

Updating the Premotor Theory: The Allocation of Attention Is Not Always Accompanied by Saccade Preparation

Artem V. Belopolsky and Jan Theeuwes
Vrije Universiteit Amsterdam

There is an ongoing controversy regarding the relationship between covert attention and saccadic eye movements. While there is quite some evidence that the preparation of a saccade is obligatory preceded by a shift of covert attention, the reverse is not clear: Is allocation of attention always accompanied by saccade preparation? Recently, a shifting and maintenance account was proposed suggesting that shifting and maintenance components of covert attention differ in their relation to the oculomotor system. Specifically, it was argued that a shift of covert attention is always accompanied by activation of the oculomotor program, while maintaining covert attention at a location can be accompanied either by activation or suppression of oculomotor program, depending on the probability of executing an eye movement to the attended location. In the present study we tested whether there is such an obligatory coupling between shifting of attention and saccade preparation and how quickly saccade preparation gets suppressed. The results showed that attention shifting was always accompanied by saccade preparation whenever covert attention had to be shifted during visual search, as well as in response to exogenous or endogenous cues. However, for the endogenous cues the saccade program to the attended location was suppressed very soon after the attention shift was completed. The current findings support the shifting and maintenance account and indicate that the premotor theory needs to be updated to include a shifting and maintenance component for the cases in which covert shifts of attention are made without the intention to execute a saccade.

Keywords: attention, saccades, premotor theory

The easiest and the most accurate way to extract information from our visual environment is by making a saccadic eye movement. These eye movements are very quick (approximately 300–500 degrees of visual angle per second) and enable us to quickly orient the part of the retina with the highest acuity to the objects of interest. Saccadic eye movements require minimum processing resources (Bekkering, Adam, Kingma, Huson, & Whiting, 1994), leading to the common notion that eye movements are also a “cheap” way to access external information.

In some situations, however, such overt orienting might be associated with certain costs. Consider a situation of crossing the road. It is often beneficial to have your attention more distributed, so that you can monitor the traffic coming from both sides. This is because making an eye movement causes most of the processing resources to be allocated to the saccade goal and the neighboring locations (Deubel & Schneider, 1996; Irwin & Gordon, 1998). In fact, overt orienting serves in a way as a very early filter of visual

information (Findlay & Gilchrist, 2003). Furthermore, covert shifts of attention are particularly useful in social situations, in which you might not want to let other people know that you are monitoring their actions. For example, if you see a person displaying aggressive behavior, you might want to avoid eye contact with that person but keep monitoring his or her location covertly.

But what are the mechanisms underlying these covert shifts of attention? The influential premotor theory (Rizzolatti, Riggio, & Sheliga, 1994; Rizzolatti, Riggio, Dascola, & Umiltà, 1987) posits that a shift of spatial attention involves all the necessary steps of saccade preparation, except for the actual motor execution (see also Klein, 1980; Klein & Pontefract, 1994). In this view spatial attention is treated as a byproduct of planning and executing saccadic eye movements. Naturally, a close interdependent relationship between covert and overt attentional orienting is predicted by this view. In recent years, a great deal of behavioral and neurophysiological evidence has been accumulated indicating a close link between covert attention and the oculomotor system.

Behavioral studies showed that the allocation of spatial attention affects saccade trajectories (Sheliga, Riggio, & Rizzolatti, 1995; Van der Stigchel & Theeuwes, 2007). Specifically, depending on the time-course, saccades tend to either curve toward or away from the attended locations (Campbell, Al-Aidroos, Pratt, & Hasher, 2009; McSorley, Haggard, & Walker, 2006), suggesting that both covertly attended locations and saccade goals share the same spatial map located in the intermediate layers of superior colliculus (SC). Furthermore, several studies have shown that before a saccade is executed there is an obligatory facilitation of perceptual processing at the location of the saccade goal (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson,

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Artem V. Belopolsky and Jan Theeuwes, Department of Cognitive Psychology, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands.

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Correspondence concerning this article should be addressed to Artem V. Belopolsky, Department of Cognitive Psychology, Van der Boerhorststraat 1, 1081 BT Amsterdam, The Netherlands. E-mail: a.belopolsky@psy.vu.nl

