

Exp Brain Res (2008) 186:431–442
DOI 10.1007/s00221-007-1243-2

RESEARCH ARTICLE

Distractor effects on saccade trajectories: a comparison of prosaccades, antisaccades, and memory-guided saccades

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Received: 27 August 2007 / Accepted: 3 December 2007 / Published online: 18 December 2007
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Abstract The present study investigated the contribution of the presence of a visual signal at the saccade goal on saccade trajectory deviations and measured distractor-related inhibition as indicated by deviation away from an irrelevant distractor. Performance in a prosaccade task where a visual target was present at the saccade goal was compared to performance in an anti- and memory-guided saccade task. In the latter two tasks no visual signal is present at the location of the saccade goal. It was hypothesized that if saccade deviation can be ultimately explained in terms of relative activation levels between the saccade goal location and distractor locations, the absence of a visual stimulus at the goal location will increase the competition evoked by the distractor and affect saccade deviations. The results of Experiment 1 showed that saccade deviation away from a distractor varied significantly depending on whether a visual target was presented at the saccade goal or not: when no visual target was presented, saccade deviation away from a distractor was increased compared to when the visual target was present. The results of Experiments 2–4 showed that saccade deviation did not systematically change as a function of time since the offset of the target.

Moreover, Experiments 3 and 4 revealed that the disappearance of the target immediately increased the effect of a distractor on saccade deviations, suggesting that activation at the target location decays very rapidly once the visual signal has disappeared from the display.

Keywords Trajectory · Anti-saccades · Memory-guided saccades · Inhibition · Superior colliculus

Introduction

Saccades do not move the eyes in a straight line: many studies have now demonstrated that saccade trajectories do not necessarily follow the shortest route from fixation to target, but deviate depending on environmental and situational factors (e.g., Aizawa and Wurtz 1998; Erkelens and Sloot 1995; Port and Wurtz 2003; Sheliga et al. 1995; Van der Stigchel et al. 2006; Viviani and Swensson 1982; Walton et al. 2005; Yarbush 1967). Perhaps distractors are the best example of such factors, stimuli that are irrelevant to the task. Several studies have shown that visual distractors close to the path between the current fixation and the target can cause a consistent deviation of saccades (e.g., Doyle and Walker 2001; Godijn and Theeuwes 2004; McSorley et al. 2005; Van der Stigchel and Theeuwes 2005). The visual distractor does not even have to be present at the time of the saccade to have its effect: saccades will deviate away from locations of covert spatial attention (Rizzolatti et al. 1994; Sheliga et al. 1995), from locations where objects are expected to appear (Van der Stigchel and Theeuwes 2006), and from locations that are held in visual short-term memory (Theeuwes et al. 2005). Moreover, distractors do not have to be visual: saccade deviations have also been induced by irrelevant lateralized auditory and somatosensory signals (Doyle and Walker 2002). Thus, it seems that saccades may deviate

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whenever there is an additional event that requires spatial processing. Whereas saccadic trajectories in most studies, including the studies referred to above, deviate away from a distractor, it has been demonstrated that saccades may also deviate toward a location. For instance, saccadic deviation toward a distractor has been shown in visual search experiments in humans (Godijn and Theeuwes 2002; McPeck et al. 2000; Walker et al. 2006) and monkeys (McPeck et al. 2003; McPeck and Keller 2001; Port and Wurtz 2003).

Deviations in saccade trajectories are considered to arise from competition between different neural populations during saccade programming, in the same manner that saccade target selection emerges from competitive interactions between populations of neurons coding possible target locations on a common motor map (e.g., Godijn and Theeuwes 2002; Kopecz 1995; Trappenberg et al. 2001). While there are multiple parallel routes and areas involved in saccade generation (Schall 1995; Sparks and Hartwich-Young 1989; Wurtz et al. 2000), the superior colliculus has often been suggested as the site of this common motor map (e.g., Godijn and Theeuwes 2002; Kopecz 1995; Trappenberg et al. 2001). The superior colliculus is topographically organized, in that the locations of neural activity within this structure correspond to specific regions in visual space in an orderly arrangement (e.g., Robinson 1972; Schiller and Stryker 1972; Wurtz and Goldberg 1972). The superior colliculus also receives input from higher visual and ocular motor cortical regions such as the frontal eye field and the lateral intraparietal area (Munoz 2002; Tehovnik et al. 2000), as well as lower visual areas such as striate cortex (e.g., Schiller 1977; Wurtz et al. 2000). Thus this structure is a plausible site for the integration of neural signals into a spatial code for saccade selection.

Several authors have proposed that a weighted average of the activity in the motor map determines the direction of saccades (e.g., Tipper et al. 2001; Van der Stigchel et al. 2006). If so, resolution of unwanted competition between multiple active locations is an important pre-requisite of accurate saccade programming. For example, activity generated by an irrelevant distractor requires inhibition at its location to preserve saccade accuracy (e.g., Godijn and Theeuwes 2002; McSorley et al. 2004; Sheliga et al. 1994; Tipper et al. 2001). As a result, the weighted average of neural populations coding different locations may incorporate both facilitation at the target location and inhibition at the distractor location. The integration of distractor inhibition into the calculation of saccade trajectory may cause the saccade vector to transiently deviate away from the inhibited location; leading to a deviation of the saccade trajectory. If however, the target location has not yet been identified and competition between multiple active locations is unresolved, the distractor location may be facilitated more than the target location. In this case, the

weighted average would cause the saccade vector to transiently deviate toward the most active location and deviation toward the distractor location may be observed as a result. For example, this may be the case when saccade latencies are short and top-down inhibition has not yet been established at the time the eye movement was programmed (McSorley et al. 2006; Walker et al. 2006).

