



# Top-down influences make saccades deviate away: The case of endogenous cues

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## Abstract

We tested a recent hypothesis suggesting that the eye deviates away from a location when top-down preparation can influence target selection. Participants had to make an eye movement to a peripheral target. Before the upcoming target, a central cue indicated the likely target location. Results show that when the target was presented at a location different from that indicated by the cue, eye movements to the target deviated away from the cued location. Because central cues are under top-down control, the present results are in line with a determining role of top-down preparation on saccade direction. These results contrast with the findings reported in a similar paradigm executed with hand movements, in which the movements were mostly initiated in the direction of the cued location. Therefore, we conclude that inhibitory effects typically observed when executing eye movements may not be observed when executing hand movements in similar conditions.

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## 1. Introduction

When examining our environment, we make rapid eye movements called saccades. The trajectory of a saccade is typically not a straight line, but shows a curved trajectory

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(Erkelens & Sloot, 1995; Viviani, Berthoz, & Tracey, 1977; Yarbus, 1967). Research has shown that the trajectory of an eye movement is influenced by the environment (for a review, see Van der Stigchel, Meeter, & Theeuwes, 2006). These modifications are regarded as a reflection of competitive processes in the oculomotor system. For instance, when a target and a distractor are placed in close proximity, the endpoint of a saccade to the target will be positioned in between the target and the distractor (Coren & Hoenig, 1972; Van der Stigchel & Theeuwes, 2005; Walker, Deubel, Schneider, & Findlay, 1997). Another example of a paradigm in which the modification of the saccade trajectory is a reflection of multiple saccade programs is visual search experiments. When participants have to search for a target presented in a search array, the saccade trajectories to the target deviate *towards* the most salient distractor (Godijn & Theeuwes, 2002; McPeck, Skavenski, & Nakayama, 2000; Walker, McSorley, & Haggard, 2006). In both situations, the competition between the distractor and the target is reflected in the saccade program, resulting in a movement that is an average of the saccade programs to both elements. Although the eye movement is correctly executed to the target, it is influenced by the competing activation caused by the distractor.

The influence of a competing saccade program does not automatically lead to a deviation *towards* the direction of the competing response. Besides deviations *towards* irrelevant distractors, deviations *away* are also frequently observed (Doyle & Walker, 2001; Godijn & Theeuwes, 2002; Van der Stigchel & Theeuwes, 2005, 2006). For instance, Doyle and Walker (2001) showed that completely irrelevant distractors can also evoke deviations *away*. Participants had to make a saccade either up or down from fixation in the presence of an irrelevant distractor. Both voluntary and reflexive saccades were accompanied by deviation *away* from the distractor.

These deviations *away* have been attributed to inhibitory processes (Godijn & Theeuwes, 2002; McSorley, Haggard, & Walker, 2004; Sheliga, Riggio, & Rizzolatti, 1994; Tipper, Howard, & Jackson, 1997). Possible target locations are represented by a large population of neurons that encode the movement towards each target location as a vector. When the competition between the different vectors is resolved, the population that loses the competition is inhibited. This inhibition of one population may shift the target vector in such a way that it affects the final response to the target which then points *away* from the inhibited location. Without the inhibitory selection the populations are combined to one mean population and the vector will point to an intermediate location, resulting in deviation *towards*.

Only recently it was investigated what determines whether saccade trajectories deviate *towards* or *away* in a certain situation (Van der Stigchel et al., 2006; Walker et al., 2006). Because deviations *away* are typically attributed to inhibition, the question arises why this inhibition does not occur in every situation. It has been hypothesized that these inhibitory components are observed when top-down preparation influences the target selection process (Van der Stigchel et al., 2006). The deviation *towards* is then caused by the unresolved competition in the oculomotor system due to a lack of top-down preparation.

