

The relationship between covert and overt attention in endogenous cuing

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In a standard Posner paradigm, participants were endogenously cued to attend to a peripheral location in visual space without making eye movements. They responded faster to target letters presented at cued than at uncued locations. On some trials, instead of a manual response, they had to move their eyes to a location in space. Results showed that the eyes deviated away from the validly cued location; when the cue was invalid and attention had to be allocated to the uncued location, eye movements also deviated away, but now from the uncued location. The extent to which the eyes deviated from cued and uncued locations was related to the dynamics of attention allocation. We hypothesized that this deviation was due to the successful inhibition of the attended location. The results imply that the oculomotor system is not only involved during the endogenous direction of covert attention to a cued location, but also when covert attention is directed to an uncued location. It appears that the oculomotor system is activated wherever spatial attention is allocated. The strength of saccade deviation might turn out to be an important measure for the amount of attention allocated to any particular location over time.

In the late 1970s and early 1980s, Posner and colleagues (Posner, 1980; Posner & Cohen, 1984; Posner, Snyder, & Davidson, 1980) developed the now classic cuing technique for manipulating spatial attention independently of eye movements. In this paradigm, participants typically have to detect or discriminate a target and respond manually by pressing the appropriate response key. The target stimulus is preceded by a cue that provides information about the location of the upcoming target. In a cuing version typically referred to as *endogenous*, a centrally displayed arrow points to the likely target location. Participants are instructed to use the arrow and focus their attention on the cued location before the appearance of the target. Results show that processing of the target is enhanced at the cued location. In the so-called *exogenous* version of the cuing paradigm, before the appearance of the target, the participant's attention is pulled to one of the locations by an uninformative peripheral cue (usually an abrupt increment or decrement in luminance). The target then appears either at the cued or the uncued location. Shortly after presentation of the cue, response times (RTs) for targets at the cued location (valid cue) are fast and accuracy is high, relative to when the target appears at the uncued location (invalid cue). However, when the interval between the cue and the target is long, RTs to targets at the cued location are delayed in comparison with those to targets at the uncued location (i.e., *inhibition of return*; Posner & Cohen, 1984).

These cuing experiments have been important for understanding spatial attention as a "spotlight." Indeed, Posner et al. (1980) described attention as a "spotlight that enhances the efficiency of detection of events within its

beam" (p. 172). Over the last 25 years, the spotlight metaphor has generated several important research questions regarding how the beam moves through space, whether the beam can split, and the extent to which it can be highly focused or not (for a review and discussion, see Cave & Bichot, 1999). Alternative approaches do not consider RT benefits and costs obtained in typical cuing tasks to be the result of a moving "spotlight," but instead to result from an efficient allocation of attention over the visual field. For example, Shaw and Shaw (1977; Shaw, 1978) proposed a parallel model of attention suggesting that attention can be allocated flexibly to multiple locations in parallel. According to their model, the attentional system has a fixed capacity for visual processing that is optimally distributed over the different spatial locations. The time it takes for a stimulus to be identified is a function of the capacity allocated to the corresponding location. Attention is divided across a visual scene on the basis of the likelihood of the target location. When chances are high that the target will be presented at a certain location, more attentional resources will be allocated to that location. Therefore, in an endogenous cuing experiment, more resources will be allocated to the valid location than to the invalid location. Because of the higher amount of resources allocated to the cued location, processing of the target will be enhanced at the cued location. A modern example of this approach is the theory of visual attention (TVA; Bundesen, 1990). TVA is a unified framework of both recognition and selection mechanisms in which all elements can be processed in parallel. The model assumes that when an object is recognized, it is selected at the same time. The weight of the attentional resources dedicated to

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an object can be enhanced by increasing the *pertinence value* linked to that element, thus increasing the current priority of attending to the element. The higher the chance that a target will appear at a certain location, the higher the priority of attention to this location will be. On the basis of the advance knowledge of the valid location in a cuing paradigm, the pertinence of the valid location value will be increased, thereby facilitating the selection of the target.

In all of the models described above, whether they adhere to a limited-capacity spotlight or to a parallel-resources approach, the mechanism underlying attention is assumed to either enhance the efficiency of processing (e.g., Posner, Nissen, & Ogden, 1978), reduce stimulus uncertainty (e.g., Eckstein, Shimozaki, & Abbey, 2002; Palmer, 1994), enhance the stimulus signal (e.g., Yeshurun & Carrasco, 1999), reduce external noise (e.g., Lu & Doshier, 1998), reduce interference from unattended locations (e.g., Theeuwes, 1991), or suppress masking at attended locations (Enns & Di Lollo, 1997). The traditional view is that the attentional system is completely modular and that specific regions of the brain are dedicated to attentional control only (Posner & Petersen, 1990). Even though the attentional system interacts with other (sensory and motor) systems, it performs operations independently of other systems and on specific inputs only (Posner & Petersen, 1990).

Although one can consider the attentional system as being separate and independent, it should be noted that there is also evidence for a close link between it and the oculomotor system. In line with the modular view, it is known that if the task requires participants only to shift attention, they can do so without moving their eyes (see, e.g., Hoffman & Subramaniam, 1995). However, if the task requires that the eyes move, they will typically move to the location at which attention is directed (Deubel & Schneider, 1996; Godijn & Theeuwes, 2003). Thus, even though attention can shift without the eyes, one fundamental question is whether the oculomotor system would be involved even in a task that only requires the shifting of covert (and not overt) attention.

If one adheres to the view that the attentional system performs its operations independently of other systems (Posner & Petersen, 1990), one would expect the oculomotor system not to be involved in a task that requires only the shifting of covert attention. Some recent studies have provided evidence for the claim that spatial attention and eye movements are independent. Hunt and Kingstone (2003a, 2003b) showed that directing covert attention to a location in space did not result in the preparation of an eye movement to that location. They found the reverse pattern as well: When observers prepared to move their eyes to a particular location, there was no evidence that covert attention was allocated there. Similarly, Juan, Shorter-Jacobi, and Schall (2004) showed that what is selected by neurons in the frontal eye fields (FEF, a brain area related to sensorimotor processing) during the allocation of covert spatial attention is different from what is selected during the subsequent preparation of a saccade. In other words, these

studies suggested that saccade preparation is not an obligatory or immediate result of directing spatial attention.

However, the premotor theory of Rizzolatti and colleagues (Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Rizzolatti, Riggio, & Sheliga, 1994) suggests a completely different role for attention. According to this theory, shifts of attention are a by-product of the preparation of an eye movement to a particular location in space. The preparation of a saccade produces a processing advantage for stimuli located at the location toward which the motor program is prepared. In terms of the premotor theory, the central arrow in Posner's endogenous cuing task that instructs participants to direct attention to a particular location implies nothing else than the preparation of an eye movement that is not executed. For invalid trials, RT costs occur because of the time it takes to cancel the oculomotor program to the cued location and to prepare another one to the uncued location. Sheliga and colleagues (Sheliga, Riggio, Craighero, & Rizzolatti, 1995; Sheliga, Riggio, & Rizzolatti, 1994, 1995) provided evidence for the premotor theory by showing that directing covert attention to a spatial location influences the trajectory of a predetermined eye movement. For instance, they had observers make vertical saccades to a target below or above the fixation point (Sheliga et al., 1994). In order to know which saccade had to be executed, participants had to attend to a cue that indicated the subsequent oculomotor behavior (the imperative stimulus). This cue was presented within one of four peripheral boxes positioned in the upper or lower visual field and to the left or right of the target locations. Results showed that the eyes deviated away from the imperative stimulus, indicating that spatial attention leads to activation within the oculomotor system (see also Van der Stigchel & Theeuwes, 2005a).

