



Saccade trajectory deviations and inhibition-of-return: Measuring the amount of attentional processing

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ABSTRACT

This study used a classic exogenous cueing task in which an abrupt onset cue indicated the target location at chance level. When there was a delay between the cue and the target, observers responded slower and less accurate to the target presented at cued than at uncued locations, signifying the occurrence of inhibition-of-return (IOR). On some trials, instead of a manual response, participants had to move their eyes to a location in space. Our findings show no saccade deviation away from the location that was inhibited due to IOR unless participants had to process the target letter presented at the inhibited location. Our findings are consistent with the notion that inhibition resulting in IOR does not occur at the saccade map level but IOR seems to reduce the input of signals going into the saccade map. We show that the strength of saccade deviation is an important measure which can reveal the amount of attentional processing taking place at any particular location in time.

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1. Introduction

It is well-known that a visual event presented with abrupt onset can have a strong effect on the attentional system. It has been argued that an abrupt onset can capture attention in an exogenous way (see e.g., Theeuwes, 1991, 1994; Yantis & Jonides, 1990). In the classic exogenous Posner cueing paradigm, observers are instructed to remain fixated at the center of the display, covertly directing their attention and respond manually to the target. Prior to the presentation of the target, a visual abrupt onset is presented as a cue (Posner & Cohen, 1984). Even though the cue does not contain any information about the upcoming location of the target, observers are faster and more accurate in responding to targets that appear at the cued than at the uncued location. Furthermore, when there is a delay between the offset of the cue and the onset of the target, observers are slower and less accurate to respond to targets at the cued than at the uncued location, a phenomenon called inhibition-of-return (IOR, cf., Posner & Cohen, 1984). It is generally agreed that the function of IOR is to bias orienting away from already inspected locations, so that visual search becomes more efficient (see, Klein, 2000). IOR places inhibitory tags on objects that recently have been inspected (either by overt or covert orienting) so that these locations no longer compete for selection and subsequent search is directed to novel objects only. Note that it takes time for this inhibitory tagging to build up and IOR is typically ob-

served when a target is presented at least 300 ms after presentation of the irrelevant cue (see e.g., Klein, 2000).

It has been argued that the occurrence of IOR is the best indicator of exogenous capture of attention. For example, Pratt, Hillis, and Gold (2001) argued that 'IOR, being beyond the reach of most short-lived sensory effects, may be the best indicator of where attention was allocated in a visual display. The suggestion that IOR occurs at previously attended (i.e., cued) locations, even if those locations do not show attentional cuing effects, is consistent with the notion that IOR aids in visual searches and foraging behavior (e.g., Klein & MacInnes, 1999)' (p. 493). Other studies have also shown that when an exogenous peripheral onset cue is used one may find IOR without any early facilitation (e.g., Tassinari, Aglioti, Chelazzi, Peru, & Berlucchi, 1994). Typically, IOR at the cued location is interpreted as evidence that the initial shift of attention was exogenous in nature (e.g., Posner & Cohen, 1984; Pratt, Kingstone, & Khoe, 1997; Theeuwes & Godijn, 2002). Moreover, according to Klein and colleagues (Klein, 2000; Taylor & Klein, 1998, 2000; see also, Rafal, Calabresi, Brennan, & Sciolto, 1989) IOR occurs at locations that have been activated within the oculomotor system.

It is also well documented that abrupt onsets exert a strong effect on eye movement behavior. In a series of experiments Theeuwes and colleagues (Godijn & Theeuwes, 2002; Theeuwes, Kramer, Hahn, & Irwin, 1998; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999) showed that an abrupt onset will capture the eyes, even when observers are instructed to look elsewhere. In this so-called oculomotor capture paradigm, observers had the explicit instruction to make an eye movement to the uniquely colored circle in the display. On some trials, an object presented with abrupt onset

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was added to the display. Observers knew that the onset was irrelevant and also knew that they had to ignore it. The condition in which the abrupt onset was presented was compared to a control condition in which no onset was added to the display. The results showed that when no onset was added to the display, observers made saccades that generally went directly to the uniquely colored circle. However, in about 30–40% of the trials in which an onset was added to the display, the eyes went in the direction of the onset, stopped briefly, and then went on to the target. The results from the oculomotor capture paradigm suggest that an abrupt onset not only captures attention (see Theeuwes et al., 1999, Experiment 2; Godijn & Theeuwes, 2002) but also captures the eyes. In the trials in which the eyes were not captured by the onset distractor (but moved directly to the target) another type of distractor interference effect was found. Relative to a condition in which no distractor was present, saccade latencies were increased indicating that it took longer to initiate a saccade to the target when a distractor was present (see e.g., Godijn & Theeuwes, 2002). Also, in those trials, the presence of a distractor had an effect on the saccade trajectory. When making a saccade to the target the eyes deviated towards to location of the distractor in some conditions (Godijn & Theeuwes, 2002; McPeck & Keller, 2001; McPeck, Skavenski, & Nakayama, 2000), while the eyes deviated away from the distractor location in other conditions (Doyle & Walker, 2001; Godijn & Theeuwes, 2002; Rizzolatti, Riggio, & Sheliga, 1994; Van der Stigchel & Theeuwes, 2005, 2006).

Saccade deviations are attributed to competitive interactions of activation within intermediate layers of the superior colliculus (SC), a midbrain oculomotor structure involved in encoding stimuli as potential saccade targets (Sparks & Hartwich-Young, 1989). Competitive interactions within SC operate between separate populations of neural activation, and are crucial to models of saccade deviation effects (Godijn & Theeuwes, 2002; McSorley, Haggard, & Walker, 2004). Deviation away from a distractor is associated with inhibition of distractor-related activation. As has been argued by Godijn and Theeuwes (2002) this inhibition is presumably top-down in nature and applied to prevent misdirected saccades towards the distractor. The overall population of activation produces a saccade vector that deviates away from the distractor location (e.g., Doyle & Walker, 2001; Godijn & Theeuwes, 2002; Van der Stigchel & Theeuwes, 2005, 2006).