The evidence for a determining role of top-down preparation in target selection comes from two reported effects: timing and prior knowledge. It has been shown that prior knowledge about the location of an upcoming target results in deviations *away*, whereas absence of this prior knowledge causes deviation *towards* a distractor (Walker et al., 2006). When the target location is known in advance, the preparation for the upcoming saccade can already begin by selecting the relevant location. This process makes the oculomotor

system less vulnerable for distractor interference and makes a successful inhibition of the distractor more likely. In line with this finding, cueing the distractor location in advance evokes the inhibition of the distractor location (Van der Stigchel & Theeuwes, 2006). When the distractor was expected but not presented, the saccades still deviated *away* from the distractor location because of the inhibition based on prior knowledge of the distractor location.

The evidence for the important role of timing comes from studies that have looked at saccade trajectories as a function of saccade latency. In visual search experiments, for instance, fast saccades deviate *towards* distractors, while slow ones deviate *away* from these elements (McSorley, Haggard, & Walker, 2006; Theeuwes & Godijn, 2004; Walker et al., 2006). Also, the deviation *away* from a distractor is modulated by target similarity when the saccade is delayed, but this effect is absent when it is not delayed (Ludwig & Gilchrist, 2003).

The above explanation regarding eye movement deviations *towards* and *away* contrasts with the findings from a hand movement study, where inhibitory components were not observed when top-down preparation influenced the target selection process (Lee, 1999). Therefore, we further test the determining role of top-down preparation by running an eye movement version of this hand movement study. Because it is generally agreed that the eye and hand movements are subject to the same selection processes (Lee, 1999; Sailer, Eggert, Ditterich, & Straube, 2002; Tipper, Howard, & Houghton, 2000; Tipper et al., 1997; Tipper, Howard, & Paul, 2001; Welsh & Elliot, 2004, 2005) a replication of the results of Lee (1999) with eye movements would pose problems for the idea that inhibitory components are observed in the presence of top-down preparation.

In the hand movement study, four circles were presented around a central circle. The movements were initiated to one of the four peripheral circles indicated by the presentation of a red target disk inside one of the peripheral circles. A central cue indicated the likely location of an upcoming target in the majority of trials. In the remaining trials, the central cue pointed to one of the other locations. When the target was presented at a location different from that indicated by the central cue, the movements with short latencies were mostly initiated *towards* the cued location (Lee, 1999). This was observed even when the target was presented 180° away from the cued location. For latencies longer than 300 ms, the movements were correctly initiated to the target without any deviation. It was therefore concluded that the location of an attentional cue was used as an initial value in the process specifying movement direction, and that this value was gradually modified by signals related to the target location.

In the study by Lee (1999), the target location was indicated by a central cue. This type of cue is typically referred to as endogenous and allows an active top-down preparation (Posner, 1980; Posner & Cohen, 1984). If it is indeed true that deviation *away* is observed in situations in which top-down preparation can influence the target selection process, the current paradigm should result in deviations *away* instead of deviations *towards*.

Moreover, one of the predictions raised by Lee (1999) with respect to eye movements is that they will deviate *towards* the cued location in a paradigm similar to his. He suggested that previous eye movement studies found the deviation *away* from the cued location, because in these studies movements were never initiated to the cued location (i.e., Sheliga et al., 1994; Sheliga, Riggio, & Rizzolatti, 1995). Therefore, the inhibitory effects of the cue dominated the facilitatory effects resulting in deviation *away*. In the study of Lee (1999), however, the fact that the cued, and presumably attended, location could become the target

location made it more likely for the facilitatory effects of attention to manifest itself in deviation *towards*. Here we directly tested this hypothesis by conducting an eye movement experiment in which the cued location became the target location in the majority of trials.

## 2. Methods

### 2.1. Participants

Seven students participated (19–34 years old, all female). All reported having normal or corrected-to-normal vision. They were naïve as to the purpose of the experiment. All persons gave their informed consent prior to their inclusion in the study.