Saccade deviations, such as those reported by Sheliga and colleagues (Sheliga, Riggio, Craighero, & Rizzolatti, 1995; Sheliga, Riggio, & Rizzolatti, 1994, 1995), have been attributed to competition between multiple target objects. It is generally assumed that possible target objects are represented by a large population of neurons encoding the movement toward each target object as a vector (Tipper, Howard, & Houghton, 2000; Tipper, Howard, & Jackson, 1997). When two possible targets are positioned in close proximity, the populations corresponding to those targets are combined into a mean population with a vector pointing to an intermediate location. Since participants are instructed to move their eyes to only one location, competition between the two active populations has to be resolved by inhibiting one of them. Because saccades are executed on the basis of the initial vector, inhibitory selection of one population over the other may shift the resulting movement vector in such a way that it affects the final response to the target. For example, in Godijn and Theeuwes (2002), saccade deviations were observed when observers had to make an eye movement to a predefined target while ignoring an abrupt-onset distractor singleton (referred to as the *oculomotor capture paradigm*; see Theeuwes, Kramer, Hahn, & Irwin, 1998). This creates a situation of competition between an endogenous and an

exogenous signal. The results showed that the eyes deviated away from the distractor location, suggesting that the location of the distractor was inhibited in order to prevent it from capturing the eyes.

The present study was designed to determine the involvement of the oculomotor system in the classic Posner cuing task. As in the Posner task, a central arrow indicated the likely target location, and participants were instructed to direct covert attention to this location. The target letters "E" and "S" needed to be discriminated, and participants responded manually to the target with the right or the left index finger. However, on a small subset of trials (20%), instead of responding manually to the target letter, the participants had to execute a vertical saccade straight up, in order to determine the extent to which the saccade deviated relative to the cued and uncued target locations. Classic attention approaches, such as the hypothesis that attention operates as a spotlight that enhances the efficiency of the detection of events within its beam (see, e.g., Posner & Petersen, 1990), do not predict the involvement of the oculomotor system. Indeed, if attention is independent of oculomotor preparation, as has been suggested (e.g., Hunt & Kingstone, 2003a, 2003b; Juan et al., 2004), there is no reason to expect that directing covert attention to a location in space would have an effect on the oculomotor system. Therefore, according to this view, allocating attention should exert no effect on the saccade deviations. Alternatively, the premotor theory of attention (e.g., Rizzolatti et al., 1987; Rizzolatti et al., 1994) predicts that, even though the participants basically performed a covert attention task involving manual responses, allocating spatial attention necessarily involves activation in the oculomotor system, and thus would cause saccade trajectories to be influenced by the location to which attention was allocated.

Regardless of whether one adheres to the classic "limited-capacity" space-based models of attention, which claim that at any given moment attention is focused on a particular area in space (e.g., Eriksen & Yeh, 1985; Posner, 1980), or the more recent "parallel-processing" models, which claim that attention may enhance the stimulus signal (e.g., Yeshurun & Carrasco, 1999) or reduce external noise (e.g., Lu & Doshier, 1998), all of these models assume that the role of attention is to prioritize processing of some objects or locations at the expense of others. Such "selection-for-perception" views can be contrasted with notions that assume that the role of attention is not so much to enhance perception but to deliver spatial information for a motor action, such as an eye movement (the "selection-for-action" view; see, e.g., Schneider, 1995; Schneider & Deubel, 2002). This view is closely related to the premotor theory of attention, except that in the selection-for-action approach the function of spatial attention is to provide a spatial code to the eye movement system, whereas in the premotor theory spatial attention is a by-product of the programming of an eye movement. The selection-for-perception theories do not assume the involvement of the eye movement system when a task involves only the covert allocation of attention. Other theories that do assume a strong connection between spatial attention and the eye movement system (such as the premotor theory) assume

that the covert allocation of attention always involves the oculomotor system, even when the eye movement system is not principally involved in executing a task. Thus, these other theories predict that any covert shift of attention will affect the eye movement trajectory.

As noted, if the allocation of covert attention affects the eye movement system, it is likely to affect the trajectory of the eyes. In the present setup, we expected the eyes to deviate away from the attended location, consistent with the effects reported by Sheliga and colleagues (Sheliga, Riggio, Craighero, & Rizzolatti, 1995; Sheliga, Riggio, & Rizzolatti, 1994, 1995). Note, however, that the eyes might instead deviate toward the location. Indeed, visual search experiments in humans (Godijn & Theeuwes, 2002; McPeck, Skavenski, & Nakayama, 2000; Walker, McSorley, & Haggard, 2006) and monkeys (McPeck, Han, & Keller, 2003; McPeck & Keller, 2001; Port & Wurtz, 2003) have shown that when a saccade is executed toward a target, a distractor may cause the eyes to deviate toward its own location. On the other hand, distractors are also able to cause eye deviations away from their location (Doyle & Walker, 2001, 2002; Ludwig & Gilchrist, 2003; Van der Stigchel & Theeuwes, 2005b). Moreover, smooth-pursuit eye movements have also been found to deviate away from an ignored distractor (Spering, Gegenfurtner, & Kerzel, 2006). The question of when eyes deviate toward and when away from a location has been the subject of several recent studies (McSorley, Haggard, & Walker, 2006; Van der Stigchel, Meeter, & Theeuwes, 2006; Walker et al., 2006). It has been hypothesized that deviations toward a location are caused by unresolved competition between populations in the oculomotor system resulting from feed-forward activation without top-down inhibition. However, when there is enough time to allow top-down preparation of a saccade, inhibitory processing may suppress the irrelevant oculomotor activity at the location of the distractor, causing the eyes to deviate away from that location (McSorley et al., 2006; Van der Stigchel et al., 2006).

Part of the evidence for the idea that top-down preparation plays an important role in the direction of saccade deviation comes from studies in which the influence of saccade latency on saccade deviation has been investigated. These studies have shown that deviations away are especially observed for eye movements with relatively long latencies (McSorley et al., 2006; Theeuwes & Godijn, 2004; Walker et al., 2006). When saccade latencies are relatively long (i.e., longer than 200 msec; see McSorley et al., 2006), there is enough time to resolve the competition in the oculomotor system. It is assumed that the top-down inhibition of the activation at the location of the distractor results in deviations away from the inhibited location (McSorley et al., 2006; Theeuwes & Godijn, 2004; Walker et al., 2006). Because the latencies in the present experiments were likely to be well over 200 msec, we expected deviation away.