For endogenous cueing, Van der Stigchel and Theeuwes (2007) investigated the role of the oculomotor system in a classic Posner cueing paradigm in which a central arrow indicated the likely target location. Observers were required to covertly direct attention to the cued location and discriminate a target letter presented at the cued or the uncued location. In some trials, instead of discriminating the target, observers had to make a saccade to another location in space. Van der Stigchel and Theeuwes (2007) found that when observers made a saccade the eyes deviated away from the attended location. As argued, finding eye movement deviation away suggests the occurrence of a process that *inhibits* oculomotor activity below baseline level prior to saccade initiation (Van der Stigchel, Meeter, & Theeuwes, 2006). Neural evidence for a link between deviation away and inhibition comes from neurophysiological studies in which a localized injection of a GABA agonist is placed at a location in the SC motor map. Such a localized inhibitor results in saccade deviation away from the injected site (Aizawa & Wurtz, 1998).

Van der Stigchel and Theeuwes (2007) showed that even when observers were only required to covertly direct attention to the cued location, the eyes deviated away from the attended location. More importantly, however, they also showed that the eyes deviated away from the uncued location. This implies that the oculomotor system is not only involved during endogenous direction of covert attention to the cued location, but that the oculomotor

system is also involved after covert attention ('the spotlight') has traveled from the cued to the uncued location. So it appears that the oculomotor activity elegantly 'travels' along with the endogenous attentional spotlight. Saccade deviation seems to reflect the amount of attentional processing at any given location in space.

Our previous study required observers to direct attention in a top-down fashion to a location in space (Van der Stigchel & Theeuwes, 2007). Rather than looking at endogenous attention, in the current study we investigated the involvement of the oculomotor system in a classic exogenous cueing task. The use of exogenous rather than endogenous cueing (as used by Van der Stigchel & Theeuwes, 2007) allows us to examine the role of oculomotor activity during the occurrence of IOR.

Note that Godijn and Theeuwes (2004) already investigated IOR and saccade deviation. In their study, the location of a peripheral onset cue presented above or below fixation on either the right or left side of fixation indicated whether observers had to make a saccade straight up or straight down. For example, a cue presented above fixation on the left side indicated that observers had to make a saccade straight up. Immediately following the onset cue, Godijn and Theeuwes (2004) showed saccade deviations away from the cued location. However, when the interval between the cue and the onset of the saccade was long (i.e., 800 ms), the effects on the saccade trajectory were absent. In other words, when IOR was at its maximum the eye trajectories were not affected anymore by the onset cue. Godijn and Theeuwes (2004) concluded that even though IOR and saccade deviations were related they were generated by different substructures because the effects occurred in different time domains.

Even though Godijn and Theeuwes (2004) provided convincing evidence that saccade deviations do not occur at the longer cue-target intervals when IOR is at its maximum (see for a similar result, Sogo & Takeda, 2006), it should be realized that the Godijn and Theeuwes (2004) task does not resemble a classic IOR paradigm. Indeed, in a classic IOR paradigm following the abrupt onset cue, participants usually have to detect or discriminate a target at either the cued or uncued location. The difference in RT between cued and uncued locations is the signature of IOR. In Godijn and Theeuwes (2004) following the onset cue participants never had to detect or discriminate a target at cued or uncued locations. It is therefore feasible that saccade deviations were not observed because no subsequent processing was required at cued and uncued locations. To overcome this concern, in the present study we employed a classic exogenous cueing task in which participants needed to respond to a target presented at cued and uncued locations.

Van der Stigchel and Theeuwes (2007) argued that saccade deviation can be used as index for the amount of attention allocated to any particular location in time. Specifically, they showed that saccade deviations were always larger for cued relative to uncued locations. In other words, top-down orienting results in the allocation of a large amount of attention to the cued location. The question addressed in the present study is whether similar attentional allocation is observed when attention is summoned in an exogenous way by an abrupt onset cue.

2. Experiment 1

We employed the classic Posner exogenous cueing task in which an abrupt onset was used as a cue. The cue had a validity of 50% suggesting that the cue indicated the target location at chance level. Observers covertly discriminated the target letter E or S. On 20% of the trials, a tone sounded indicating that observers had to execute a saccade straight up as soon as possible. We used two intervals: a short (100 ms) and a long (800 ms) interval. The

paradigm employed was similar to the paradigm used by Sheliga and colleagues (1997).

2.1. Method

2.1.1. Participants

Twelve observers, aged between 18 and 27 years old, served as paid volunteers. Four of the observers were male. All reported having normal or corrected-to-normal vision. They were naïve as to the purpose of the experiment.

2.1.2. Apparatus

A Pentium IV computer with a processor speed of 2.3 GHz controlled the timing of the events and recorded response times. Displays were presented on an Iiyama 21" SVGA monitor with a resolution of 1024×768 pixels and an 85-Hz refresh rate. A second computer controlled the registration of eye movements' data on-line. Eye movements were registered by means of a video-based eye tracker (SR Research Ltd, Canada). The EyeLink2 system has a 500-Hz temporal resolution and a spatial resolution of about 0.1° . Only data from the left eye were analyzed. Although the system compensates for head movements, the observer's head was stabilized using a chin rest. The distance between monitor and chin rest was 75 cm. The experiment was conducted in a sound-attenuated and dimly lit room.