### 2.2. Apparatus

A Pentium IV computer with a processor speed of 2.3 GHz controlled the timing of the events and recorded response times. Displays were presented on an Iiyama 21" SVGA monitor with a resolution of  $1024 \times 768$  pixels and an 85-Hz refresh rate. A second computer controlled the registration of eye movements' data on-line. The eye movements were registered by means of a video-based eye tracker (SR Research Ltd., Canada). The Eye-link2 system has a 500 Hz temporal resolution and an accuracy probability of  $0.5^\circ$ . The system used an infrared video-based tracking technology to compute the pupil center and pupil size of both eyes. An infrared head mounting tracking system tracked the head motion. Although the system compensates for head movements, the participant's head was stabilized using a chin rest. The distance between the monitor and chin rest was 75 cm. Participants performed the experiment in a sound-attenuated and dimly lit room.

### 2.3. Stimuli

See Fig. 1 for an illustration of the display sequence. All figures were presented in light gray on a black background. Each trial started with the presentation of a star-shaped fixation stimulus ( $0.27^\circ \times 0.27^\circ$ ) in the center of the screen. After 600 ms, five equidistant circles ( $1.39^\circ$  of visual angle in diameter) were presented positioned on an imaginary circle with a radius of  $6.94^\circ$  around the central fixation point. A centre line segment ( $0.92^\circ$ ) appeared 500 ms later pointing to one of the five circles ('cue'). A variable delay occurred (of 150–300 ms), followed by the onset of a filled circle at one of the five circle locations ('target').

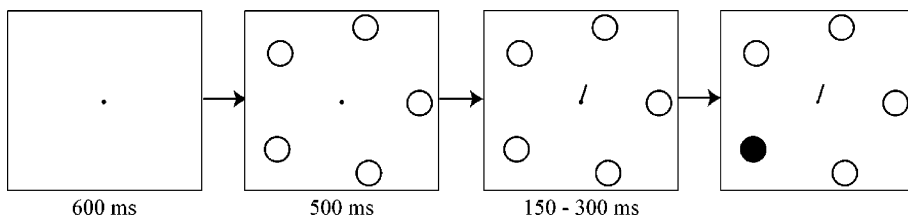


Fig. 1. An example of the display sequence. The central line segment indicated the likely target location. After a variable delay, the target ('filled circle') was presented and observers were required to make a fast eye movement to the target.

## 2.4. Procedure and design

Participants first received oral instructions. They were instructed to fixate the fixation stimulus until the target onset and to then move their eyes to the target location. It was stressed that one had to make a single accurate saccade towards the target element. The experiment consisted of a training session of 24 trials and an experimental session of 1000 trials. In 60% of the trials, the target was presented at the cued location (a validity of 60%). For the four other locations, the probability of target appearance was 10%. The sequence of trials was randomized for each participant. Participants heard a short tone when the saccade latency was higher than 600 ms.

## 2.5. Data analysis

Saccade latency was defined as the interval between target onset and the initiation of a saccadic eye movement. If saccade latency was lower than 80 ms, higher than 600 ms or further than two and a half standard deviations away from the mean latency, the trial was removed from the analysis. Moreover, trials were excluded from the analysis in which no saccade or a too small first saccade ( $<3^\circ$ ) was made. If the endpoint of the first saccade had an angular deviation of more than  $30^\circ$  from the center of the target, the saccade was classified as an error and also not analyzed. Furthermore, the initial saccade starting position had to be within  $1^\circ$  from the center fixation point.

To examine the influence of the different conditions on saccade trajectories, we used three different measures: saccade deviation, overall direction and initial direction. This enabled us to explore on what part of the saccade the influence of the distractor location might be observed: for the trajectory as a whole (saccade deviation), for the beginning of the trajectory (initial direction), or for the end of the trajectory (overall direction). For an overview of all different measures and how to compute them, see [Van der Stigchel et al. \(2006\)](#) and [Ludwig and Gilchrist \(2002\)](#):

- Saccade deviation was defined as the mean angle of the actual saccade path relative to the angle of a straight line between the saccade starting position and the target location. 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.
- The overall direction was defined as the angular difference between the angle of a straight line from the fixation to the saccade endpoint and the angle of a straight line from saccade starting position to the target location.
- The initial direction was defined as the difference between the angle of the saccade at 10 ms after saccade initiation and the angle of a straight line between the saccade starting position and the target location.