Dosher, & Blaser, 1995; Shepherd, Findlay, & Hockey, 1986). Importantly, several studies have demonstrated a functional relationship between the oculomotor system and covert attention. For example, in a study by Craighero and colleagues (Craighero, Nascimben, & Fadiga, 2004) the ability to make eye movements was precluded by asking participants to fixate a location far out in the periphery. As a result, they were not able to make eye movements to one side of the display, while they were not limited in making eye movements to the other side. The authors used the classic Posner cueing task (Posner, 1980), which robustly shows that cueing a location in the periphery leads to facilitation of processing of targets at that location. However, when a location to which no eye movement could be executed was cued, no benefits in processing were observed, while the standard cueing effect was shown on the "intact" side. Similarly, Smith et al. (Smith, Rorden, & Jackson, 2004) showed that covert attention was disrupted in a patient who from birth lacked the ability to make eye movements. Finally, several neurophysiological studies showed that subthreshold stimulation of several oculomotor structures such as frontal eye fields (FEF) and superior colliculus (SC) resulted in enhanced visual sensitivity at the corresponding retinotopic location (Cavanaugh & Wurtz, 2004; Moore & Fallah, 2001, 2004; Müller, Philiastides, & Newsome, 2005).

However, a completely different view posits that spatial attention represents a separate cognitive function which mechanisms could not be reduced to the operation of the low-level specialized oculomotor system (Hunt & Kingstone, 2003; Klein, 1980; Klein & Pontefract, 1994; Posner, 1980). Despite the fact that the two systems are often coupled during the everyday activities, it is assumed that covert attention operates independently and can be dissociated from the eye movement system, so that affecting one system would not have any consequences for the other system. Therefore, covert attention is treated as a supramodal higher cognitive function that interacts with the eye movement system only for the purpose of input and output and can be functionally distinguished from it (Klein & Pontefract, 1994). Substantial behavioral and neurophysiological evidence for dissociation between saccade preparation and spatial attention has also been accumulated.

Several behavioral studies using a dual-task design showed that preparing a saccade to a specific location on a majority of trials does not result in enhancement of occasional probe detection at that location as measured by manual responses (Hunt & Kingstone, 2003; Klein, 1980; Klein & Pontefract, 1994; Posner, 1980). Furthermore, it has been demonstrated that maintaining covert attention at a specific location in expectation of manually detecting a target on a majority of trials does not result in facilitation of occasional saccades to the attended location. Dissociation has also been demonstrated at the neurophysiological level. For example, it has been shown that within FEF and SC some neurons indeed followed the movements of attention (visual and visuomotor neurons), whereas other neurons (pure motor neurons) were either not modulated or even were inhibited during shifts of covert attention (Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Juan, Shorter-Jacobi, & Schall, 2004; Thompson, Biscoe, & Sato, 2005).

The relationship between attention and the oculomotor system remains an ongoing controversy (for a review see Awh, Armstrong, & Moore, 2006). In our previous study (Belopolsky & Theeuwes, 2009a) we have suggested that the controversy can be

resolved if a distinction is made between the shifting of attention to a location and maintenance of attention at a location. The idea is that shifting of attention to a location obligatory results in activation of a specific oculomotor program, which is consistent with the premotor theory (Rizzolatti et al., 1987). However, the voluntary maintenance of covert attention that occurs after attention is shifted may be more flexibly (economically) related to the oculomotor system, which suggests some dissociation between the attentional and the oculomotor systems.

To test this idea Belopolsky and Theeuwes (2009a) used a task that allowed simultaneous measurement of attentional allocation and saccade preparation, avoiding the typical problems of prioritizing one task over the other, associated with the dual-task designs (Pashler, 1989). Participants had to covertly shift their attention according to the central pointer cue which indicated a location where the target was likely to appear (80% of the trials). Depending on the identity of the target (numbers "1," "2," "3," or "4") they had to make a saccade to one of the locations. We showed the classic Posner like cueing effect: the saccadic reaction time (SRT) on validly cued trials was shorter than on invalidly cued trials (Posner, 1980). To measure saccade preparation we compared the SRT for the eye movements directed either toward (match) or away from the target location (mismatch). Note that participants did not have any advantage for preparing a voluntary eye movement to a specific location, because saccades to each location in the display were equally likely.

On validly cued trials, on which covert attention was already maintained at the target location, there was either facilitation of the saccade program when the probability of making an eye movement to the target location was 50% (Experiment 1) or suppression of the saccade program when this probability was low (i.e., 25% in Experiment 2). On invalidly cued trials, on which attention had to be shifted from the initially cued location to the target location, saccades were always initiated faster when the target and saccade locations matched, suggesting activation of a saccade program. Based on these results we concluded that shifting attention is accomplished through activation of an oculomotor program, but after attention is shifted, the oculomotor program can be suppressed if the probability of its execution is low.

In addition, the dynamics of facilitation and suppression were strongly affected by the match between the attended and saccade location on the previous trial. Specifically, saccades were prepared to the attended location when on the previous trials saccades were made to the target location. However, saccades to the attended location were suppressed when on the previous trial saccade were made away from the target location. This suggested that the onset of suppression of saccades is largely determined by the association formed on the previous trial.