This concept of trajectory deviation away as arising from an interaction between facilitatory activity at the target location and inhibitory activity at the distractor location has been investigated primarily by studies manipulating the distractor. Results have shown that when the distractor is successfully inhibited, saccades deviate away from its location. Moreover, the amount of deviation away from a location was found to be correlated with the amount of inhibition applied to that location. For example, in a study conducted by Ludwig and Gilchrist (2003) observers made saccades to a colored target in one of two positions on the vertical meridian, while an irrelevant distractor that was similar or dissimilar in color to the target appeared on some trials left or right of the vertical meridian. Saccade deviation away from the distractor was larger when the onset was similar in color to the target, which was attributed to a need for greater inhibition when the distractor was more likely to be confused with the target (see also, Godijn and Theeuwes 2004).

While variations in trajectory deviation as a function of the irrelevant distractor provide useful support for the interaction hypothesis, it is also true that the hypothesis predicts that deviation should vary as a function of the target. If saccade deviation emerges from the balance of activity between target and distractor locations, then the level of activation at the target location should modulate saccade deviation just as distractor activation does. However, the effect of different activation levels at the target location has never been directly investigated.

In the present study we contrast the efficacy of distractors on prosaccades, antisaccades and memory-guided saccades. In both the antisaccade and the memory-guided saccade task, there is no visual stimulus at the location of the saccade goal, and behavioral data show longer reaction times and reduced accuracy compared to prosaccades (e.g., Gnadt et al. 1991; Krappmann et al. 1998; White et al. 1994). These facts suggest that the degree of activation at the goal location of antisaccades and memory-guided saccades may be reduced compared to prosaccades. Indeed, there are neurophysiologic data to support this assertion. For example, saccade-related discharges in the superior colliculus are reduced when there is no visual stimulus at the saccade endpoint (Edelman and Goldberg 2001, 2003), and neurons in the superior colliculus show attenuated stimulus- and saccade-related activity during antisaccades, compared with prosaccades (Everling et al. 1999). If saccade

deviation is explained by a balance between excitatory activity at the goal location and inhibitory activity at the distractor location in a motor map, then reduced goal location activity should cause the same distractors to generate greater trajectory deviation in antisaccades and memory-guided saccades than in prosaccades. More specifically, the distractor location will be relatively more active in the anti- and memory-guided saccades, as the target stimulus is either further away in space (i.e., antisaccade) or in time (i.e., memory-guided saccade) from the distractor and the saccadic goal. Competition thus strongly favors the distractor item. As such, relative to the pro-saccade, to execute a correct antisaccade or memory-guided saccade requires more inhibition to overcome the increased activity at the distractor location, and this is expected to cause greater deviation away from the distractor in the anti- and memory-saccade.

Experiment 1

Participants completed a prosaccade, an antisaccade and a memory-guided saccade block. In the antisaccade task, observers are required to make an eye-movement in the direction opposite to that where the visual target is located (Hallet 1978; Hallet and Adams 1980). In the memory-guided saccade task, participants are shown a visual target but are required to withhold the immediate orienting response, and to make this eye-movement only after a short time-interval during which the location of the target must be held in short-term memory (Fischer and Boch 1981). Participants thus make an eye-movement to a memorized, empty location in space. In all three tasks (i.e., prosaccade, antisaccade and memory-guided saccade) trajectories to the saccade goal when no additional distractor was present were compared to trajectories to the saccade goal when the irrelevant distractor was present. The difference in curvature between the distractor present and absent condition yielded a measure of deviation. Whereas a visual target is present at the saccade goal in the prosaccade task, there is no visual target at the saccade goal in both the antisaccade and memory-guided saccade task. If saccadic deviation is modulated by the presence of a visual stimulus at the saccadic goal-location, we expect to find differences between trajectories in the prosaccade task compared to the antisaccade and the memory-guided saccade task.

Method

Participants

Ten observers, aged between 20 and 47 years old, participated in the experiment. Five of the participants were

females. All reported having normal or corrected-to normal vision. All subjects gave informed consent and the protocol was approved by the institutional review board of the university, and conducted in accordance with the principles of the Declaration of Helsinki.

Apparatus

Participants performed the experiment in a dimly lit room and viewed the display monitor from a distance of 70 cm. Eye movements were recorded by an Eyelink-II system (SR Research Ltd, Canada), an infra-red video-based eye tracker that has a 500 Hz temporal resolution and a spatial resolution of 0.01° . The subject's head was stabilized with a chin and forehead rest, and an infrared head-mounted tracking system compensated for any residual head motion. The left eye was monitored in all subjects.

Stimuli

All figures (fixation, target, distractor) were white (40 cd/M2) elements on a black background of luminance (0.6 cd/M2), as measured with an OptiCal photometer (Model OP200-E, Cambridge Research Systems). Each trial started with the presentation of a “plus” character ($0.94^\circ \times 0.94^\circ$) in the center of the screen that functioned as the fixation stimulus. After a variable period of 400–800 ms, the target appeared (a solid circle with a diameter of 0.94°) located at an eccentricity of 8.1° on the vertical meridian, either in the upper or lower field. In a third of trials, the target was the only element presented. In the remaining two-thirds, a diamond-shaped distractor (sides measuring $1.09^\circ \times 1.09^\circ$) appeared at the moment the fixation-point offset. The distractor was presented 6.26° away from fixation in the horizontal direction and 4.69° away in the vertical direction: half of the distractors were located to the left of the saccade goal and half to the right.

Procedure and design

Each block started with a nine-point grid calibration procedure. 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.