To compute the influence of the cue on saccade trajectories, the trajectory differences were computed between valid trials and invalid trials. Valid trials were considered as the baseline condition on the basis of which trajectory deviations were calculated for each target location. For all measures, the trials in which the outcome of that particular trajectory measure was two and a half standard deviations away from the mean outcome were removed from the analysis. Positive and negative values refer to measurements towards

and away from the cued location, respectively. Separate calculations were made for the two possible distances between the cued and the target location: ‘close’ (72°) and ‘far’ (144°).

### 3. Results

The exclusion criteria led to a total loss of 14% of trials.

#### 3.1. Saccade latency

To determine whether the cue had an effect on saccade latency, an ANOVA with cue condition (‘valid’, ‘invalid close’ or ‘invalid far’) as a factor was performed. There was a main effect of cued condition ( $F(2,12) = 17.71$ ;  $p < 0.001$ ). Saccade latencies to the valid location were faster than to the invalid close (201 ms (SEM = 18 ms) vs. 221 ms (SEM = 14 ms);  $t(6) = 20.34$ ;  $p < 0.01$ ) and the invalid far location (201 ms (SEM = 18 ms) vs. 226 ms (SEM = 16 ms);  $t(6) = 20.01$ ;  $p < 0.01$ ).

#### 3.2. Saccade deviation

An analysis of variance (ANOVA) on mean saccade deviation with cue condition (‘far’ vs. ‘close’) and the five target locations as factors showed a main effect of cue condition (see Fig. 2;  $F(1,6) = 72.46$ ;  $p < 0.001$ ). In the close condition, the saccade trajectories deviated more strongly away from the cue condition ( $-0.033$  rad, SEM = 0.011), than in the far condition ( $-0.002$  rad, SEM = 0.006). There was also a significant target location  $\times$  cue condition interaction ( $F(4,24) = 2.98$ ;  $p < 0.05$ ) caused by a larger cueing effect for the three top locations compared to two bottom locations. There was no main effect of target location ( $F < 1$ ).

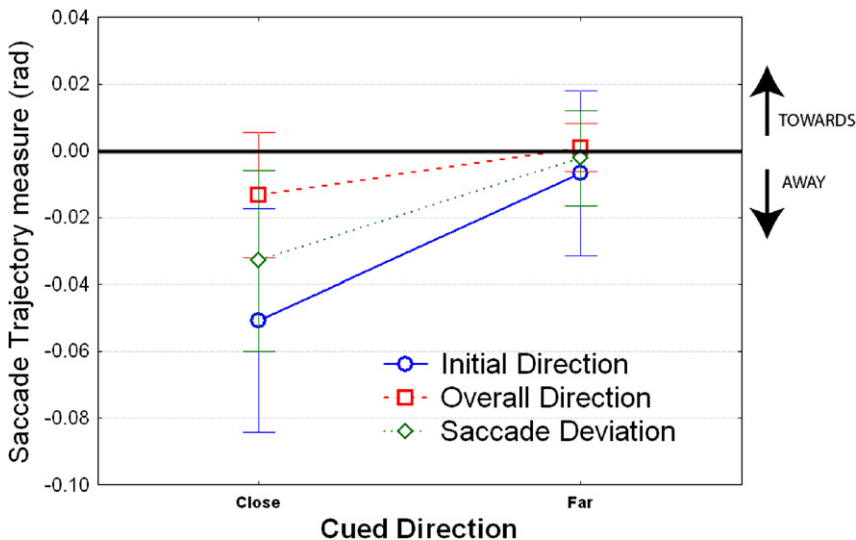


Fig. 2. Results of the two cue conditions for all three measures of saccade deviations. Negative values refer to deviations away. See text for further details.