Furthermore, in the present experiment, eye movements were executed on the basis of voluntary control, because they were initiated in response to a go signal. A saccade was executed because of successful processing of this go signal, so all eye movements were completely voluntary

and subject to top-down processes. This setup should lead to successful top-down inhibition of the to-be-canceled eye movement, resulting in deviation away.

EXPERIMENT 1

In Experiment 1, a central arrow indicated the likely target location, and participants were instructed to direct their attention to the cued location without making an eye movement. In most trials (66.6%) the cue was valid, so the target letter “E” or “S” was likely to appear at the cued location. In a subset of the trials (16.7%), the cue was invalid, and the target letter appeared at the uncued location. In the remaining 16.7% of trials, instead of a target letter being presented at a validly or invalidly cued location, a tone sounded to indicate that the participant should make a saccade straight up to a marker 7.2° above the fixation point.

The goal of Experiment 1 was to determine whether the mere allocation of covert attention would affect the oculomotor system. In the classic studies of Sheliga and colleagues (Sheliga, Riggio, Craighero, & Rizzolatti, 1995; Sheliga, Riggio, & Rizzolatti, 1994, 1995) demonstrating saccade deviation, participants knew that they had to make a saccade in every trial. In other words, it may not be surprising that the oculomotor system was involved in those studies, because the task was basically an eye movement task. Also, in most of Sheliga and colleagues’ conditions, the imperative stimulus that indicated that a saccade had to be executed was presented at one of the cued locations. Thus, in these conditions, the observed saccadic deviation away from the cued location may not have been the result of simply allocating endogenous attention; it may also have resulted from the actual processing of the imperative stimulus located at that location. In 83.3% of the trials in our Experiment 1, participants did not make an eye movement, but only directed attention covertly. In the 16.7% of trials in which they did have to execute a saccade, there was nothing to process at the location of the cue, since the imperative stimulus to execute the saccade was a tone. Therefore, this setup presented adequate con-

ditions in which to determine whether the mere allocation of endogenous attention in a classic manual-RT Posner task has an effect on the oculomotor system. According to the premotor theory, even though there was nothing to process at the location of the cue, allocating spatial attention should cause the eyes to deviate away from that location. Alternatively, a finding that the cue had no effect on the oculomotor system would support the conclusion that covert and overt attention are not linked (see Hunt & Kingstone, 2003a, 2003b; Juan et al., 2004).

Method

Participants. Eight observers (5 females and 3 males, between 19 and 32 years of age) served as paid volunteers. All reported having normal or corrected-to-normal vision and were naive with respect to the purpose of the experiment.

Apparatus. A Pentium IV computer with a processor speed of 2.3 GHz controlled the timing of the events and recorded RTs. Displays were presented on an Iiyama 21-in. SVGA monitor with a resolution of 1,024 × 768 pixels and an 85-Hz refresh rate. A second computer controlled the registration of the eye movement data online. Eye movements were registered by means of a video-based eyetracker, the Eyelink2 (SR Research Ltd., Canada). The Eyelink2 system has a 500-Hz temporal resolution and a spatial resolution of 0.01°. The system uses an infrared video-based tracking technology to compute the pupil center and pupil size of both eyes. An infrared head-mounted tracking system tracks head motion. For our experiments, only data from the left eye were analyzed. Although the system compensates for head movements, each participant’s head was stabilized 75 cm from the monitor using a chinrest. All experiments were conducted in a dimly lit sound-attenuating room.

Stimuli. See Figure 1 for an illustration of the display sequence. In the present experiment, the display started with the presentation of a fixation “star” character (0.28° × 0.28°) in the center of the screen. This fixation point was presented in light gray (CIE *x/y* chromaticity coordinates of .280/.314; 15.5 cd/m²) on a black background (0.0 cd/m²). After 600 msec, two pattern masks were presented (1.11° × 0.92°) that were the same color as the fixation point. The two were positioned around the central fixation point on an imaginary circle of radius 6.85°. In addition, a line cue (0.42° × 0.83°) pointed in the direction of one of the two pattern masks. After a delay of 800–1,300 msec, one of the patterns masks was replaced by a letter character. The color of this letter was the same as the fixation point and pattern masks. The letter was sampled from the char-

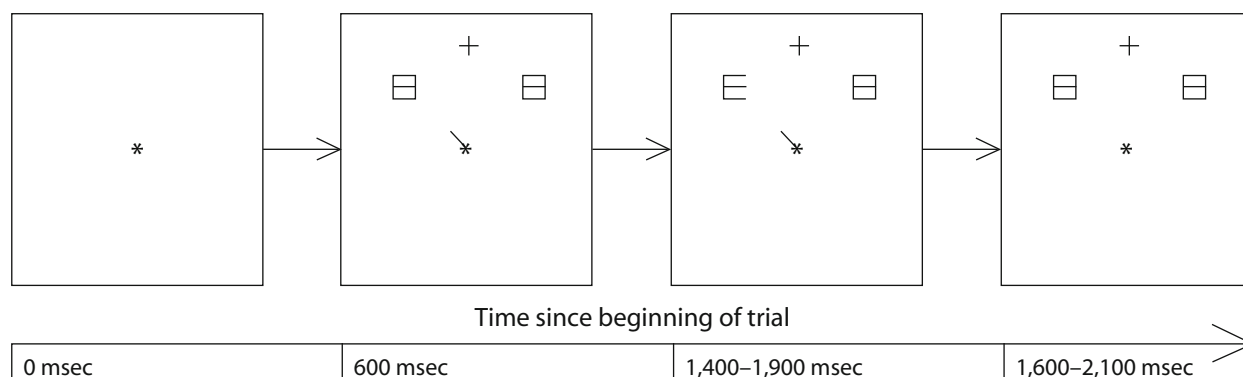


Figure 1. Example of the display sequence in Experiment 1. Each trial started with the presentation of a fixation screen. After 600 msec, a central cue indicated the likely target location. The interval between the cue and the target was 800–1,300 msec, after which the target was presented for 200 msec. Participants responded manually to the target letters “E” or “S,” which could appear at the cued or the uncued location. On a small subset of trials a tone sounded, indicating that a saccade had to be made straight up to the “+” marker.

acters “E” and “S” and was sufficient in size to identify it without foveating. After 200 msec, the letter was removed with a postmask. Participants were required to indicate which letter was present (by pressing the “z” key for the letter “E” and “/” key for the letter “S”). In some of the trials, no letter was presented, but instead a short beep sounded. In these trials, participants had to saccade to a “+” 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 2,000 msec when no response was made.

Procedure and Design. Participants received oral instructions before the start of the experiment. They were instructed to fixate the center fixation point during the whole trial, except for when they heard the beep. In that case, they had to move their eyes to the designated cross above the fixation point. We stressed that they had to make a single accurate saccade toward 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 could be seen as a “go signal” for the eye movement. There was a 66.7% chance that the “E” or “S” character would appear at the cued location. In 16.7% of the trials, one of the two letters appeared at the uncued location, and in the remaining 16.7%, the beep was presented. Participants were told that the to-be-identified letter would mostly appear at the cued location.