2.1.3. Stimuli

See Fig. 1 for an illustration of the display sequence. In the current experiment, the display started with the presentation of a 'star' character ($0.28^\circ \times 0.28^\circ$) in the center of the screen together with two pattern masks. The fixation point was presented in light gray (CIE x,y chromaticity coordinates of 0.280/0.314; 15.5 cd/m^2) on a black background (0.6 cd/m^2). The two pattern masks ($1.11^\circ \times 0.92^\circ$) were of the same color as the fixation point. They were positioned around the central fixation point on an imaginary circle of radius 6.85° . After 1000 ms one of the pattern masks was shortly replaced by a filled square with the same size and color as the pattern masks. This square served as a 'peripheral cue'. This cue was replaced after 50 ms by a pattern mask. After a delay of either 100 or 800 ms, both pattern masks were replaced by a letter character. On each trial, either the target letter 'E' or 'S' was presented accompanied by a randomly selected distractor letter 'P' or 'H'. The color of the letters was the same as the fixation point and pattern masks. The letters were sufficient in size to identify them without foveating. After 200 ms the letters were removed with a post-mask. Observers were required to indicate which target letter was present ('z' key for the letter 'E' and '/' key for the letter 'S').

In some of the trials (20%), no letter was presented but a short beep sounded. In these trials, observers had to saccade to a 'plus' character ($0.28^\circ \times 0.28^\circ$) positioned 7.2° straight above the fixation point. The display remained visible until a response was made or for 2000 ms when no response was made.

2.1.4. Procedure and design

Observers received oral instructions before the start of the experiment. They were instructed to fixate the central fixation point during the whole trial except when they heard the beep. In that case, they had to move their eyes to the designated cross above the fixation point. It was stressed that they had to make a single accurate saccade towards this element when they heard the beep or to respond as soon as possible by pressing the correct key if they detected the 'E' or the 'S' character. In other words, the beep can be seen as a 'go-signal' for the eye movement. In the 80% of the trials in which a target letter appeared, there was a 50% chance that the 'E' or the 'S' character was presented at the cued location, making the cue non-predictive of the target location. In 20% of the trials the beep was presented.

The experiment consisted of a training session of 40 trials and an experimental session of 640 trials. Each session started with a nine-point grid calibration procedure. Observers were required to saccade towards nine fixation points sequentially appearing at random in a 3×3 grid. In addition, simultaneously fixating the center fixation point and pressing the space bar recalibrated the system at the start of each trial. Feedback about the observer's performance on the identification of the letters was given every 20 trials.

2.1.5. Data analysis

An eye movement was considered a saccade when either eye velocity exceeded $35^\circ/\text{s}$ or eye acceleration exceeded $9500^\circ/\text{s}^2$ (as determined by the EyeLink 2 system). For trials in which a saccade had to be made, trials in which saccade latency was lower than 80 ms (anticipatory saccades) or higher than 800 ms were removed from the analysis. Saccade latency was defined as the interval between beep onset and initiation of a saccadic eye movement. Moreover, trials were excluded from further analysis in which no saccades, too early or small saccades ($<3^\circ$) were made. If the endpoint of the saccade had an angular deviation of less than 30° from the center of the target, the saccade was classified as correct and further analyzed. Furthermore, the initial saccade starting position had to lie within 2° from the central fixation point. For trials in which no saccade had to be made, trials were removed in which a saccade ($>3^\circ$) was made and in which the manual response was slower than 1000 ms.

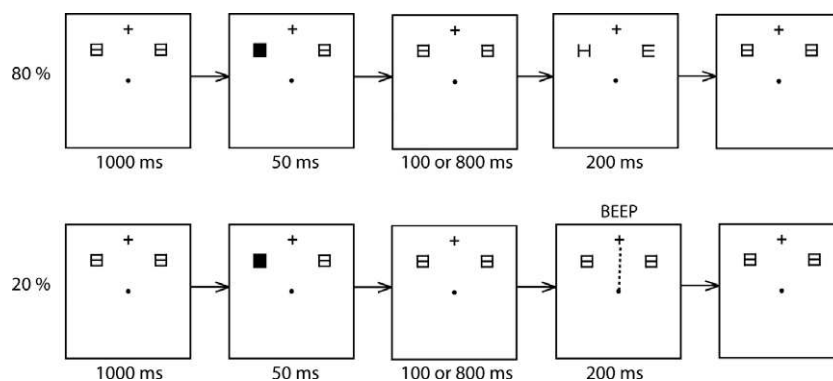


Fig. 1. Example of the display sequence in Experiment 1. Each trial started with the presentation of a fixation screen. After 1000 ms, a peripheral cue was presented for 50 ms. The interval between the cue and the target was either 100 or 800 ms. In 80% of the trials a target letter was presented after this interval. In these trials observers had to respond manually to the target letters 'E' or 'S' which could appear at the cued or the uncued location. On a small subset of trials (20%) a tone sounded, indicating that a saccade had to be made straight up to the '+'-marker.

Saccade trajectories to the target location were examined by calculating the mean angle of the actual saccade path relative to the mean angle of a straight line between the starting point of the saccade and the saccade target. The angle of the actual saccade was calculated for each 2 ms sample point by examining the angle of the straight line between fixation and the current sample point. Angles were averaged across the whole saccade and subtracted with the angle of the straight line between fixation and the target location (for a more detailed overview of saccade trajectory computation, see Van der Stigchel et al., 2006). Positive and negative deviations refer to deviations towards and away from the target location, respectively.

To compute the influence of the cue on saccade trajectories, differences between the deviations of the leftward and the rightward cue condition were analyzed. For instance, no difference in saccade trajectories between whether the left or the right location was cued would mean that the cue had no influence on saccade deviation. This would imply that an identical trajectory was observed whether the left or the right location was cued. Trials with saccade latency, response time or angular deviation of more than 2.5 standard deviations away from the mean were excluded from the analysis.