Participants were instructed to fixate the center fixation-cross and to make a saccade to the appropriate goal of each trial when the fixation-cross disappeared: it was stressed that they should try to do this with a single accurate saccade. In prosaccade trials, the saccade goal was the target circle presented throughout the duration of the trial. In anti-saccade trials, the saccade goal was the location opposite to that of where the visual target was presented (i.e., the

mirrored position across the horizontal midline). In both prosaccade and antisaccade trials, the target appeared at the same time that the fixation-cross disappeared, after a variable period of 400–800 ms of fixation. In memory-guided saccade trials, the target appeared after a variable period of 400–800 ms of fixation and remained visible for 500 ms, following which the fixation point remained on, disappearing after an additional 1,500 ms. Participants had to maintain fixation until the fixation cross disappeared, and then make a saccade to the location where the target had been presented. If a distractor was presented, it always appeared in the vertical half containing the saccade goal. In all conditions, the distractor appeared with offset of the fixation point.

The experiment consisted of three blocks each consisting of a training session of 24 trials and an experimental session of 192 trials. Participants heard a short tone when their saccade latency on a given trial was longer than 600 ms or shorter than 80 ms. The sequence of trials was randomized for each participant, in terms of both target location (upper or lower field) and distractor condition (distractor left, right or absent). Participants were instructed prior to the experiment block and were allowed to take breaks in between blocks.

Data analysis

An eye movement was considered a saccade when either eye velocity exceeded $35^\circ/\text{s}$ or eye acceleration exceeded $9,500^\circ/\text{s}^2$. Saccade latency was defined as the interval between the offset of the fixation point and the initiation of a saccade eye movement. If saccade latency was shorter than 80 ms, or longer than 600 ms or 2.5 standard deviations from the subject's mean latency, the trial was removed from analysis. Trials were excluded if there was no saccade or the first saccade was too small ($<3^\circ$). 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 2° from the center fixation point for the vertical and 1° for the horizontal direction. Based on these criteria, 6.3% of trials were removed in the prosaccade block, 14.7% in the antisaccade block, and 15.9% of the trials were excluded in the memory-guided saccade block.

Deviation was defined as the difference in mean angle of the observed saccade path and the shortest path (i.e., straight line) measured from the saccade starting position and the target location. The mean angle of the saccade path in a single trial was calculated by averaging the angles of the straight line between the saccade starting position and the different sample points (for a more detailed overview of saccade trajectory computation, see Van der Stigchel et al.

2006). For each saccade in a trial with a distractor we compared its mean path angle to that of the averaged mean-path-angles of all saccades in trials without a distractor, to determine if the saccade in that specific distractor trial deviated toward or away from the location of the distractor. This then represented the distractor-induced deviation for that trial. Deviations were signed so that a positive value indicated deviation toward the distractor, and a negative value deviation away. Results were analyzed by a repeated measures ANOVA, with saccade type as a within-subject factor and subject as a random effect.

Distractor effects on latency were also assessed from the included trials. These were subjected to a repeated measures ANOVA with saccade type (prosaccade, antisaccade, and memory-guided saccade) and distractor condition (absent, present) as within subject factors, and subject as a random effect.

Results

The upper panel of Fig. 1 depicts the measure of distractor-induced deviation for the pro, anti, and memory saccade block. The negative values indicate that the eyes deviated away from the distractor. Distractor-induced deviation was

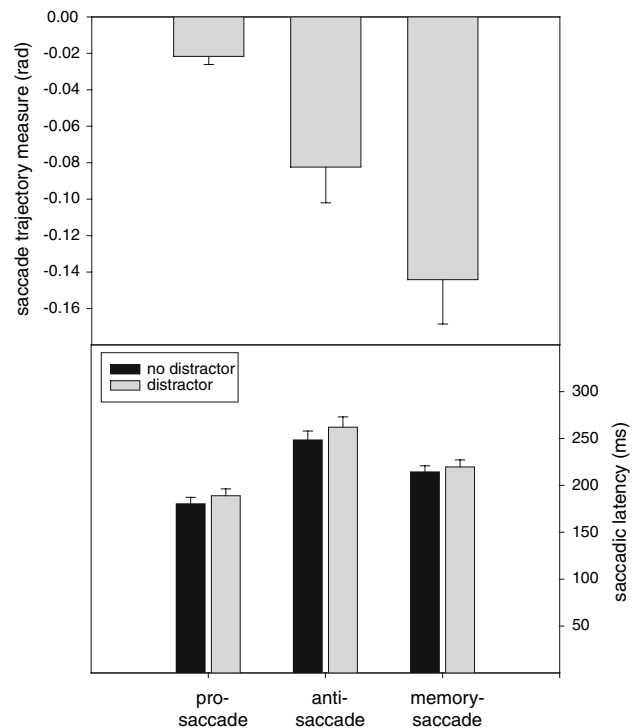


Fig. 1 Shows the results of the different saccade trajectory measures (*upper panel*) and the saccadic latency in the distractor present and absent conditions (*lower panel*) for the three different conditions in Experiment 1. Negative saccade trajectory measures indicate saccades deviated away from the distractor. *Error bars* represent standard errors of the mean

significantly different across the three saccade types ($F(2, 18) = 20.07$, $p < 0.0001$). Planned comparisons revealed larger deviation in antisaccades than in prosaccades ($F(1, 9) = 11.27$, $p < 0.01$), and yet larger deviation in memory-guided saccades compared to antisaccades ($F(1, 9) = 12.41$, $p < 0.01$).

For saccade latency, there was a significant main effect of saccade type ($F(2, 18) = 49.28$, $p < 0.0001$). Planned comparisons revealed that latencies were longer for antisaccades than prosaccades ($F(1, 9) = 93.70$, $p < 0.001$) or memory-guided saccades ($F(1, 9) = 21.80$, $p < 0.001$), and latencies of memory-guided saccades were longer than those of prosaccades ($F(1, 9) = 28.76$, $p < 0.001$). Such results are consistent with numerous reports comparing latencies of these different saccade types (e.g., Everling and Fischer 1998; Massen 2004; Mokler and Fischer 1999; Munoz and Everling 2004; Olk and Kingstone 2003). There was also a significant main effect of distractor condition ($F(1, 9) = 19.00$, $p < 0.005$), due to longer latencies when distractors were present. However, there was no significant interaction between condition and distractor ($F(2, 18) = 1.20$, $p > 0.1$).