### 3.3. Overall direction

The same analysis repeated with overall direction as a measure showed a main effect of cue condition (see Fig. 2;  $F(1,6) = 13.11$ ;  $p < 0.02$ ) but not for the target location, and no interaction ( $F < 1$ ). In the close condition, the overall direction was more negative in the cue condition ( $-0.013$  rad, SEM = 0.008) than in the far condition (0.001 rad, SEM = 0.003).

### 3.4. Initial direction

There was again a main effect of cue condition (see Fig. 2;  $F(1,6) = 93.46$ ;  $p < 0.001$ ) when the initial direction was used as measure of deviation. In the close condition, the saccade trajectories deviated away from the cue condition ( $-0.051$  rad, SEM = 0.014). This deviation away was greater than in the far condition ( $-0.007$  rad, SEM = 0.010). There was no main effect of target location ( $F < 1$ ) and no interaction  $F(4,24) = 1.40$  ( $p > 0.2$ ).

### 3.5. Relation between saccade deviation and saccade latency

To quantify the relation between saccade deviation and saccade latency, we calculated for each participant the mean correlation between these two measures for the close and far cue conditions. For each individual trial, its saccade deviation was measured with respect to the mean baseline deviation. Both correlations were not significantly different from zero (close cue condition: mean = 0.013;  $t(6) = 0.77$ ;  $p > 0.45$ ; far cue condition: mean =  $-0.055$ ;  $t(6) = 2.36$ ;  $p = 0.06$ ). There was no difference between the two conditions ( $t(6) = 2.19$ ;  $p = 0.07$ ).

To further examine the relationship between the saccade deviation and latency, we ordered the latencies in different bins. On the basis of their latency (fastest to slowest) and cue conditions (close and far cue condition), the trajectory deviations were divided in two times three bins. By examining the three bins, we could determine whether saccade trajectories change as a function of saccade latency for the two conditions. An ANOVA on mean saccade deviation with cue condition (“far” vs. “close”) and latency bins as factors showed a main effect of cue condition (see Fig. 3;  $F(1,6) = 49.14$ ;  $p < 0.001$ ). There was no main effect of latency bin ( $F(2,12) = 1.90$ ;  $p > 0.15$ ) and no significant interaction between the cue condition and latency bin ( $F < 1$ ).

## 4. Discussion

The present study was modeled after a hand movement study of Lee (1999), but instead of making hand movements, participants made eye movements in our study. Participants had to make a saccade to a gray circle presented at one of five possible target locations. A central cue indicated the likely target location in advance. The saccades were faster to this cued location than to other locations. This indicates that the cue-evoked programming of a saccade to the cued location.

When the target was presented close to the cued location, the trajectory deviated *away* from the cued location. This effect was observed for all three measures (initial direction, overall direction and saccade deviation) indicating that this deviation exists at both beginning and end of the movement trajectory. However, these effects were only observed for movements to the locations close to the cued location. For the locations far from the cued