2.2. Results

In this experiment 16.6% of the trials were excluded from the key press condition; most of the trials were excluded because eye movements were made during the trial (13.7%). In the eye movement condition, 14.5% of trials were excluded; most of these trials were excluded due to the above mentioned restrictions on saccade latency (8.3%). See Table 1 for all results.

With respect to response times, an ANOVA was run with cue-target interval (100 versus 800 ms) and cue validity (cued, uncued) as factors. There was a main effect of cue-target interval ($F(1,11) = 7.57, p = .018$) indicating that observers responded slower with the 100 ms interval compared to the 800 ms interval. There was no effect of cue validity ($F(1,11) = 2.83, p = .12$). The interaction between cue-target interval (CTI) and cue validity reached near significance ($F(1,11) = 3.34, p = .094$). With respect to the 800 ms interval, responses were significantly slower for the cued than for the uncued location ($t(11) = 2.95, p = .013$). An effect of cue was not present for the 100 ms interval ($t(11) = 0.57, p = .58$).

Saccade latencies were slower in response to the go-signal on trials with the 100 ms interval compared to trials with the 800 ms interval ($t(11) = 4.09, p = .0018$).

An ANOVA with interval (100 versus 800 ms) and cue validity (cued, uncued) revealed no effects on percentage correct. There was no effect of interval ($F(1,11) = 3.39, p = .095$) or cue validity ($F < 1$). Also the interaction between interval and cue validity was not significant ($F(1,11) = 1.41, p = .26$).

For the 100 ms interval, saccade deviation differences for eye movements triggered by a go-signal revealed a significant difference from zero ($t(11) = 2.87, p = .015$). Eye movements deviated

away from the cued location. For the 800 ms interval, saccade deviations differences for eye movements triggered by a go-signal revealed no significant difference from zero ($t(11) = 0.05, p = .96$). There was a significant difference between the deviations of the 100 versus 800 ms interval ($t(11) = 2.54, p = .027$).

In addition to the measure of saccade deviation as we typically have used in our studies (see e.g., Van der Stigchel & Theeuwes, 2005, 2006, 2007), we also calculated two other often used measures of eye movement trajectory deviation. Fig. 2 presents these results. As is clear from Fig. 2, the two other measures 'overall initial direction' and 'maximum deviation' basically show the same effect at the 100 and 800 cue-target interval. This is consistent with previous studies in which we have shown that the various measures of saccade trajectory deviation show similar effects suggesting that each measure represents the same underlying mechanism (Van der Stigchel, Meeter, & Theeuwes, 2007; Van der Stigchel & Theeuwes, 2006).

2.3. Discussion

In the present experiment in which observers had to covertly discriminate between the letters E and H, the abrupt onset cue caused IOR. At the 800 ms interval, observers were slower to respond to a target presented at a cued location (628 ms) than at an uncued location (614 ms). However, the cue did not result in the typical RT benefits at the 100 ms interval. Even though others also failed to find facilitation and at short intervals (Danziger & Kingstone, 1999; Dorris, Klein, Everling, & Munoz, 2002; McAuliffe & Pratt, 2005; Pratt et al., 2001; Tassinari et al., 1994) the occurrence of IOR is typically interpreted as evidence that attention was captured in a purely exogenous way (see e.g., Posner, 1980; Theeuwes & Godijn, 2002). In addition, as noted, the occurrence

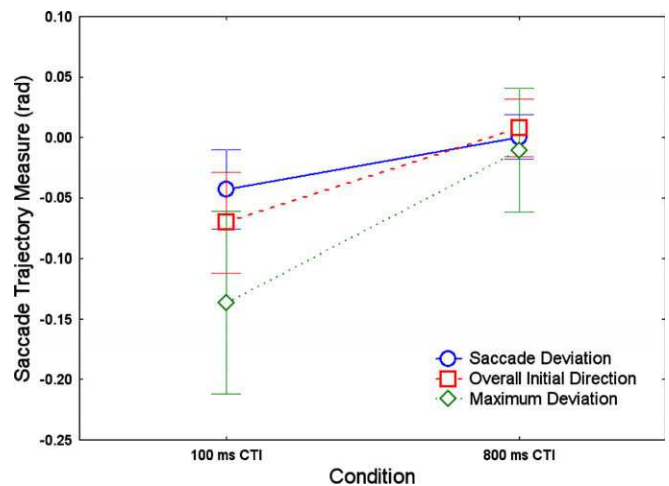


Fig. 2. Saccade trajectory deviation for 100 and 800 ms cue-target interval (CTI). Error bars represent standard errors of the mean. The three different measures of saccade trajectory deviation show deviation at the 100 ms CTI and basically no deviation at 800 ms CTI.

Table 1

Experiment 1: Manual reaction time and accuracy for targets presented at cued and uncued locations with a 100 or 800 ms cue-target interval (CTI)

	100 ms Cue-target interval		800 ms Cue-target interval	
	Valid	Invalid	Valid	Invalid
Manual response time (in ms)	633 (60)	637 (62)	628 (52)	614 (56)
Accuracy (in %)	84 (8)	84 (11)	80 (11)	83 (13)
Saccade latency (in ms)	416 (29)		366 (33)	
Saccade deviation relative to the location of the onset (in rad)	-0.043 [*] (0.052)		0.000 (0.029)	

Saccade latencies and saccade deviations for trials in which observers made a saccade straight up. ^{*}Indicates deviation values significantly different from zero. (Standard deviation in brackets.)