The aim of the present study was to critically examine the shifting and maintenance account. Specifically, the shifting component of the account needed to be tested directly, since in our previous study shifting of attention was inferred from invalidly cued trials. This could have been a special case of shifting of attention to the target location after it had been disengaged from the cued location. To investigate this issue we used a paradigm similar to Belopolsky & Theeuwes (Belopolsky & Theeuwes, 2009a; Experiment 2) and asked participants to shift their attention in a variety of ways. In Experiment 1 participants shifted their attention as is typically done in covert visual search, in Experiment

2 attention was shifted by means of exogenous cue, and in Experiments 3 and 4 by means of endogenous cue. In all experiments the probability of executing an eye movement to the attended location was low (25%). Therefore, if shifting of attention obligatory activates the oculomotor system (consistent with the premotor theory) then it should always (and independent of how it is shifted) be evident in facilitation of saccades to the attended location.

Second, we wanted to investigate at what time point shifting of attention transfers into maintenance of attention (Experiment 3 and 4). This was possible because our previous results showed that in contrast to attention shift, attention maintenance was sensitive to probability manipulation. Specifically, it was associated with suppression of the saccade program (Belopolsky & Theeuwes, 2009a) when the probability of making an eye movement to the attended location was low. Such suppression of the oculomotor program is not consistent with the classic version of the premotor theory and indicates that premotor theory needs to be updated. By looking at the dynamics of facilitation and suppression of the oculomotor system as a function of time between the endogenous cue and the target (Experiment 3 and 4) we examined at which point shifting of attention turns into attention maintenance.

Experiment 1: Visual Search

In the previous study (Belopolsky & Theeuwes, 2009a) it was proposed that shifting of attention is always accompanied by saccade preparation. However, this was inferred from the performance on the invalidly cued trials, in which attention presumably had to be disengaged from the cue and then shifted to the target location (Posner, 1980). Because in the cueing paradigms attention shifts are systematically manipulated by using an external stimulus, it is important to examine whether this effect generalizes to conditions such as covert visual search. Typically in visual search participants covertly shift their attention freely across the display, which is very much unlike the situation in which attention is externally controlled by cues (as was the case in our previous cueing study). The need for attention in visual search is especially strong when the target is defined by a conjunction of features (Treisman, 1988) or when it shares many of its features with distractors (Duncan & Humphreys, 1989). In such situations it has been demonstrated that visual search is accomplished through a series of shifts of attention until the target is found (Treisman, 1988; Wolfe, 1994; Woodman & Luck, 1999). While some studies demonstrated common attention mechanisms being involved in shifting attention in the cueing and the visual search tasks (Briand & Klein, 1987; Luck, Fan, & Hillyard, 1993), several differences have been also noted (Duncan, Ward, & Shapiro, 1994; Theeuwes, Godijn, & Pratt, 2004; Wolfe, Alvarez, & Horowitz, 2000).

To examine whether shifting attention during visual search is associated with saccade preparation participants were asked to covertly perform a visual search for a target. We adapted the task of Belopolsky and Theeuwes (2009a) in such a way that participants had to covertly search for the target. They had to search for a number among three letters made up from the Figure 8 pre-masks. The target and distractor were similar to each other, requiring focal attention to be shifted repeatedly in order to find the target. The target number could be number "1," "2," "3," or "4" and indicated the location to which saccade had to be made (top left, top right,

bottom right, or bottom left, respectively). As in the previous study, saccades to each location in the display were equally likely, eliminating any advantage for preparing a voluntary eye movement to any specific location. Therefore, participants first had to search covertly by shifting attention serially from one element to another and after finding the target make an eye movement to the appropriate location. Note that the probability of making an eye movement to the target location was low (25%). If shifting of attention during visual search is mandatory accompanied by an active saccade program, then this should be evident in the facilitation of saccades to the target location even if the actual probability of executing the saccade program is low.

Method

Participants

Fourteen participants (7 females) from the Vrije Universiteit Amsterdam, with normal or corrected-to-normal vision, participated in the experiment. Their age varied between 19 and 25, with a mean age of 21.

Apparatus

The stimuli were presented on a 21-inch monitor running at 75 Hz with a 1024×768 pixels resolution. Eye movements were recorded with the head-mounted EyeLink-II system (SR research, Mississauga, Ontario, Canada) with 500 Hz temporal and 0.2° spatial resolution. An automatic algorithm detected saccades using minimum velocity and acceleration criteria of $35^\circ/s$ and $9,500^\circ/s^2$, respectively.