The experiment consisted of a training session of 24 trials and an experimental session of 360 trials. Each session started with a nine-point grid calibration procedure in which a participant was required to saccade toward nine fixation points sequentially appearing at random in a 3×3 grid. In addition, simultaneously fixating the center fixation point and pressing the space bar recalibrated the system at the start of each trial. Feedback about the participant’s performance on the identification of the letters was given every 24 trials.

Data analysis. For trials in which saccades had to be made, those with a saccade latency lower than 80 msec were removed from the analysis. *Saccade latency* was defined as the interval between beep onset and the initiation of a saccadic eye movement. Moreover, trials were also excluded from further analysis if no saccade was made or if the saccade was too early or too small ($<3^\circ$). If the endpoint of the saccade had an angular deviation of less than 30° from the center of the target, and if the saccade’s starting position lay within 1° of the center fixation point, the saccade was classified as correct and analyzed further. For trials in which no saccade had to be made, trials were removed in which a saccade $>3^\circ$ was made.

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-msec 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 from 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 toward and away from a given location, respectively.

To compute the influence of the cue on saccade trajectories, differences between the deviations of the leftward and rightward cue conditions were analyzed. For instance, no difference in saccade trajectories when the left or the right location was cued would mean that the cue had no influence on saccade deviation. Such a lack of effect would imply that identical trajectories were observed, whether the left or the right location was cued. Trials with a saccade latency, RT, or angular deviation more than 2.5 times the mean for that measure were excluded from the analysis.

Results

The prerequisites made on saccade latency, RT, saccade amplitude, saccade deviation, and saccade classification led to the average loss of 10.6% of trials. See Table 1 for all results. RTs were faster for letters presented at the val-

Table 1
Experiment 1: Manual Response Times for Targets Presented at Validly and Invalidly Cued Locations

	Valid Location	Invalid Location
Manual response time	421 msec	449 msec
Accuracy	92%	94%
Saccade latency		441 msec
Saccade deviation		-0.05 rad*

Note—Saccade latencies and saccade deviations are for trials in which participants made a saccade straight up. *Deviation value significantly different from zero.

idly cued than at the invalidly cued location [$t(7) = 3.56$, $p < .01$]. The mean RT for letters at the valid location was 421 msec ($SD = 107$ msec), whereas it was 449 msec ($SD = 115$ msec) for letters at the invalid location. Mean saccade latency was 441 msec ($SD = 51$ msec). There was no significant difference in the percentages correct for the valid and invalid location cuing conditions [$M = 93\%$ correct; $t(7) = 1.21$, $p > .20$].

Saccade deviation differences for eye movements triggered by a go signal revealed a significant difference from zero [$t(7) = 5.13$, $p < .01$]: Eye movements deviated away from the cued location ($M = -0.05$ rad, $SD = 0.05$ rad).

Discussion

The present results showed a classic Posner cuing effect on manual RTs, revealing faster RTs for targets presented at a validly cued than at an invalidly cued location. Finding a location cuing effect indicates that participants followed the instructions and endogenously directed attention to the cued location. At the same time, there was a clear saccade deviation away from the cued location, suggesting that the mere endogenous allocation of attention to a location in space has an influence on the oculomotor system. Whereas previous studies showed saccade deviations away from locations at which an imperative stimulus was presented, the present study showed that it is not necessary to process information at a location: Simply directing attention to the location is enough to elicit a saccade deviation. Note that in the present experiment, participants had to make a manual response in most trials, and in the small subset of trials in which a saccade had to be made, the saccade never had to be executed to the cued location. Therefore, from a task perspective, there was no need to prepare an eye movement to the cued location. If anything, preparing such an eye movement would have made it harder to remain fixated at the fixation point.

Finding saccade deviations in a condition in which participants only had to direct attention to a location in space provides strong evidence for the premotor theory of attention. The saccade deviation is caused by the need to inhibit the automatically programmed eye movement to the cued location in order to be able to execute an accurate saccade to the target (Doyle & Walker, 2001; Godijn & Theeuwes, 2002; Theeuwes & Godijn, 2004; Van der Stigchel et al., 2006; Van der Stigchel & Theeuwes, 2005b). The present findings suggest that directing attention to a location in space automatically results in a saccade deviation. This finding is consistent with recent work by Theeuwes,

Olivers, and Chizk (2005), who showed that keeping a location in spatial working memory also causes a saccade deviation away from this location.

EXPERIMENT 2

In Experiment 2, the notion of covert attention and its relation to the oculomotor system was tested further. In Experiment 1, the imperative stimulus to execute a saccade was presented auditorily. In Experiment 2, we presented the imperative stimulus to execute a saccade visually at the cued or the uncued location. This manipulation enabled us to examine the effect on saccade deviations when attention is initially directed to the valid location and—when the trial is invalid—is then directed to the invalid location. According to classic approaches, no effect would be expected on the saccade deviation, since directing attention has nothing to do with the preparation of a saccade. With respect to the premotor theory, however, the predictions are less clear. In case of a validly cued location, we would expect the same effect observed in Experiment 1; we should observe an effect on saccade deviations, because participants should endogenously direct attention (and therefore program a saccade) to the upcoming target location. However, it is less clear what would happen when attention (and therefore a saccade) was prepared to a location that turned out to be invalid. The endogenously prepared saccade would need to be canceled, and attention would need to be shifted to the invalid location. The question is whether this shifting of attention to the invalid location would involve activation in the saccade map so that the eyes would now deviate away from the invalidly cued location.

Method

Participants. Eight observers (all females between 19 and 23 years of age) served as paid volunteers. All reported having normal or corrected-to-normal vision and were naive with respect to the purpose of the experiment.

Stimuli, Procedure, Design, and Data analysis. The present experiment was similar to Experiment 1 except that, in addition to the target letters “E” and “S,” an “H” could also be presented at the cued or uncued location. Again, participants were required to respond manually to the letters “E” and “S.” When they identified the “H,” though, they had to saccade to the “+” character positioned above the fixation point. In this experiment, the “H” character replaced the beep signal and could be seen as the go signal for the eye movement. There was a 60% chance that an “E” or “S” character would appear at the cued location. In 20% of the cases, one of these two letters appeared at the uncued location, and in the remaining 20% the “H” character was presented. When the “H” appeared, in 50% of the trials it did so at the cued location, and in the other 50% of the trials it appeared at the uncued location. The cue signal disappeared on letter onset. The experiment consisted of a training session of 24 trials and an experimental session of 480 trials.

Results

The prerequisites made on saccade latency, RT, saccade amplitude, saccade deviation, and saccade classification led to the average loss of 14.0% of trials. See Table 2 for all results. RTs were faster for letters presented at the validly cued than at the invalidly cued location [$t(7) = 8.56, p < .001$]. The mean RT for letters at the validly cued location

Table 2
Experiment 2: Manual Response Times, Saccade Latencies, and Saccade Deviations for Targets Presented at Validly and Invalidly Cued Locations

	Valid Location	Invalid Location
Manual response time	476 msec	528 msec
Accuracy	93%	94%
Saccade latency	494 msec	530 msec
Saccade deviation	-0.19 rad*	0.05 rad

*Deviation value significantly different from zero.

was 476 msec ($SD = 130$ msec), whereas it was 528 msec ($SD = 139$ msec) for letters at the invalidly cued location.