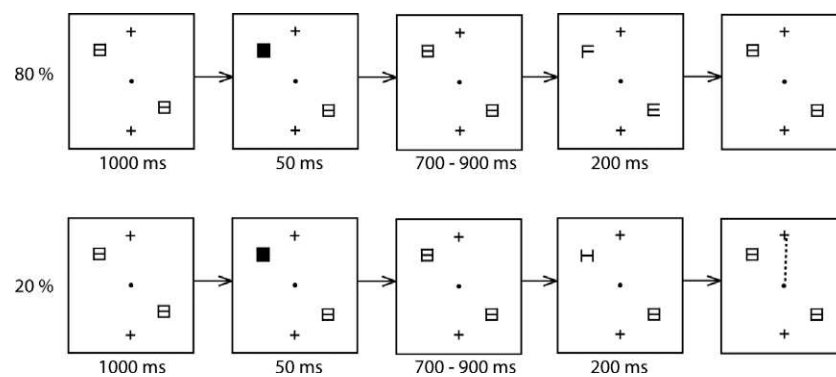


Fig. 3. Example of the display sequence in Experiment 2A. Each trial started with the presentation of a fixation screen. After 1000 ms, a peripheral cue was presented for 50 ms. The interval between the cue and the target was varied between 700 and 900 ms. In 80% of the trials a target letter was presented after this interval. In these trials observers had to respond manually to the target letters 'E' or 'S' which could appear at the cued or the uncued location. On a small subset of trials (20%) the letter 'H' was presented, indicating that a saccade had to be made to the location of the '+'-marker on the site at which the letter was presented.

of IOR is the best indicator of exogenous capture of attention (Pratt et al., 2001). The observed saccade deviation away from the location at which the onset was presented at the 100 ms interval indicates that the exogenous capture of attention by the abrupt onset causes oculomotor activity, a result that is consistent with previous findings (e.g., Godijn & Theeuwes, 2002; Van der Stigchel & Theeuwes, 2005). Note however, that at the 800 ms interval in which IOR is present, there was no saccade deviation. This result is consistent with Godijn and Theeuwes (2004) who also observed significant saccade deviations at short but not at long cue–target intervals. On the basis of this dissociation in time (saccade deviation at short cue–target intervals while IOR at long cue target intervals) Godijn and Theeuwes (2004) concluded that the inhibition underlying IOR and the inhibition which causes the saccade trajectory deviations have to operate at different levels within the oculomotor system.

Before we can conclude that the eyes do not deviate away from a location that is inhibited due to IOR, one has to consider two features of our current design that may have made the occurrence of saccade deviation at this interval less likely. First, in the current experiment the two potential target locations were both in the upper hemifield. It is feasible when the cue–target interval is relatively long (i.e., at 800 ms) that on some trials attention moves from the cued location to the uncued location (especially because the cue is only valid on 50% of the trials). On other trials however attention may reside at the cued location. If one calculates the mean saccade deviation over these different types of trials one may not observe any saccade deviations because *averaged over trials* these effects will cancel each other out. For example, recent work by McSorley et al. (2004) showed that when a vertical saccade has to be made when two distractors were presented at mirrored locations in both the left and the right hemifield, saccade trajectories tend to be straight. A similar result was reported by Van der Stigchel and Theeuwes (2007) when investing endogenous cueing. They showed that when cued and uncued target locations were presented both in the upper or lower hemifields no saccade deviations were observed while moving them to separate upper and lower visual fields caused reliable saccade deviations.

To test this possibility, similar to Van der Stigchel and Theeuwes (2007), we moved the cued and uncued target locations to the upper and lower visual fields (see Fig. 3). For example, the cued location would be in the upper right field while the uncued location would be in the lower left visual field. The saccades which we used to determine the saccade trajectory deviations would either be made to the upper visual field (in this example reflecting the deviation caused by the cued location) or the lower visual field (reflecting the deviation caused by the uncued location). By placing the cued and uncued locations in the upper and lower visual fields we are able to examine the effect of the exogenous onset cue

when—in case of an invalid trial—attention needs to move away from the (cued) visual field in which the onset cue was presented to the other (uncued) visual field in which there is no exogenous activity. This manipulation allows us to disentangle the exogenous effect of the cue from the endogenous shift of attention required to identify the target positioned at the uncued location.

Second, in our Experiment 1 in the condition in which a saccade had to be made, observers only executed a saccade when a tone sounded. This implies that when the tone sounded observers did not have to process information at cued or uncued locations. There was only attentional processing at cued and uncued locations for the manual response in trials in which no saccade was executed. Obviously, the saccade deviation that we observed in our Experiment 1 is the result of the presentation of the abrupt onset, but does not represent the subsequent processing at the cued location following the abrupt onset that occurs in typical IOR paradigms. To address this issue, in our Experiment 2 in addition to the manual E–S discrimination task, observers were presented in 20% of the trials the letter H at cued and uncued which signaled that they had to make a saccade. This ensured that before a saccade was launched attentional processing was needed at either the cued or the uncued location. This also enabled us to determine the oculomotor involvement after attentional processing at the uncued location. Since we focused on the oculomotor involvement in IOR we only used a long cue target interval in Experiment 2.

