectation* that a distractor will appear at a specific location is enough to generate saccade deviations away from this location. The crucial finding is that there was a significant deviation even when no physical object was present. In addition, when an actual distractor would appear at the expected location, the saccade deviation was even stronger. We have further provided evidence that the trajectory effects cannot be attributed to either the saccade latency variations or to the residual inhibition from the previous trial.

In terms of the vector theory the current findings indicate that on the basis of the expectancy of the distractor, the vector representing the distractor location is inhibited before the distractor presentation. As the target and the distractor vectors are represented by overlapping populations, inhibition of the distractor vector will result in the reported saccade trajectory modifications. When the distractor is not only expected but also presented, the activity evoked by the onset of the distractor will be suppressed by the reactive feedback mechanism as proposed by the vector theory (Houghton and Tipper 1994; Tipper et al. 1997). This inhibition will summate with the inhibition that was applied on the basis of expectancy, resulting in a greater deviation away from the distractor location. Although the explanation remains speculative, the present findings seem to elaborate on the vector theory by showing that the mere expectancy of distractor presentation can already evoke the inhibition of the vector coding for the possible distractor location.

To examine the influence of the different conditions on saccade trajectories, we used four different measures: saccade deviation, overall direction, initial direction and saccade curvature. Results show that the most pronounced results were obtained for saccade deviation and initial direction. With respect to the measure "overall saccade direction", there was no effect of the different conditions. This measure uses the actual saccade endpoint and compares it to a straight line from the saccade starting point to the target location.

Although the different conditions had an effect on curvature measure (Van Gisbergen et al. 1987), these effects were not as pronounced as the effects of the initial saccade direction and the deviation measure. The adopted curvature measure computes the difference between the initial direction of a saccade and the overall direction. As the most important findings were due to the initial direction of the saccade, introducing a measure that computes the difference with saccade endpoint (which showed no significant effects) might have introduced additional noise to the data. The deviation measure (Godijn and Theeuwes 2002b) takes all data points of the saccade into account and might therefore be less sensitive to noise.

There was no effect of the different distractor conditions on saccade latency. Typically, saccade latencies are longer in conditions in which distractors are present (see e.g., Godijn and Theeuwes 2002b). The reason that we did not find an effect of the presence of a distractor in the current experiment may be due to the fact that in the current experiment the appearance of a distractor was highly predictable and if it was presented it was always presented at the same location. Our results indicate that under these conditions, observers may endogenously inhibit the location of the distractor before it is actually presented. This inhibition may be sufficient for the distractor to have no effect on the speed with which observers can generate an eye movement.

Many models have assumed that saccadic target selection is the result of competitive interactions among groups of neurons coding the possible target locations on a common motor map (Godijn and Theeuwes 2002b; Kopecz 1995; McSorley et al. 2004; Trappenberg et al. 2001). The superior colliculus (SC) is thought to operate as a motor map according to theoretical models of saccade target selection (Schall 1991; Sparks and Hartwich-Young 1989). This mid-brain structure contains a retinotopically organized map and neural activity in the SC is correlated with target selection (McPeek and Keller 2004; Wurtz et al. 1980). Furthermore when multiple targets are present, activity at the site of the target in the SC is increased, whereas it is decreased at other sites (Basso and Wurtz 1997), leading to the hypothesis that the SC is involved in target selection. To accomplish this, the SC integrates input from many cortical areas such as the frontal eye fields, the supplementary eye fields, the posterior parietal cortex and occipital visual areas (Munoz 2002). It sends the result of this integration process to the brainstem premotor

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[1]To test whether there was a difference in the magnitude of the expectation effect on the saccade trajectory deviations between the two experiments, we run a mixed ANOVA with Experiment as a between-subjects factor. There was no interaction between Experiment and condition ($F < 1$) suggesting that the magnitude of the expectation effect was similar in both experiments. There was no main effect of Experiment ($F < 1$).

circuitry where the eye movement is programmed (Moschovakis 1996). New evidence suggests that the region of maximal activity determines which target is going to be foveated, but not how this is to be brought about (e.g., via a saccade, or a combined eye and head movement, or via smooth pursuit) (Bergeron et al. 2003).

Although the SC does not determine the exact trajectory of a saccade (Bergeron et al. 2003; Goossens and Van Opstal 2000; Quaia et al. 1998), its activity does seem to play an important role in the oculomotor process of the programming of an eye movement. For example, McPeek et al. (2003) conducted single-cell recordings in the SC and found deviation toward a second onset location. They showed that this deviation was accompanied by increased presaccadic activity at the location where the trajectory curved toward. More important, the magnitude of this deviation was correlated with the level of activity recorded at this location. Further evidence was provided in the same study by microstimulation of the SC. Eye movements that were initiated to a different location, curved toward the stimulated location. The magnitude of this deviation was correlated with the induced activity.

McSorley et al. (2004) proposed a model in which the initial saccade direction is controlled by the SC, but the cerebellum takes care of the deviation back toward the target (see also Quaia et al. 1998). The cerebellum monitors saccade progress and compensates for directional errors by adjusting the motor signal. So, while initially the direction of the saccade is programmed to a location that is not the target location, on-line cerebellum feedback takes care of the correct landing position. This notion fits well with our finding that the endpoint of the saccade, in contrast to the initial saccade direction, was not influenced by the presence of a distractor. This suggests some type of independence between the mechanisms that control the saccade endpoint and those that control the initial direction.

The crucial finding of the present study is that the mere *expectation* that a distractor will appear at a specific location is enough to generate saccade deviations away from the location of the expected distractor. The results suggest that higher-order cognitive processes such as top-down expectancy can interact with low-level eye movement structures. One of the most likely neurophysiological candidates for this higher-order influence is the frontal eye fields (FEF) which send major projections to the SC. Input of the FEF to the SC is mediated through the substantia nigra of the basal ganglia (Basso and Wurtz 1997, 2002). It has been assumed that the FEF send inhibitory connections to the SC via the basal ganglia (Munoz and Schall 2003). The FEF input shows a coarse topology in that nearby cortical cells tend to project to the same region of the SC (Komatsu and Suzuki 1985). Responses in the FEF are responsive to task demands which are shown for example by different responses to targets and distractors (Bichot and Schall 2002). In visual search, the FEF have been shown to select one population of activity as the target and inhibit the distractor location (Schlag-Rey et al. 1992).

On the basis of neurophysiological findings, it can be concluded that the FEF provide a possible source for top-down modulation of target selection and distractor inhibition. Many models have therefore incorporated the FEF as a possible source of how higher-level processes can influence the saccade generation (Gancarz and Grossberg 1999; Godijn and Theeuwes 2002b; McSorley et al. 2004). On the basis of the results of the current study, we hypothesize that if a distractor is expected to appear at a certain location, in anticipation of the distractor appearance, FEF inhibits the population of neurons coding for that location. The top-down inhibition that enters the motor map facilitates correct responding when target and distractor are presented, because activity at the distractor location will already be lowered on distractor onset. The activity evoked by the distractor will therefore be much less than without top-down inhibition and the competition between the target and distractor can then be correctly won by the target location. When the distractor is actually presented along with the target, the activity evoked by the onset of the distractor will also be inhibited by the FEF to facilitate responding. This inhibition summates with the top-down expectancy inhibition and results in a deviation away that is greater than when the distractor is only expected and not presented.

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