Discussion

The key finding from Experiment 1 was that distractor-induced deviations in saccade trajectory varied significantly with the type of saccade. Distractors caused greater deviation in both memory-guided saccades and antisaccades compared to prosaccades, fulfilling the prediction of the interaction hypothesis and the results anticipated based on neurophysiological data that memory-guided saccades and antisaccades have less excitatory activity at the saccade goal than prosaccades (Edelman and Goldberg 2003; Everling et al. 1999).

However, the results also showed differences between memory-guided saccades and antisaccades. Distractor-induced deviation was largest in memory-guided saccades, followed by antisaccades, and smallest in prosaccades. Such results could be interpreted as indicating that the balance between distractor and saccade goal activity was most heavily tilted in favor of the distractor in memory-guided saccades and most heavily tilted in favor of the saccade goal in prosaccades, with the effect in antisaccades being intermediate.

What could lead to such a difference in distractor effects between all three types of saccades? One possibility to consider is the relationship between saccade latency and distractor-induced deviations. Some studies have found that short-latency saccades deviate toward while high-latency saccades deviate away from irrelevant distractors (McSorley et al. 2006; Theeuwes and Godijn 2004), and for saccades that deviate away from the distractor, higher latencies are

associated with greater deviation (McSorley et al. 2006). These latency effects could contribute to the reduced distractor-induced deviations seen with prosaccades, which have the shortest latencies of all three saccade types. However, while antisaccades had the longest latencies, they did not have the greatest distractor-induced deviations. Thus the pattern of results across all three saccade types does not resolve to a simple single correlation of distractor-induced deviation with latency (Walker et al. 2006).¹

Could there be additional factors at play during the complex antisaccade task that mitigate against a larger distractor-induced deviation? To execute an antisaccade, one must both create a novel response and simultaneously inhibit the stimulus-driven prosaccade to the visual stimulus (Everling and Fischer 1998). In contrast, during a memory-guided saccade one must also initially inhibit the prosaccade to the visual stimulus while maintaining fixation, but then release the saccade upon perceiving the disappearance of the fixation light. One possibility then, is that, during an antisaccade, inhibitory resources are being divided between inhibition at the distractor location and simultaneous inhibition at the stimulus site located opposite to the saccade goal. However, while this explanation may account for why antisaccades have less distractor-induced deviation than memory-guided saccades, it would also predict that antisaccades should have less rather than more distractor-induced deviation than prosaccades. Hence division of resources because of simultaneous inhibition at the stimulus location also cannot be the sole explanation of the distractor effects across all three saccade types.

A second possibility is that the more modest excitatory activity at the saccade goal of memory-guided saccades and antisaccades, due to the lack of a visual target, has a temporal dynamic. As with the programming of prosaccades, antisaccade programming may begin immediately upon presentation of the visual stimulus and identification (and activation) of the saccade goal. In contrast, a considerable period has passed since target identification occurred before the eyes are set in motion for a memory-guided saccade. It may be that the reduced activity at the target location for a memory-guided saccade declines further with the time elapsed since target presentation. If so, then the interval of 1,500 ms that we chose may have been associated with very weak target-related activity, allowing distractor effects to dominate the generation of saccade trajectory.

This explanation predicts that the amount of distractor-induced deviation observed in memory-guided saccades

¹ It should be noted, however, that the results of Walker et al. (2006) regarding a relationship between deviation and latency did not show a linear trend. Instead, it appeared that the amount of deviation away from a distractor reached an asymptote; it is conceivable that at longer latency the amount of deviation may start to decrease again.

should vary as a function of the duration of the memory-interval. To examine this, we conducted three studies of the effect of memory-interval duration in memory-guided saccades.

Experiment 2

We tested four memory-intervals in Experiment 2: 500, 1,000, 1,500 (the same interval used in Experiment 1) and 3,000 ms. We hypothesized that as the memory-interval increased, the excitatory activation at the location of the target would weaken, leading to larger effects of the distractor on saccade trajectory.

Method

Participants

Nine observers, aged between 18 and 25 years old, participated in the experiment. Six of the participants were females. All reported having normal or corrected-to normal vision.

Apparatus, stimuli

These were identical to Experiment 1.

Procedure and design

Participants performed memory-guided saccades only. Memory-guided saccades were constructed as in Experiment 1, but with the memory-interval (the interval between target offset and fixation offset) set at 500, 1,000, 1,500 and 3,000 ms. These different memory-intervals were tested in the same blocks, in randomized order. The experiment consisted of a training session of 24 trials and an experimental session of 576 trials. Participants heard a short tone when the saccade latency was higher than 600 ms or lower than 80 ms. The sequence of trials was randomized for each participant, in terms of both target location (upper or lower field) and distractor condition (distractor present or absent) and memory interval (500, 1,000, 1,500 and 3,000 ms).

Data analyses

Based on the exclusion criteria for trials described for Experiment 1, 27.0% of trials were removed for further analyses. Distractor-induced deviation measures from the remaining trials were subjected to repeated-measures ANOVA with interval (500, 1,000, 1,500 and 3,000) as the within-subject factor. Latency was assessed with repeated-measures ANOVA, with interval and distractor condition (present, absent) as within-subject factors.