3. Experiment 2

In Experiment 2 we focused on IOR and used a cue–target interval that randomly varied between 700 and 900 ms. We presented the pre-masks (the potential target locations) in the upper and lower visual field. Because we did not have an adequate baseline in Experiment 2A to account for the natural variation in eye movement trajectories, we were not able to calculate saccade deviations.¹ Therefore, in Experiment 2B we solely focused on saccade

¹ Since it is known that natural directional biases exist in saccade trajectories (e.g., Erkelens & Sloop, 1995; Minken, Van Opstal, & Van Gisbergen, 1993; Viviani, Berthoz, & Tracey, 1977), the effect of the cue on saccade trajectories has to be corrected for this natural variation. In Experiment 1, we computed the difference between the mean deviation for the leftward and the rightward cue. In this experiment, a deviation of zero indicates no difference between these two trajectories. However, in Experiment 2A, there was no leftward and rightward cue for each participant because the two potential target locations were presented in the upper and lower visual field with one in the left and one in the right hemifield (see Fig. 3). In Experiment 2B, this condition was changed by running two blocks (block 1: a pattern mask in the upper visual field located on the left and a pattern mask in the lower visual field on the right; block 2: a pattern mask in the upper visual field located on the right and a pattern mask in the lower visual field on the left). This allowed us to calculate the saccade deviations in a same way as in Experiment 1.

deviations. We balanced the locations of the pattern masks such that in one block the pattern mask would appear in the top-left or bottom-right and in another block in the top-right and bottom-left. This enabled us to calculate an adequate baseline, because saccade trajectories in response to activity at the left or right pattern masks could be compared to saccade trajectories evoked by activity at their mirrored locations as recorded in a different block (see, Van der Stigchel et al., 2007). In Experiment 2B we used the same timing and set-up as Experiment 2A except that observers had to make saccades on every trial.

4. Experiment 2A

4.1. Method

4.1.1. Participants

Twelve observers, aged between 19 and 25 years old, served as paid volunteers. Two of the observers were male. All reported having normal or corrected-to-normal vision. They were naive as to the purpose of the experiment.

4.1.2. Stimuli: procedure, design, and data analysis

In the current experiment, the two potential target locations were presented in the upper and lower visual field with one in the left and one in the right hemifield. The locations were counter-balanced between observers, but it was ensured that the pattern masks were always diagonally separated like in Fig. 3. In addition to the target letters 'E' and 'S', an 'H' was presented on 20% of the trials at the cued or uncued location. Observers were required to respond manually to the letters 'E' and 'S'. However, when the observers identified the 'H', they had to saccade to the plus character positioned in the same upper or lower hemifield as where the 'H' was presented. In this experiment, the 'H' character replaced the beep signal and could be seen as the 'go-signal' for the eye movement. The interval between the cue and the letters was varied between 700 and 900 ms. The experiment consisted of 600 trials and 40 training trials. For data analyses, the same prerequisites as in Experiment 1 were applied.

4.2. Results

In Experiment 2A, 20.9% of the trials were excluded from the key press condition; most of the trials were excluded because eye movements were made during the trial (15.7%). In the eye movement condition, 30.4% of trials were excluded; most of these trials were excluded because the eye movement was not directed to the correct target location (9.86%), because the amplitude of the eye movement was too small (5.90%) and due to the above mentioned restrictions on saccade latency (11.60%). See Table 2 for all results.

With respect to response times, observers were slower to respond to letters at the cued location than at the uncued location ($t(11) = 4.29$, $p = .0013$), indicating the existence of a reliable IOR effect.

Table 2

Experiment 2A: Manual reaction time and accuracy for targets presented at cued and uncued locations

	Cued	Uncued
Manual response time (in ms)	639 (65)	627 (70)
Accuracy (in %)	83 (10)	87 (9)
Saccade latency (in ms)	549 (87)	559 (79)

Saccade latencies for trials in which observers made a saccade straight up. (Standard deviation in brackets.)

Saccade latencies were not significantly different in response to the go-signal at the cued location than at the uncued location ($t(11) = 1.58$, $p = .14$)

Consistent with the effect of IOR on RT, observers were more accurate in responding to letters at the uncued location than at the cued location ($t(11) = 4.15$, $p = .0016$).

5. Experiment 2B

5.1. Method

Six observers, aged between 19 and 27 years old, served as paid volunteers. Two of the observers were male. In the current experiment, the two pattern masks were presented in the upper and lower visual field. Two blocks were run with one block in which the pattern mask in the upper visual field was presented on the left and the pattern mask in the lower visual field was presented on the right and one block in which this situation was reversed (the pattern mask in the upper visual field was presented on the right and the pattern mask in the lower visual field was presented on the left). The order of the blocks was counterbalanced. At either the cued or the uncued location, an 'H' was presented (the target letter). No other non-target letters were presented. When the target letter H was localized, observers were required to saccade to the plus character positioned in the same upper or lower visual field as where the target letter was presented. The interval between the cue and the letters was varied between 700 and 900 ms. The experiment consisted of 400 trials and 40 training trials. For data analyses, the same prerequisites as in Experiment 1 were applied.

5.2. Results

In Experiment 2B, 15.2% of the trials were excluded; most of these trials were excluded because the eye movement was not directed to the target location (4.37%), because the amplitude of the eye movement was too small (5.29%) and due to the above mentioned restrictions on saccade latency (4.75%). See Table 3 for all results.

Saccade latencies were not significantly different in response to the go-signal presented at the cued location relative to the uncued location ($t(5) = 1.06$, $p = .34$).

For the cued location, saccade deviations differences for eye movements triggered by a go-signal were significantly different from zero ($t(5) = 2.15$, $p = .042$; one-tailed). A significant difference was obtained for the uncued location ($t(5) = 3.28$, $p = .012$, one-tailed). There was a significant difference between the deviations for the cued and the uncued locations ($t(5) = 3.18$, $p = .024$) with stronger deviations for the uncued location compared to the cued location. For completeness, Fig. 4 presents two additional measures of saccade deviation.

5.3. Discussion

Experiment 2A showed that in the present experimental set-up the abrupt onset causes IOR on manual responses: observers were

Table 3

Experiment 2B

	Cued	Uncued
Saccade latency (in ms)	318 (49)	310 (39)
Saccade deviation (in rad)	-0.054* (0.061)	-0.090* (0.067)

Saccade latencies and saccade deviations for trials in which observers made a saccade straight up. *Indicates deviation values significantly different from zero. (Standard deviation in brackets.)