There was no significant difference in percentages correct on letter identification for the valid and invalid location cuing conditions [$M = 93\%$ correct; $t(7) = 0.39, p > .70$].

With respect to saccade latencies, eye movements were faster when the go signal was presented at the validly cued location ($M = 494$ msec, $SD = 56$ msec) rather than the invalidly cued location ($M = 530$ msec, $SD = 61$ msec). This difference was statistically significant [$t(7) = 8.49, p < .0001$].

Separate deviations were calculated according to whether an eye movement was triggered by a go signal at the validly or the invalidly cued location. Deviation differences revealed a significant difference from zero for eye movements triggered by a go signal at the cued location [$t(7) = 5.13, p < .01$]. In this condition, eye movements deviated away from the cued location ($M = -0.19$ rad, $SD = 0.11$ rad). If the eye movement was triggered by a go signal at the invalidly cued location, there was no reliable difference from zero [$M = 0.049$ rad, $SD = 0.11$ rad; $t(7) = 1.30, p > .20$]. A comparison of both conditions showed that they were significantly different [$t(7) = 3.34, p < .02$]. See Figure 2 for a plot of the mean trajectories of 1 participant.

Discussion

Like Experiment 1, the present experiment showed a classic Posner cuing effect on manual RTs. Manual RTs to targets presented at a cued location were faster than those to targets presented at an uncued location. In addition, the present findings elegantly showed a similar effect on saccade latencies: When the imperative stimulus to execute a saccade was presented at a cued location, the saccades were initiated faster than when the imperative stimulus appeared at an uncued location.

Our measure of saccade deviation only showed an effect when the imperative stimulus appeared at the cued location. Indeed, the eyes deviated away from the validly cued location but not from the invalidly cued location. This raises the question of why no saccade deviation should occur away from the invalidly cued location, although participants responded accurately to the letter targets. If spatial attention and eye movement are closely coupled, one would expect that in the invalid cue condition, saccades would also deviate away from the attended location, but in this case away from the uncued location. There are

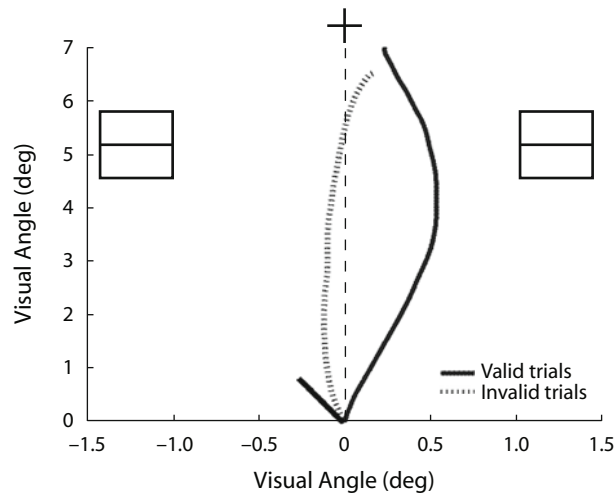


Figure 2. Mean eye movement trajectories for 1 observer. Trajectories were averaged for left-side trials. Separate trajectories are plotted for the valid and invalid trials. The cue and possible target locations are also indicated, although not drawn to scale.

number of possible explanations. First, it should be noted that spatial attention to the cued location was sustained for a long period during the cue–target interval, whereas it moved to the uncued location only briefly. Second, one way to explain these findings is to assume that saccade deviations result purely from the endogenous allocation of attention in response to the cue (as in our Experiment 1), and not so much from target processing. In both Experiments 1 and 2, we found saccade deviations away from the cued location. It is feasible that directing attention in response to the cue results in enough activity within the oculomotor system to observe saccade deviations. If this is true, the exact location of the target would not influence the saccade deviation, because this deviation is only observed in response to the cue.

However, we should consider one other alternative possibility. If spatial attention was necessary for processing the target at the invalid location, it could be feasible for some residual attention to remain at the cued location, thereby canceling out the attention generated at the invalidly cued location. Indeed, previous work by McSorley, Haggard, and Walker (2004) showed that when a vertical saccade was to be made in the presence of two distractors presented at mirrored locations in the left and right hemifields, saccade trajectories tended to be straight. The present result of a straight vertical saccade in the invalid cue condition could very well be explained by activation at both the valid and invalid mirrored locations.

To test this possibility, we conducted a third experiment in which the cued and uncued target locations were presented in the upper and lower visual fields. For example, the cued location could be in the upper right field while the uncued location was in the lower left visual field. The saccades we used to determine the saccade trajectory deviations could be made either 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). Because the cued and uncued locations were no longer both within the upper or the lower visual field, the activations within the saccade map would no longer have influenced each other. When the to-be-inhibited vector was remote and in the opposite (upper or lower) hemifield, the resulting vector would not be affected. For instance, Doyle and Walker (2001) did not find an effect of an irrelevant distractor in the opposite hemifield. Moreover, deviations are only present when the attended location is close to the saccade goal (Van der Stigchel, Meeter, & Theeuwes, 2007).

EXPERIMENT 3

Experiment 3 had the same setup as Experiment 2, except that the possible target locations were changed (see Figure 2): The cued and uncued locations were positioned on diagonals. Thus, when the upper right location was cued, the invalid target location was the lower left position, and vice versa. In addition, when the upper left location was cued, the lower right location was the uncued position. Moreover, participants could make a saccade to either the upper or to the lower visual field. When the imperative stimulus for the saccade was presented at one of the two lower-field positions, a vertical saccade to the lower visual field had to be made. If the imperative stimulus was presented to the upper visual field, a vertical saccade to the upper visual field had to be made.

Method

Participants. Nine observers (all females between 16 and 32 years of age) served as paid volunteers. All reported having normal or corrected-to-normal vision and were naive with respect to the purpose of the experiment.

Stimuli, Procedure, Design, and Data analysis. See Figure 3 for an illustration of the display sequence. In the present experiment, four pattern masks were presented around the central fixation point, on an imaginary circle of radius 6.85° . Furthermore, a line cue appeared that pointed in the direction of one of the four pattern masks. A delay of 800–1,300 msec then occurred, followed by the disappearance of the cue. Simultaneously with this change, a letter character replaced either the pattern mask that the line cue pointed to or the pattern mask positioned diagonal to this element (the uncued location). The remaining two pattern masks did not change.

The probabilities were the same as in the previous experiment. Participants were instructed that letters would mostly appear at the cued location but that in some trials the letter would appear at the uncued location. The experiment consisted of a training session of 24 trials and an experimental session of 984 trials. For data analyses, the same prerequisites were applied as in Experiment 2.