Results

For the distractor-induced deviation measures depicted in Fig. 2, an ANOVA showed no effect of interval ($F(3, 21) < 1$, $p = \text{n.s.}$). The analysis of saccade latency showed an effect of distractor condition ($F(1, 7) = 5.73$, $p < 0.05$), with longer latencies when distractors were present, as well as an effect of memory interval ($F(3, 21) = 11.81$, $p > 0.001$) (Fig. 2). Linear contrasts revealed that there was a significant overall linear trend between saccade latencies and memory interval across the four conditions, such that as memory-interval increased, saccade latencies decreased ($F(1, 7) = 11.30$, $p < 0.05$).

Discussion

Experiment 2 showed that saccade deviation did not vary as a function of the memory-intervals between 500 and 3,000 ms, even though saccade latency did. This excludes a linear relationship between memory-interval and distractor-induced deviation over this period. However, it does not rule out the possibility of a more rapid decline in excitatory target-related activity over the initial 500 ms of a memory interval. To determine if distractor-induced deviation

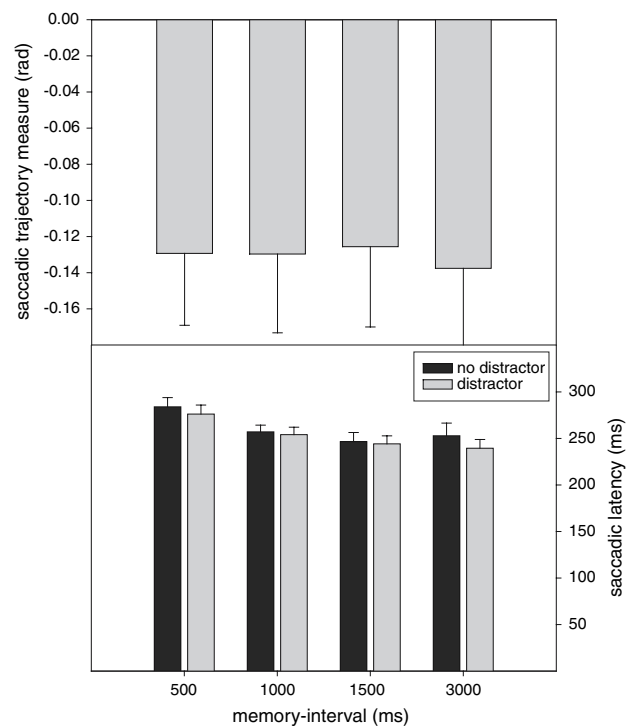


Fig. 2 Shows the results of the different saccade trajectory measures (*upper panel*) and the saccade latency in the distractor present and absent conditions (*lower panel*) for the three different conditions in Experiment 2. Negative saccade trajectory measures indicate saccades deviated away from the distractor. Error bars represent standard errors of the mean

increased rapidly during the first 500-ms that the target was absent, we performed a third experiment.

Experiment 3

This experiment contained four types of saccade trials, a prosaccade condition and three memory-guided saccades, with memory intervals of 0, 250 and 500 ms. In the 0 ms condition, the target appeared for 500 ms, as in all the other memory-guided saccades, but its disappearance coincided with the offset of the fixation stimulus. This contrasted with the standard prosaccade trial, in which the offset of the fixation stimulus coincides with the appearance (rather than the disappearance) of the target, which then remains visible until the end of the trial. If target-related activity declines within the first 500 ms of target offset, we expect to see an increase in the amount of saccade deviation between the memory intervals 0 and 500 ms. Based on the results of Experiment 1 we expect that saccadic deviation will have reached its asymptote at 500 ms.

Method

Participants

Eleven observers, aged between 18 and 35 years old, participated in the experiment. All but one participant was female. All reported having normal or corrected-to normal vision.

Apparatus, stimuli

These were identical to Experiments 1 and 2.

Procedure and design

The procedure and design were identical to Experiment 2, except for that the tested intervals between target and fixation-point offset were now set at 0, 250 and 500 ms. In addition, a prosaccade condition was included in which the target appeared simultaneous to fixation offset and remained visible until the end of the trial (1,200 ms). The sequence of trials was randomized for each participant, in terms of both target location (upper or lower field) and distractor condition (distractor present or absent) and condition (standard prosaccade, interval 0, 250, and 500 ms).

Data analysis

Based on the set exclusion criteria, 17.3% of trials were removed for further analysis.

We analyzed distractor-induced deviations with a repeated-measures ANOVA with saccade type (prosaccade,

memory-interval 0 ms, memory-interval 250 ms, memory-interval 500 ms) as a within-subject factor. Latency was assessed with repeated measures ANOVA with interval and distractor condition (present, absent) as within-subject factors.

Results

For distractor-induced deviation (Fig. 3) there was a main effect of condition ($F(3, 21) = 5.2.4$, $p < 0.01$). Post hoc comparisons (Fisher LSD) revealed that prosaccades differed significantly from each of the memory-interval conditions (0, 250 and 500 ms) (all $p < 0.05$). However, no significant differences were found between the different interval conditions.