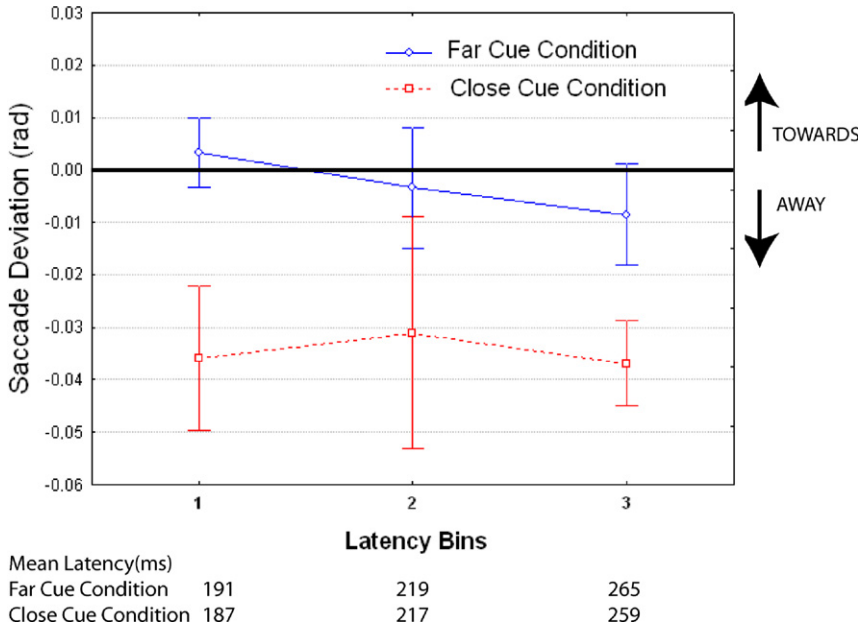


Fig. 3. Saccade deviations for the two cue conditions divided in three latency bins. Mean saccade latencies for the bins are given in the bottom of the figure.

location, saccade trajectories were not influenced. Finally, there was no relation between saccade deviations and saccade latencies. This is consistent with the recent findings that such a relation is not observed for eye movement when voluntary cues are used (Walker et al., 2006).

Because the present study used cues that are subject to top-down preparation, the present results are in line with a determining role of top-down influence on the direction of the saccade trajectory. Because participants knew the likely target location in advance, top-down preparation could influence the target selection process. When the target location differed from the cued location, the 'endogenous' saccade program could be successfully inhibited. This inhibition then resulted in deviation *away* from the cued location. Furthermore, the finding that saccade deviation is not influenced by saccade latency indicates that this inhibition does not build up and is already present in the eye movements with the shortest latencies.

As noted before, saccade deviations were only observed for movements to target locations close to the cued location and not for saccades to target locations far from the cued location. This finding is consistent with the idea that saccade deviations are caused by the competition between overlapping movement vectors (Tipper et al., 1997, 2001). In response to the central cue, an eye movement is programmed to the cued location. The corresponding population of neurons encodes this motor program as a vector. When the target is subsequently presented at an uncued location, an eye movement will be programmed to this target location. To correctly execute this movement, the vector to the cued location has to be inhibited. When the distance between the target and the cued location is small, the population coding the 'target vector' and the 'cue vector' will overlap. Therefore, the inhibition of the cue vector shifts the target vector in such a way that it points *away* from the cued



location. When the distance between the cued and the target location is large, the vectors do not overlap and inhibition of the cue vector will not affect the trajectory of the eye movement to the target.

The present results contrast with those reported by Lee (1999) who investigated hand movement trajectories. In that study, in trials in which the target was presented at an uncued location, fast hand movements were mostly initiated in the direction of the cued location. This was observed for both far and close cued locations. For longer latencies, the movements were correctly initiated to the target location. Lee (1999) hypothesized that similar findings would be observed in an eye movement variant of that study. However, none of these results were observed in the present experiment: we observed no differences between fast and slow responses, the movements were mostly initiated *away* from the cued location and an influence of the cue was only observed for the close cued locations.

On the basis of these findings, it can be questioned whether similar inhibitory influences are present in the corresponding situations for hand and eye movements. Other studies have also obtained diverging results between hand and eye movements. These studies have investigated the influence of irrelevant distractors on movement trajectories. Participants typically make a motor movement to a predictable target location in the presence of an irrelevant distractor. Hand trajectories typically deviate *towards* the distractor (Chang & Abrams, 2004; Chieffi, Ricci, & Carlomagno, 2001; Tipper et al., 2000; Welsh & Elliot, 2004, 2005). For instance, Welsh, Elliot, and Weeks (1999) conducted an experiment in which the participants executed a hand movement to a target while they had to ignore a simultaneously presented distractor. In this study, the distractors and the targets were lights (i.e. LEDs). It was shown that the hand trajectory deviated *towards* the distractor. In similar paradigms, eye movement trajectories have generally been found to deviate *away* from irrelevant distractors (Doyle & Walker, 2001, 2002; Ludwig & Gilchrist, 2003; McSorley et al., 2004; McSorley, Haggard, & Walker, 2005; Van der Stigchel & Theeuwes, 2006).