Results

The prerequisites on saccade latency, RT, saccade amplitude, saccade deviation, and saccade classification led to an average loss of 19.5% of the trials. See Table 3 for all results.

RTs were faster for letters presented at the validly rather than the invalidly cued location [$t(8) = 8.00, p < .001$]. The mean RT for letters at the cued location was 492 msec ($SD = 54$ msec), whereas the mean was 570 msec ($SD = 67$ msec) for letters at the uncued location.

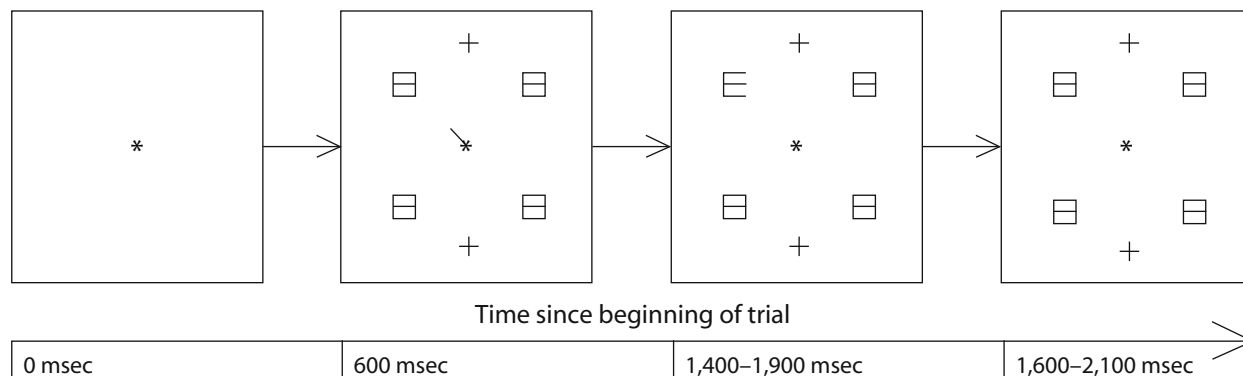


Figure 3. Example of the display sequence in Experiment 3. Each trial started with the presentation of a fixation screen. After 600 msec, a central cue indicated the likely target location. The interval between the cue and the target was 800–1,300 msec, after which the target was presented for 200 msec. The target letter could either appear at the cued location or at the location diagonally opposite the cued location. Participants were required to remain fixated during the whole trial sequence and to indicate as fast as possible which letter was presented. In a small number of trials an “H” was presented at the cued or the uncued location, which indicated that the participant had to make an eye movement either straight up or straight down to the marker. Which movement was required depended on the location of the letter “H” (the go signal): If the go signal was presented at one of the two upper locations, an upward saccade had to be executed. However, if it was presented at one of the two lower locations, a downward saccade had to be made.

There was no significant difference in percentages correct on letter identification for the validly and invalidly cued conditions [$M = 95\%$ correct; $t(8) = 1.92, p > .05$].

With respect to saccade latencies, eye movements were faster if the go signal was presented in the validly cued location ($M = 646$ msec, $SD = 112$ msec) rather than the invalidly cued location ($M = 672$ msec, $SD = 113$ msec). This difference was statistically significant [$t(8) = 2.46, p < .05$].

Before calculating saccade deviations, saccades to the upper and lower visual fields were collapsed. Then, saccade deviations were calculated according to whether an eye movement was triggered by a go signal at the cued or the uncued location. Deviation differences revealed a significant difference from zero for eye movements triggered by a go signal at the cued location [$t(8) = 2.58, p < .05$]. In this condition, eye movements deviated away from the cued location ($M = -0.06$ rad, $SD = 0.07$ rad). If the eye movement was triggered by a go signal at the uncued location, there was no reliable difference from zero [$M = 0.00$ rad, $SD = 0.08$ rad; $t(8) = 0.07, p > .90$]. A comparison of these conditions showed that they were significantly different [$t(8) = 3.45, p < .01$].

Discussion

Like Experiment 2, the present experiment showed a classic Posner cuing effect both on manual RTs and saccade latencies. By presenting cued and uncued targets in the different hemifields, we ensured that the oculomotor activity at the cued location could not cancel out oculomotor activity at the uncued location during processing of the invalidly cued target. Even though we implemented these conditions, our data indicated that processing at the uncued location did not result in enough oculomotor activity to cause the eyes to deviate from that location. These findings suggest that actual processing of the target at cued or uncued locations may not cause the saccade deviation, but instead that the endogenous direction of attention in

response to the cue could be the cause. This suggests that endogenously directing attention in response to a cue may be functionally different from directing attention needed to process a target letter.

Even though this is feasible, such a conception would be somewhat unsatisfactory theoretically. An alternative interpretation would be that observing saccade deviations could require that *enough* attentional resources be active at a particular location. It is possible that the task of letter discrimination was too easy, so participants did not have to focus their spatial attention strongly. Obviously, this lack of focusing would only occur at the invalid cue condition; in the valid cue condition, the participants would be expected to focus their attention in response to the predictive cue. To test this idea, we made the letter discrimination task more difficult. If our hypothesis is correct that a minimum amount of attention at a particular location is necessary in order to obtain saccade deviations, and our manipulation of making the letter discrimination task harder is thus successful, we would expect to also find saccade deviations for targets presented at the uncued location.

EXPERIMENT 4

The present experiment had the same setup as Experiment 3; the only difference was that the letter discrimination task was made more difficult. To this end, the pre-

Table 3
Experiment 3: Manual Response Times, Saccade Latencies, and Saccade Deviations for Targets Presented at Validly and Invalidly Cued Locations

	Valid Location	Invalid Location
Manual response time	492 msec	570 msec
Accuracy	95%	94%
Saccade latency	646 msec	672 msec
Saccade deviation	-0.06 rad*	0.00 rad

*Deviation value significantly different from zero.

sentation time of the target was now 100 msec instead of 200 msec. Furthermore, all elements were presented with less luminance, making it harder for the participants to recognize the letters.

Method

Participants. Nine observers (8 females and 1 male, between 19 and 31 years of age) served as paid volunteers. All reported having normal or corrected-to-normal vision and were naive with respect to the purpose of the experiment.

Stimuli, Procedure, Design, and Data analysis. The present experiment was similar to Experiment 3, except for the luminance of the different elements and the target duration. The fixation point and the cue were presented in darker gray than in the previous experiments (new CIE x/y chromaticity coordinates of .280/.314; 6.5 cd/m²). Furthermore, the gray color of the pattern masks and the letters was even more dark than the other elements in the visual display (CIE x/y chromaticity coordinates, .280/.314; 4.6 cd/m²). The target letter was presented for 100 msec.

Results

The prerequisites made on saccade latency, RT, saccade amplitude, saccade deviation, and saccade classification led to the average loss of 17.0% of the trials. See Table 4 for all results.

RTs were faster for letters presented at the validly than at the invalidly cued location [$t(8) = 3.08, p < .02$]. The mean RT for letters at the cued location was 583 msec ($SD = 122$ msec), whereas this was 625 msec ($SD = 91$ msec) for letters at the uncued location.