For latency there was no effect of distractor condition ($F(1, 7) = 2.76$, $p > 0.1$); however, there was a significant effect of saccade type ($F(3, 21) = 17.14$, $p < 0.0001$). Post hoc comparisons revealed that significant differences were found in latency between the standard prosaccades condition and the 0, 250 and 500 ms memory-guided saccade condition, as well as between the 0 and 500 ms memory-guided saccade condition ($p < 0.005$); the comparison between the 0 and 250 ms interval condition, as well as

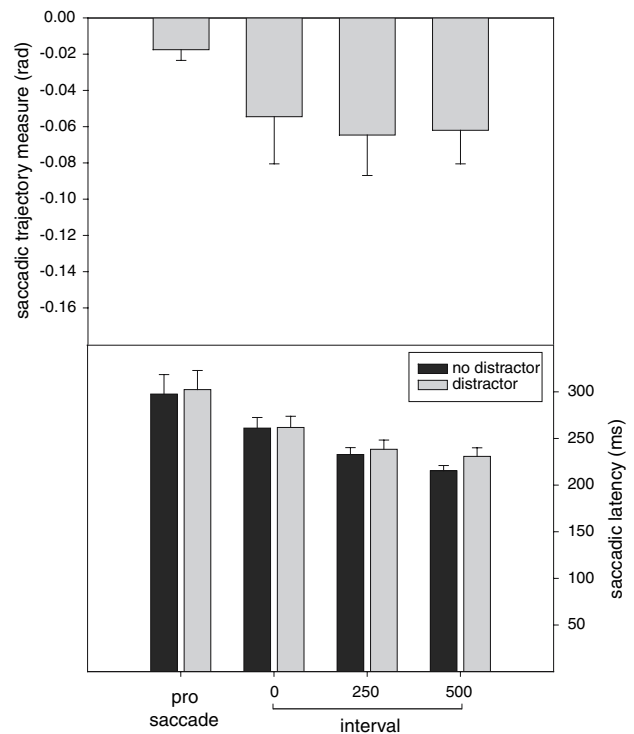


Fig. 3 Shows the results of the different saccade trajectory measures (*upper panel*) and the saccade latency in the distractor present and absent conditions (*lower panel*) for the three different conditions in Experiment 3. Negative saccade trajectory measures indicate saccades deviated away from the distractor. *Error bars* represent standard errors of the mean

between 250 and 500 ms interval condition did not reach significance ($p > 0.1$). Observers were faster to initiate saccades when the target disappeared in the memory-interval conditions than in prosaccades, where the target remained visible during saccade preparation.

Discussion

The results of Experiment 3 showed that distractor-induced deviation is increased relatively to that for prosaccades the moment the visual target signal has disappeared. The main difference between prosaccades and the 0 ms interval condition is whether the target is visible after the signal to make the saccade (i.e., the fixation offset). The direct removal of the target on fixation offset in the 0 ms interval condition means that this is not truly a memory-guided saccade. Nevertheless, the small difference between this condition and the prosaccade was sufficient to generate a nearly threefold increase in the magnitude of the distractor-induced deviation.

Experiment 3 again provided evidence that the difference in distractor-induced deviation between prosaccades and memory-guided saccades is not due to differences in saccade latency. In this experiment, distractor-induced deviations continued to be largest in the memory-guided saccades, while latency was now the longest in prosaccades.

We considered potential explanations for these unexpected long prosaccade latencies, which were around 300 ms in Experiment 3 compared with 200 ms in Experiment 1. This may have reflected protocol differences between Experiments 1 and 3: the different saccade conditions were presented in different blocks in Experiment 1, but randomly mixed in Experiment 3. Subjects may be better prepared to make fast responses in blocks of uniform prosaccades. An additional factor is that in the trials of memory-guided saccades in Experiment 3, the fixation offset that was the “go” signal was preceded or accompanied by a target offset, which itself could be used to prime saccade readiness (Kingstone and Klein 1993). The frequent occurrence of such a priming event may have placed prosaccades, which lack such a prime, at a disadvantage. To learn whether the results of Experiment 3 were confounded by strategies induced by a mixed design, we conducted Experiment 4.

Experiment 4

The conditions tested in Experiment 4 were identical to the ones tested in Experiment 3, the only difference being that the conditions were presented in a blocked design in Experiment 4. As a result, in Experiment 4, observers were

perfectly aware of the upcoming condition and as such were better prepared to program the saccade the moment the fixation offset. If strategies influenced the (in)ability to ignore the irrelevant distractor in Experiment 3, we predict that observers should be better able to ignore the distractor in Experiment 4. Hence, the pattern of deviation away from the distractor across the different memory-interval condition may be decreased in Experiment 4 compared to Experiment 3.

Method

Participants

Eight observers, aged between 19 and 29 years old, participated in the experiment. All except for one of the participants were females. All reported having normal or corrected-to normal vision.

Apparatus, stimuli

These were identical to Experiments 1–3.

Procedure and design

The procedure and design were identical to Experiment 3 except that the tested conditions (prosaccade, interval 0, 250, and 500 ms) were run in different blocks. Blocks were counter-balanced across participants. Within each block, target location (upper or lower field) and distractor condition (distractor present or absent) was randomized for each participant.

Data analysis

Based on the set exclusion criteria, 18.7% of trials were removed for further analysis. Analysis of distractor-induced deviation and latency was identical to Experiment 3.

Results

For distractor-induced deviation (Fig. 4) the ANOVA showed a main effect of saccade type ($F(3, 21) = 10.53$, $p < 0.001$). Post hoc comparisons (Fisher LSD) revealed that the prosaccades differed significantly from each of the interval conditions (0, 250 and 500 ms) (all $p < 0.05$). However, no significant differences were found between the different interval conditions.