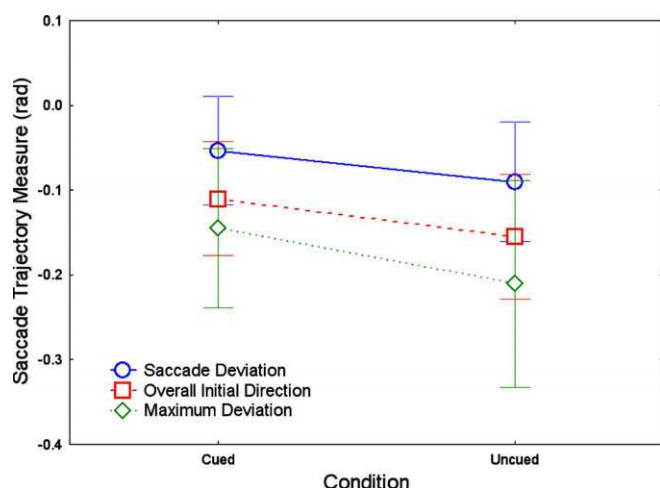


Fig. 4. Saccade trajectory deviation for cued and uncued conditions. Error bars represent standard errors of the mean. The three different measures of saccade trajectory deviation show more deviation away from the uncued than from the cued location.

slower and less accurate to respond to targets presented at the cued location than to targets presented at the uncued location. Experiment 2B shows that, with respect to the uncued location at which no exogenous cue was presented, the eyes deviated away from this location quite strongly. Note that this effect is unrelated to IOR, because exogenous attention was never at this location. In order to respond to the target letter, it has to be assumed that after attention has been captured by the exogenous onset at the cued location, observers had to redirect their attention in an endogenous way from the cued to the uncued location. This caused the deviation away from the uncued location. This finding is consistent with Van der Stigchel and Theeuwes (2007) who showed in an endogenous cueing task saccade deviations away from the uncued location. In their study, after attention was endogenously directed to the location indicated by a central arrow, in invalid trials observers had to redirect attention away from the cued location towards the uncued location. They concluded that oculomotor activity as revealed by the saccade deviations travels along with the ‘attentional spotlight’.

The current Experiment 2B also shows saccade deviation away from the cued location. This deviation is relatively small and significantly smaller than the deviation away from the uncued location. The important point here is that on the basis of the RT differences between the cued and uncued locations in Experiment 2A, we have evidence that the abrupt onset caused IOR at the cued location. Still, even though IOR was present at this location the eyes deviated away from this location, a result which is inconsistent with Godijn and Theeuwes (2004).

6. General discussion

In the present study we used the classic Posner exogenous cueing paradigm in which an abrupt onset was presented at a peripheral location followed by a target that appeared with equal probability at the location of the cue (validly cued location) or at another location (invalidly cued location). The current findings indicate that at short intervals, exogenous capture of attention by the peripheral onset causes saccade deviations away from this location (Experiment 1). These results are explained by assuming that the onset causes a burst of exogenous activity in the SC saccade map that needs to be inhibited when shortly after the presentation of the onset a saccade has to be executed (see also, Godijn & Theeuwes, 2004). At long intervals, we show the occurrence of IOR:

observers are slower and less accurate to respond to targets appearing at cued than at uncued locations (see Experiment 1 and 2A). The occurrence of IOR is a signature that the abrupt onset captured attention in a purely exogenous way (see, Posner & Cohen, 1984; Theeuwes & Godijn, 2002). Our Experiment 2B shows that even though IOR caused inhibition at the cued location, there was still a small deviation away from this location. However, saccade deviations were much stronger at the uncued location at which no IOR was present.

The present findings showing deviation away from the inhibited (IOR) location seem to be inconsistent with the current Experiment 1 and with Godijn and Theeuwes (2004). In these experiments there were no saccade deviations from the inhibited (IOR) location. For example, Godijn and Theeuwes (2004) reported only saccade trajectory deviations at short intervals between the cue and saccade execution (as in our current Experiment 1). Consistent with our Experiment 1 at longer delays when the cued location was inhibited (IOR), saccades did not deviate away from the location. As noted, there are important differences between the experimental tasks used in these experiments. Identical to the current study, Godijn and Theeuwes (2004) used a peripheral onset cue to summon exogenous attention to the cued location. However, in our Experiment 1 and in Godijn and Theeuwes (2004) following the presentation of the onset observers did not have to perform a discrimination task at cued or uncued locations. In our Experiment 1, observers initiated a saccade after a tone sounded. In Godijn and Theeuwes (2004) observers received a central arrow which indicated the location to which they had to execute a saccade. The crucial point is that after attention was summoned by the abrupt onset, in our Experiment 1 and in Godijn and Theeuwes (2004), attention never had to go back to this location to discriminate a target letter. In our current Experiment 2 (and in more classic IOR studies), after the long delay following the peripheral onset cue, observers typically have to perform a discrimination task (i.e., determining whether the target letter was an E, S, or H). Obviously, in order to discriminate the target letter attention needed to go back to the inhibited location. We assume that the return of attention at the cued location which was required in our Experiment 2 causes a small, yet reliable, saccade deviation from this location. The deviation is relatively small because the oculomotor activity associated with this attentional processing rides on top of the inhibition caused by IOR. Note that saccade deviations were much stronger at the uncued location because at this location attentional processing occurs without any inhibition (IOR). These findings are consistent with the notion suggested by Godijn and Theeuwes (2004) that IOR and saccade deviations are related but operate at different levels within the oculomotor system.