There was no significant difference in percentages correct on the letter identification task for letters presented at the cued or the uncued location [$M = 87\%$ correct; $t(8) = 1.03, p > .30$].

With respect to saccade latencies, eye movements were initiated faster if the go signal was presented in the cued location ($M = 585$ msec, $SD = 121$ msec) rather than the uncued location ($M = 633$ msec, $SD = 157$ msec). This difference was statistically significant [$t(8) = 2.58, p < .04$].

Saccade deviation differences revealed a significant difference from zero for eye movements triggered by a go signal at the cued location [$t(8) = 6.61, p < .001$]. In this condition, eye movements once again deviated away from the cued location ($M = -0.12$ rad, $SD = 0.05$ rad). For eye movements triggered by a go signal at the uncued location, this time there was also a reliable difference from zero [$M = -0.05$ rad, $SD = 0.05$ rad; $t(8) = 2.98, p < .02$]. A comparison of the conditions showed that they were significantly different from each other [$t(8) = 9.23,$

$p < .0001$]. Note that both deviations are negative, indicating that the eyes deviated away from the cued but also from the uncued location.

Discussion

In line with the previous experiments, we once again found the classic Posner cuing effect both for manual and saccadic responses. In addition, our manipulation to make the letter discrimination task more difficult was successful: Manual RTs were about 80 msec slower than in Experiment 3, and the mean accuracy rate dropped from 94% to 87%.

In line with Experiments 2 and 3, saccades deviated away from the cued location on valid trials. More importantly, however, the eyes also deviated away from the uncued location on invalid trials. Obviously, our manipulation of making the letter discrimination task harder resulted in more attention to being allocated to the invalidly cued location. These results suggest that when enough attention needs to be focused at the location of the target, researchers will obtain saccade deviations even from an uncued location.

Although eye movements deviated away from the uncued location, deviations away from a target location were higher for valid than for invalid trials. This implies that more attentional resources were allocated at a cued than at an uncued location. It is important to note that the strength of saccade deviation may turn out to be an important measure that can reveal the amount of attention that is allocated to any particular location over time.

GENERAL DISCUSSION

In the present study, a classic Posner cuing task was used in which participants had to direct covert attention to a location in space. In all four experiments, we found the classic endogenous cuing effects both for manual RTs and saccade latencies. More importantly, even though participants were required to only direct covert attention to the cued location, we found that under these conditions the oculomotor system was also involved. More specifically, on those trials in which a saccade had to be made straight up or down, the eyes deviated away from the cued location. In other words, the allocation of covert attention to the cued location resulted in eye movements that deviated away from this location.

It is important to note that our Experiment 4 shows that the eyes can also deviate away from stimuli appearing at the uncued location. This implies that the oculomotor system is not only involved during the endogenous direction of covert attention to the cued location, but also after covert attention is allocated to the uncued location. It appears that the oculomotor system is activated wherever spatial attention is allocated. Keep in mind that in our experiments there was never a need to have oculomotor activity at the cued or the uncued location, because on those few trials in which a saccade was required, the saccade never had to be directed to either of those locations. Overall, these findings provide strong evidence for the premotor theory of attention (Rizzolatti et al., 1987;

Table 4
Experiment 4: Manual Response Times, Saccade Latencies, and Saccade Deviations for Targets Presented at Validly and Invalidly Cued Locations

	Valid Location	Invalid Location
Manual response time	583 msec	625 msec
Accuracy	88%	86%
Saccade latency	585 msec	633 msec
Saccade deviation	-0.12 rad*	-0.05 rad*

*Deviation value significantly different from zero.

Rizzolatti et al., 1994), which suggests that shifts in covert attention are a by-product of the preparation of an eye movement. Even when there is no need to program an eye movement to a location, according to this theory the process of directing spatial attention always involves the oculomotor system. Note that in our study there was not only no need to make a saccade, participants were also explicitly instructed to keep their eyes on the fixation point. In terms of the premotor theory, the cuing effects on manual RTs and saccade latencies and the observed saccade deviations relative to the uncued location represent the process of canceling a saccade to the cued location and programming a new saccade to the uncued location. Saccade deviations from the uncued location were thus expected, because covert attention is a by-product of the preparation of a saccade.

It is important to note that our Experiment 1 showed that saccade deviations were observed in conditions in which nothing was processed at the location to which attention was directed. This is an important finding, since it suggests that, even in a task that is basically a classic Posner manual-RT task that only requires the allocation of covert attention, the endogenous shift of attention (without the need to process anything) is enough to generate oculomotor activation. This finding suggests that even when only covert attention is directed to a location in space, the oculomotor system is involved. These findings seem inconsistent with some of the conclusions of a study by Rafal, Calabresi, Brennan, and Sciolto (1989) investigating the role of the oculomotor system in the generation of inhibition of return (IOR). In one of Rafal et al.'s conditions, a central (endogenous) cue required participants to direct covert attention to a peripheral location in space. There were two types of instructions. In one condition, participants were instructed to covertly direct attention to the cued location *and* to prepare a saccade to the location; in the other condition, participants only had to direct covert attention. Rafal et al. showed the occurrence of IOR with the former but not with the latter type of instructions. In other words, with central cues, IOR was observed when a saccade had been prepared or executed to the cued location, but not when only covert attention had been directed to the cued location. They concluded that IOR only occurs when the oculomotor system is activated and that IOR does not occur in conditions in which participants only direct covert attention to a cued location. Given this conclusion, Rafal et al. implicitly assumed that the oculomotor system is not activated when only covert attention is directed to a location in space. Our findings show, however, that this implicit assumption may not be correct, and that even during covert endogenous orienting of attention the oculomotor system is involved. Our conclusion is in line with a recent study by Theeuwes et al. (2005), who showed that merely remembering the location of an object can affect the eye movement system (see also Theeuwes, Van der Stigchel, & Olivers, 2006). Theeuwes et al. (2005) showed that the eyes deviated away from a location that was kept in spatial working memory. These findings led to the conclusion that the process of remembering a certain

location may be the same as the process of programming an eye movement to that location, a claim that extends the premotor theory of attention.

Overall, the present study provides strong evidence that the oculomotor system is involved in the classic Posner endogenous cuing task, in line with the premotor theory of attention (Rizzolatti et al., 1987; Rizzolatti et al., 1994). The results are inconsistent with more classic theories of spatial attention that assume that covert and overt attention are not necessarily linked (Hunt & Kingstone, 2003a, 2003b; Posner & Dehaene, 1994; Posner & Petersen, 1990). In our experiments, we assume that the central cue indicating the location of the upcoming target elicited a motor program toward the expected location. This program would specify the direction and amplitude of a saccade that—in our experiments—never needed to be executed. According to the premotor theory, the presence of this motor program has two effects: (1) Through backward connections, the location of the expected stimulus becomes more salient, and (2) responses to stimuli presented at that location can be faster. The ability to respond faster not only holds for saccades, it also extends to more classic responses, such as manual RTs. The notion that the presence of a motor program toward a cued location increases the salience of stimuli presented at that location fits very well with the classic “spotlight of attention” notion, which assumes that attention can enhance the efficiency of processing (see, e.g., Posner, 1980; Posner et al., 1978). In line with this idea, Carrasco, Ling, and Read (2004) recently showed that location cuing alters the apparent stimulus contrast. These results imply that directing spatial attention results in greater neuronal sensitivity (i.e., a decreased threshold), changing the strength of the stimulus by increasing its salience.