For latency, the ANOVA showed no effect of distractor ($F(1, 7) = 1.50$, $p > 0.1$); however, a significant effect of saccade type was found ($F(3, 21) = 4.39$, $p < 0.05$). Post hoc comparisons revealed that the only significant difference between the different saccade types was between the

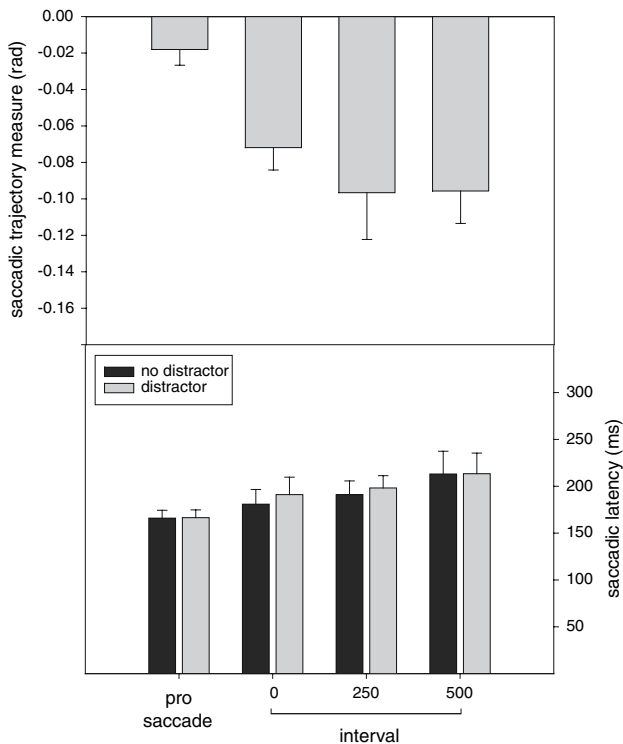


Fig. 4 Shows the results of the different saccade trajectory measures (*upper panel*) and the saccade latency in the distractor present and absent conditions (*lower panel*) for the three different conditions in Experiment 4. Negative saccade trajectory measures indicate saccades deviated away from the distractor. *Error bars* represent standard errors of the mean

standard prosaccade condition and the 500 ms memory-guided saccade condition ($p < 0.05$); no other comparisons reached significance.

To determine if the results were influenced by whether the different saccade types were tested in a mixed or a blocked design, we conducted an ANOVA on distractor-induced deviation with experiment as a between-subject factor and condition (standard prosaccade, interval 0, 250, and 500 ms) as a within-subject factor. No effect of experiment was found ($F(1, 14) < 1$, $p = \text{n.s.}$), showing that the results for distractor-induced deviation were not confounded by the method. Similarly, we conducted an ANOVA on latency with experiment as a between-subject factor and distractor (present vs. absent) and saccade type (prosaccade, interval 0, 250, and 500 ms) as within-subject factors. An effect of experiment was found ($F(1, 14) = 12.93$, $p < 0.01$), with latencies longer in Experiment 3 (average 255 ms) than in Experiment 4 (average 190 ms). There was an interaction between experiment and saccade type ($F(3, 42) = 18.30$, $p < 0.001$). Post hoc comparisons showed that the difference in latency between experiments was significant in prosaccades and the 0 ms interval condition, (both $p < 0.05$) but not in the 250 and 500 ms interval condition (both $p > 0.1$). No other main effects or interactions reached significance.

Discussion

The results of Experiment 4 replicated the results of Experiment 3 and showed that saccade deviation increased dramatically the moment the visual target has disappeared from the display. While saccade latencies were affected by the design of the experiment (i.e., mixed in Experiment 3 vs. blocked in Experiment 4), distractor-induced deviation was not. Again, this reinforces the conclusions from Experiments 1 and 3 that a previously reported relationship between latency and distractor-induced deviation (e.g., McSorley et al. 2006; Walker et al. 2006; however, see footnote 1) is not responsible for the difference in distractor effects on trajectory that we find between memory-guided saccades and prosaccades.

In the Discussion of Experiment 1 we hypothesized that the difference in trajectory deviation between the antisaccades and the memory-guided saccades may have been due to temporal dynamics of activity at the target location as a function of memory-interval. However, the results of Experiments 2–4 showed that distractor-induced deviation did not vary linearly with memory-interval. As such, these results suggest that temporal dynamics do not explain the finding of larger deviations for memory-saccades than for antisaccades in Experiment 1. In turn, it appears that perceptual differences between the two conditions may best explain the observed findings. In the antisaccade task, the target is visible throughout the duration of the trial, whereas in the memory-guided saccade task the target is absent: the only stimulus present on the screen in the memory-guided saccade, the moment a saccade is initiated, is the distractor. Relative activity at the location of the distractor vs. the location of the saccadic goal may thus be higher in the memory-guided saccade than in the antisaccade, resulting in a need for more inhibition and greater deviation in the former. Alternatively, it may be the case that overall activation in the SC is reduced and more wide-spread in the memory-saccade task compared to the anti-saccade task. An overall lower level of saccade related activation in the SC would relatively increase irrelevant activity at the distractor location. This relative increase may in turn require the need for more inhibition and therefore lead to greater deviation in the memory-saccade task.

General discussion

Our experiments were designed first to test the hypothesis that antisaccades and memory-guided saccades would have greater distractor-induced deviations in saccade trajectories than prosaccades. This hypothesis was derived from a concept that such deviations emerge from an interaction between facilitatory activity at the location of the saccade

goal and inhibitory activity at the location of the distractor in a motor map. If so, reduced activity at the location of the saccade goal should lead to greater deviation of saccade trajectories in the presence of a distractor. Behavioral and neurophysiologic data suggest that, compared to prosaccades, memory-guided saccades and antisaccades have less neural activity at the location of their saccade goal in the motor map of the superior colliculus (Everling and Fischer 1998) at least in part due to the absence of a visual stimulus at the saccade goal (Edelman and Goldberg 2001, 2003). This leads to the prediction that these types of saccades should then have greater deviation of their trajectories on trials with distractors. The results of Experiment 1 fulfilled this prediction.

However the results of Experiment 1 also showed that distractor-induced deviation was significantly greater for memory-guided saccades than for antisaccades. Previous work suggested that this result would be opposite to what might be expected on the basis of latency differences between these two types of saccades (McSorley et al. 2006; Theeuwes and Godijn 2004; Walker et al. 2006). Instead we considered the possibility that either a division of inhibitory resources might reduce the effect of the distractor during antisaccades, or that the additional delay between goal activation and saccade execution might reduce the effect of the target in memory-guided saccades. Experiments 2–4 were designed to evaluate the latter possibility, as well as to explore the temporal dynamics of goal-related activity in memory-guided saccades.