Consistent with these findings is the claim made by Van der Stigchel and Theeuwes (2007) who argued that the strength of saccade deviation may be an important measure that can reveal the amount of attention that is allocated to any particular location in time. Note that in their endogenous cueing task, Van der Stigchel and Theeuwes (2007) showed that the eyes deviated away from both the cued and uncued location. Yet, opposite to what we found here with exogenous cueing, deviations away from a target location were higher for cued than for uncued locations. This implies that with endogenous cueing more attentional resources are allocated at the cued than at the uncued location. The current findings show that with exogenous cueing the reverse effect is found. Deviations away from the uncued (uninhibited) location were stronger than deviations away from the cued (inhibited) location. This confirms the idea that saccade deviation may reflect the amount of attention allocated to any particular location in time.

The current findings are consistent with the notion that saccade trajectory deviations are caused by inhibition applied to the SC saccade map, and inhibition resulting in IOR is caused by inhibition at

higher levels within the oculomotor system. Because saccade trajectory deviations are only observed immediately following attentional processing, it has to be assumed that inhibition at the saccade map is only needed to inhibit the immediate activation caused by attentional processing. Because the short burst of exogenous activity in the SC will fade rapidly (see e.g., Theeuwes, Van der Stigchel, & Olivers, 2006) there is no need to inhibit any activity within the SC after a long delay. Therefore, consistent with Godijn and Theeuwes (2004) one does not expect saccade deviations after an abrupt onset at long intervals. Therefore, at the moment in time at which IOR is observed one does not observe saccade deviations. This is consistent with the idea that inhibition in the SC saccade map is different from inhibition resulting in IOR. Note however, if, as in our Experiment 2, attentional processing is required to discriminate a target letter at the inhibited location (IOR), we show that attentional processing causes a small but reliable deviation away from the inhibited location.

Godijn and Theeuwes (2004; Theeuwes and Godijn, 2004) presented a framework that can explain the different inhibitory mechanisms operating within different subsystems. This framework consists of three subsystems: a preculomotor attentional map, a saccade map, and an inhibitory control system. In the saccade map (the SC) the final saccade programming takes place. This saccade map is also responsible for activating a tag required for inhibition to occur. The inhibitory control system receives the inhibitory tag from the SC and applies the inhibition. We speculate that this inhibitory control system may include the dorsolateral prefrontal cortex (dlPFC) and the frontal eye fields (FEFs). These areas have been implicated in saccade inhibition. For example, lesions in the FEFs (e.g., Guitton, Buchtel, & Douglas, 1985; Rafal, Machado, Ro, & Ingle, 2000) or the dlPFC (e.g., Pierrot-Deseilligny, Rivaud, Gaymard, & Agid, 1991; Walker, Husain, Hodgson, Harrison, & Kennard, 1998) result in disinhibition of saccades. The preculomotor attentional map (presumably LIP) provides input to the saccade map (for details see, Godijn & Theeuwes, 2004; Theeuwes & Godijn, 2004).

In the current experiments, the abrupt onset is assumed to capture attention in an exogenous way. The capture of attention implies that there is exogenous activation within the preculomotor attentional map (i.e., LIP). This in turn generates oculomotor activation within the saccade map (i.e., SC) corresponding to the location in space where the abrupt onset was presented. At the short delay, when observers have to execute a saccade, the oculomotor activation in the saccade map has to be inhibited causing saccade deviations. However, at the long delay, as long as observers do not have to make an eye movement, the oculomotor activity within the SC has no consequences other than the generation of an inhibitory tag corresponding to the location of activation within the saccade map. The inhibitory control system receives this location-specific tag and in turn inhibits the preculomotor attentional map. This inhibitory control system inhibits within the preculomotor attentional map the location at which the initial abrupt onset was presented. This mechanism of inhibitory control is what is typically referred to as IOR: after attention is reflexively shifted to the location of the initially presented onset, there is delayed responding to stimuli subsequently presented at that location. The current study shows that when attention has to return to the inhibited location in order to process the letter identity, significantly less activation will be transferred to the saccade map resulting in a relatively small saccade deviation. At the uncued location at which there is no inhibition, the saccade deviation was significantly larger. The crucial point is that the inhibition in the preculomotor map causes a reduced input in the SC causing a relatively small saccade deviation.

The current interpretation is consistent with findings from a single cell study of Dorris and colleagues (2002). In this study,

monkeys performed an IOR task that required a saccade to a peripheral target while neural activity was measured in the SC. During the interval between cue and target, neural activity at the cued location was higher than at the uncued location suggesting that there was no active inhibition of neural activity within the SC during the cue–target interval. However, when the target appeared, the target-related burst of activity of SC cells was greater when the target was presented at an uncued location than at a cued location. Consistent with our interpretation, the inhibition resulting in IOR was not caused by active inhibition of SC cells but by reduced input into the SC.

The interpretation is also consistent with results of Theeuwes and Godijn (2004) who showed that distractors presented at inhibited (IOR) locations produced less interference than distractors at new locations. IOR seems to reduce the exogenous activation of irrelevant distractors within the SC. They concluded that IOR reduces competition within the oculomotor system such that observers are biased to orient away from already inspected locations (see, Klein, 2000).

In summary, the present study shows that immediately after attention is exogenously allocated to a location in space, saccades deviate away from this location. Consistent with a recent suggestion of Sogo and Takeda (2006) the function of inhibition underlying these deviated saccade trajectories may be the same as the function of IOR, that is, preventing revisiting already inspected locations. At longer intervals following the exogenous capture of attention, saccade deviations are no longer observed; yet at these time intervals (e.g., 800 ms after the presentation of the cue) the mechanism of IOR prevents revisiting already inspected locations. If attention has to return to the inhibited location to allow the subsequent processing of a target letter, again saccade deviation is observed yet this saccade deviation is less pronounced because attention has to go back to a location that is tagged with IOR. The observed reduced saccade deviation is consistent with the idea that IOR at a particular location reduces competition of that location within the SC (Theeuwes & Godijn, 2004).

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