The premotor theory can also explain delayed manual and saccadic responses to uncued locations. According to this theory, a response can only be emitted after a new motor program has been set up. Thus, for invalid trials, the original motor program toward the cued location needs to be canceled, and a new program toward the uncued location has to be set up. Obviously this takes time, causing delayed responding for both manual and saccadic responses.

Although the present study supports a strong link between covert attention and eye movements, the direction of the relationship is basically unknown. Only recently have researchers investigated a possible causal relationship between the capacity to perform a saccade and the capacity to orient attention (Craighero, Carta, & Fadiga, 2001; Craighero, Nascimben, & Fadiga, 2004). Participants in these studies were tested in a standard Posner cuing task with the eyes rotated in the orbit. In this setup, because the eyes were fully rotated to one of the temporal sides, participants could not make an eye movement toward the temporal hemifield. Note that visual acuity of the target locations was not affected in these experiments. Under these conditions, participants were unable to direct their attention to the temporal hemifield, as indicated by the lack of a difference between valid and invalid trials (Craighero et al., 2004). These results

indicate that when an eye movement cannot be executed, attention also cannot be allocated, which seems to point to a causal relationship between attention and eye movements.

There is also ample neurophysiological evidence for a connection between spatial attention and eye movements (see, e.g., Kustov & Robinson, 1996). For example, Corbetta et al. (1998) showed overlapping activation in both the parietal and frontal lobes in conditions in which participants either shifted attention or shifted the eyes (see also Nobre, Gitelman, Dias, & Mesulam, 2000). Furthermore, microstimulation of the FEF, an area involved in saccade preparation (Bruce, Goldberg, Bushnell, & Stanton, 1985), enhances visual excitability and attention (Armstrong, Fitzgerald, & Moore, 2006; Moore & Armstrong, 2003; Moore & Fallah, 2004). More recently, Müller, Philiastrides, and Newsome (2005) showed a similar result for the superior colliculus (SC), a subcortical oculomotor structure (Moschovakis, 1996). In addition, transcranial magnetic stimulation in humans affected the neural activity evoked by visual stimuli (Taylor, Nobre, & Rushworth, 2007). These studies all point to a link between spatial attention and eye movements. On the other hand, there is heavy debate whether (for instance) the lateral intraparietal area known to be involved in visual attention (Colby, Duhamel, & Goldberg, 1996; Robinson, Bowman, & Kertzman, 1995) is also directly involved in the generation of eye movements (Bisley & Goldberg, 2003; Goldberg, Bisley, Powell, Gottlieb, & Kusunoki, 2002).

Saccade trajectory deviations are assumed to reflect the competition between the different possible target locations within intermediate layers of the SC, which is involved in encoding stimuli as potential saccade targets (for a review, see Van der Stigchel et al., 2006). The SC is a lower-level structure that operates as a motor map for the generation of eye movements. Its intermediate layers have direct projections to and from the posterior parietal cortex (Paré & Wurtz, 1997), a region closely related to attentional selection. Competitive interactions within SC have been shown to operate between separate populations of neural activation and are central to models of saccade deviation effects (Arai & Keller, 2005; Godijn & Theeuwes, 2002; McPeck et al., 2003; McSorley et al., 2004). McPeck et al. (2003) showed that, when a saccade deviated toward a distractor during visual search, there was increased presaccadic activity at the location of the distractor in the SC. Also, microstimulation of the SC below the threshold for saccade generation caused saccades to deviate toward the stimulated location, and the magnitude of this deviation correlated with the activity induced at the stimulated location.

The observed saccade deviations in the present study can be understood in terms of the competitive integration model suggested by Godijn and Theeuwes (Godijn & Theeuwes, 2002, 2004; Theeuwes & Godijn, 2004). It is assumed that saccade trajectory deviations are caused by location-specific inhibition applied to a spatial map in which saccade programming occurs (a saccade map). The competitive integration model presumes that the SC represents the saccade map even though other structures,

such as the FEF and the supplementary eye field, could serve the same function (see, e.g., Schall, Stuphorn, & Brown, 2002). In our experiments, the mere allocation of endogenous attention to the cued location resulted in activity in the oculomotor map. In most trials, this endogenous allocation of attention was sufficient to discriminate between the target letters and to generate the appropriate manual response. When—in 20% of the trials—a saccade has to be executed, the eyes started moving in the direction of the mean vector of activity within the saccade map. Because there was oculomotor activation at the cued location, location-specific inhibition had to be applied to ensure that the eyes went up and not to the cued location. This location-specific inhibition resulted in a subbaseline level of activation within the saccade map. This subbaseline activation was reflected in a saccade trajectory deviation away from the inhibited location. Evidence for this idea has been provided by Aizawa and Wurtz (1998), who found similar saccade trajectory deviations after local inactivation of a region of the SC.

For invalid trials, the same processing occurred. Because the stimulus appeared at the uncued location, spatial attention was directed to that location. Once attention resided there, oculomotor activity was generated at that location. In terms of the premotor theory, once a new saccade program had been set up for the invalid location, spatial attention as a by-product of oculomotor programming resided at the uncued location. Because a saccade had to be made in some trials, this oculomotor activation had to be inhibited, causing subbaseline activation that was reflected in saccade deviations away from the uncued location. The strength of inhibition that needed to be applied depended on the level of activation of the to-be-inhibited location. In our Experiment 4, the eyes deviated more strongly away from the cued (-0.12 rad) than from the uncued (-0.05 rad) location, suggesting that the activation at the cued location was much stronger than the activation at the uncued location. This may not be surprising, because attention was directed to the cued location during the cue interval, and the cued location also had a validity three times higher than the uncued location. The important point is that the more oculomotor activation is generated at a location in space, the stronger the inhibition that must be applied, causing larger saccade deviations. These findings are consistent with Godijn and Theeuwes (2004), who required participants to ignore exogenous cues. They showed that more salient exogenous cues (such as an abrupt onset) resulted in larger trajectory deviations than did less salient cues (such as a color singleton).

In sum, whether one believes that covert spatial attention is a “spotlight” that can travel and can enhance the efficiency of the detection of events within its beam (Posner, 1980) or that spatial attention is a by-product of oculomotor programming (Rizzolatti et al., 1987; Rizzolatti et al., 1994), the present findings add to the growing body of literature showing that the attentional and oculomotor systems are strongly related, both at the behavioral level (see, e.g., Godijn & Theeuwes, 2002, 2004; Theeuwes et al., 2005; Van der Stigchel & Theeuwes, 2005a) and the neural level (e.g., Corbetta et al., 1998).

AUTHOR NOTE

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