These experiments showed that distractor-induced deviation did not systematically change as a function of the time elapsed from the disappearance of the target to the signal to execute the memory-guided saccade. In fact, Experiments 3 and 4 revealed that even a “memory interval” of 0 ms generated a significant increase in the effect of the distractor on saccade trajectory, compared to a prosaccade. Thus the impact on saccade trajectories of the visual stimulus at the goal location of memory-guided saccades appears to vanish (or at least decline rapidly to an asymptotic minimum) as long as the target stimulus disappeared before the go-signal and the appearance of the distractor.

This rapid decline in the impact of a previously visible stimulus at the location of the saccade goal may seem surprising given data on the effects of a previously visible stimulus at the location of the distractor. Distractors can still induce significant deviation away from their location even if they have disappeared 1,000 ms before the go signal to make a saccade (Theeuwes et al. 2005). In this study, the distractor induced deviation only when the location of the distractor had to be remembered, but had no effect when the location of the distractor did not have to be remembered. Note that in both conditions, no distractor was presented at the time the saccade was initiated. The difference

thus seems to be related to the additional modulation at the distractor location that is required in the memory condition. Similarly, the mere expectancy of a distractor at a particular location can cause deviations in saccade trajectories (Van der Stigchel and Theeuwes 2006). In this study, even though no visual stimulus was presented at the location of the distractor, saccades deviated away from the location where the distractor was expected to appear. While one may argue this effect may be due to residual stimulus-related activity at the distractor site, additional inter-trial analyses did not reveal an effect of the location of the distractor in a previous trial on the current trial (Van der Stigchel and Theeuwes 2006). This result thus suggests that the effect of expectancy is most likely due to top-down modulation that is not directly related to perceptual effects of the visual stimulus.

The difference between the results of these two studies and the results of the present results may lie in the need for active and sustained top-down modulation at the location of the distractor. For example, in the study conducted by Theeuwes et al. the location had to be actively remembered throughout the trial as participants were required to judge whether a later presented stimulus was presented at the same or a different location as the to-be-remembered stimulus. In the present experiment, there were only two possible target locations, in the upper and lower field, and there was no secondary memory task. As such, one may argue that the memory-guided saccade in the present study did not require such active maintenance of the saccade goal location. If there is no need to keep the target location active for the duration of the memory interval, we would not expect an effect of memory-interval. Similarly, one may predict that expectancy also evokes more sustained patterns of activation at the relevant locations (Van der Stigchel and Theeuwes 2006) compared to the method employed in the current experiments. To summarize, in the present study, an effect of relevant activation at the saccade goal may only have influenced saccade trajectories once the fixation-point disappeared, which served as the command to initiate the saccade. Because participants did not need to keep the saccade goal active for the duration of the trial, the eye-movement program was not modulated by additional influences that modulate activity prior to the movement-trigger. Further studies may be able to provide insight in the role of relevant target activity in saccade deviation.

Nevertheless, the results of the present study do reveal the important role of stimulus-related activity at the saccade location. What do our results for memory-guided saccades tell us about the temporal dynamics of stimulus-related activity at the saccade goal in a motor map? Clearly, the timing of visual stimulation at the saccade goal prior to the triggering of the saccade and/or the onset of the distractor (note that these two events were not dissociated in our

experiments) has no effect on saccade trajectory. Given that the memory-guided saccade occurs approximately 200–300 ms after the triggering event, there are at least two possible interpretations of this lack of effect. These depend upon whether one views the effects on trajectory as deriving from an integration of motor-map activity during the entire interval between the command to make the saccade and the onset of the eye movement (i.e., including the 200–300 ms saccade initiation time, also referred to as “blank time” by Edelman and Goldberg 2001), or from the instantaneous balance between distractor- and goal-related activity at the moment of saccade initiation (i.e., at the end of the blank time).

If one favors the “integration of activity” account, then the results suggest that activity generated by the visual stimulus decays nearly immediately, since its impact on the interaction between distractor- and goal-related activity in generating saccade deviation is minimal. This suggests that for a visual stimulus at the saccade goal to modulate distractor-induced deviation, it must overlap in time with the presence of the distractor. Furthermore, this account would predict that the greater the period of overlap, the larger the reduction in distractor-induced deviation.

If one favors the “instantaneous activity” account, then what matters is how strong goal-related activity is at the time of saccade onset, about 200–300 ms after the triggering signal. Our memory-guided saccade experiments only explored the effects of visual stimuli up to the moment of the triggering signal. Hence they do not exclude the possibility that visual stimuli that disappear AFTER the triggering signal but shortly BEFORE saccade onset may have some effect on distractor-induced deviation (Ludwig et al. 2007). If so, this would indicate a rapid (but not immediate) decay in the effect of visual stimuli at the saccade goal occurring with a time course of less than 200–300 ms. This account would predict that what is significant is not the period of overlap between distractor and target, but the time elapsed between target offset and saccade onset (Edelman and Goldberg 2001).

Thus, further work is clearly required to explore the temporal dynamics of goal/distractor interactions. Nevertheless, our study underlines the contribution of a visual stimulus at the saccade goal to the generation of saccade trajectory in the presence of a distractor, in keeping with the hypothesis that deviations arise from an interaction between inhibitory activity at the location of the distractor and excitatory activity at the location of the goal in a motor map for saccade generation.

Acknowledgments W. v. Zoest was supported by the Michael Smith Foundation for Health Research (MSFHR). J. B. was supported by a Canada Research Chair and a Senior Scholar Award from the MSFHR. The authors wish to thank Elizabeth Roy and Guido Peek for testing participants.

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