It must be noted that deviations *away* have been observed in hand movements in some circumstances. Tipper et al. (1997) found that hand movements deviated *away* from near distractors in movements to far targets, but deviated *towards* far distractors for movements to near targets. However, these experiments differed from the other hand movement experiments in that they were executed with physical stimuli that could obstruct the movement. Tresilian (1998) explained these results by stating that participants keep a minimal distance to physical stimuli to avoid obstruction. A second study in which deviation *away* was observed is an experiment in which the distractor was presented at a different time point before the target (Welsh & Elliot, 2004). When the distractor was presented 750 ms before the target, the movements deviated *away* from the distractor. When the distractor was presented less than 750 ms before the target, movements were again shown to deviate *towards* the distractor.

There has been one study that has monitored eye and hand movement trajectories simultaneously (Tipper et al., 2000). In this study, the participants attended to a spatial cue without making an eye movement and subsequently executed a hand movement to a target location indicated by the cue. In line with other studies, hand movements deviated *towards* the attended location and eye movements deviated *away* from this location. So, although it is generally agreed that eye and hand movements are subject to the same selection processes (Franz, Gegenfurtner, Bulthoff, & Fahle, 2000; Lee, 1999; Sailer et al., 2002; Schneider & Deubel, 2002; Tipper et al., 1997, 2001), movement trajectories studies seem to

indicate that the role of inhibitory mechanisms differs between hand and eye movements. As noted before, deviations *away* are assumed to be reflections of high amounts of inhibition, whereas deviations *towards* indicates a relative lack of inhibition. It might be that inhibitory processes are more potent in the eye movement system than in the hand movement system. This explains why we observed deviation *away* in the current experiment instead of deviation *towards* as was observed in the hand movement version of the paradigm. Moreover, this also explains why the influence of an irrelevant distractor seems to differ between the two motor responses.

From the neuroscience point of view, differences between the selection processes for hand and eye movements are not surprising given that hand and eye movements are generated in anatomically separate areas in the brain. Systems that code for a specific direction of an eye movement response have been located in the FEF and the superior colliculus (SC) (Schall, 1991; Sparks & Hartwich-Young, 1989). The role of the SC in saccade trajectories was revealed by McPeck, Han, and Keller (2003), who showed that when a trajectory deviated *towards* a distractor location in a visual search experiment, there was increased pre-saccadic activity at that location. Also, micro-stimulation of the SC below the threshold for saccade generation resulted in eye movements that deviated *towards* the stimulated location. Although eye movement trajectories deviate *away* from a distractor location have not been reported in monkeys, the SC may be assumed to underlie such deviations as well. Indeed, after deactivating of a location by an injection of a GABA agonist, muscimol, the eyes deviate *away* from this location in monkeys (Aizawa & Wurtz, 1998). The SC does not play a role in hand movements. Instead, cells in area 5 of the parietal cortex and in the motor cortex code for a specific direction of a hand movement response (Georgopoulos, 1990), and these areas may have a different physiology from those in the eye movement system.

To summarize, the present study found saccade deviations *away* from the cued location in a task in which top-down preparation could influence the target selection process. In a similar experiment with hand movements, deviations *towards* the cued location were observed (Lee, 1999). The functional significance of such a difference is currently unclear, but it can be concluded that similar inhibitory influences are not present in the corresponding situations for hand and eye movements.

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