Stimuli, Design, and Procedure

Participants viewed a display with four figure 8 pre-masks ($1^\circ \times 1.5^\circ$, 58 cd^{-2}) positioned on a black background 5.7° from the fixation point and 8° from each other (see Figure 1). After a random interval of 800–1300 ms, line segments of the figure 8 pre-masks were removed, revealing the target (a number) along with distractor letters for 2000 ms. The target could be either number "1," "2," "3," or "4" and distractors could be letters "H," "P," "U," or "F." Participants had fixate in the center and covertly search for the target, which was verified by continuous eye movement monitoring. They remained fixated in the center until the target was found and depending on the target identity a single saccade had to be made to the location indicated by the target number. Target "1" indicated that saccade had to be made to the location on the top left, target "2" indicated that saccade had to be made to the location on the top right, target "3" indicated that saccade had to be made to the location on bottom right, and target "4" indicated that saccade had to be made to the location on bottom left. The factors of the target location and saccade end point were manipulated orthogonally. This means that the probability that the target and saccade locations coincided was 25%. Participants completed two practice and 10 experimental blocks (32 trials each).

Results and Discussion

Trials with saccades faster than 80 ms and slower than 1000 ms, saccades that did not start within 1° away from fixation point, and

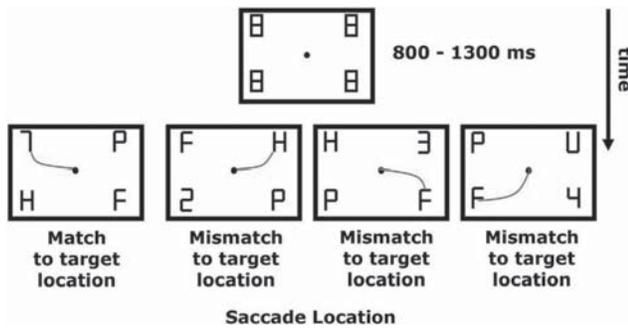


Figure 1. Experiment 1: Illustration of events occurring on a typical trial. Participants had to fixate the center and after a variable interval, characters were revealed by removing line segments from the figure 8 premasks. Participants had to covertly (without moving their eyes) search for a target number (“1,” “2,” “3,” or “4”) among letter distractors. Depending on the identity of the target participants had to make a saccade to one of the locations, “1” meant make a saccade to the top left location, “2” – saccade to the top right location, “3” – saccade to the bottom right location, “4” – saccade to the bottom left location (correct saccade is illustrated by a thin line). Note that in the ‘match’ condition the number identified by covert attention indicated that a saccade had to be made to the same location at which covert attention was allocated necessary to identify the digit. The ‘mismatch’ condition represents a situation in which the number identified by covert attention indicated that a saccade had to be made to another location.

with anticipatory saccades were discarded from further analyses. This resulted in an average loss of 11% of trials. One participant was replaced because of excessive anticipatory saccades (>10%).

Mean correct saccade RT data are presented in Figure 2 (left panel). One-way repeated-measures ANOVA with saccade location (match to target location, mismatch to target location) showed that saccades were initiated faster when the target location and saccade location matched, $F(1, 13) = 8.19, p < .05$.

On average participants made 16% of errors. Saccade was considered erroneous if it did not land within 45 degrees from the saccade target location. Participants made fewer errors when saccade and target locations matched than when they mismatched (12.4% vs. 19.8%, respectively, $F(1, 13) = 30.92, p < .001$), which is consistent with the SRT results.

The results of Experiment 1 clearly demonstrate that shifting covert attention in visual search was associated with saccade preparation even though there was no incentive to prepare a saccade to the target location and the probability of making an eye movement to the attended location was low. The pattern of results is similar to the previous findings using the cueing paradigm (Belopolsky & Theeuwes, 2009a), suggesting that shifts of attention during visual search and shifts of attention away from the invalidly cued locations are similar in their relation to the oculomotor system. In both cases covert attention was disengaged from one location and then shifted to the next location until the target was detected. Although on the majority of trials the shift of attention to the target location was not followed by an eye movement, the saccade program to the that location was facilitated. The obligatory activation of the oculomotor program during attention shifts while covertly searching a display is by and large consistent with both the premotor theory and our shifting and maintenance account.

Another way that attention can be shifted is by means of an exogenous cue, such as an abrupt onset (Posner, 1980; Yantis & Jonides, 1984). Such cues are able to capture attention, meaning that they cause an attention shift even when they are completely irrelevant to the task at hand (Theeuwes, 1991). Experiment 2 examined whether shifting of attention in this fashion is also accompanied by an active oculomotor program.

Experiment 2: Exogenous Cueing

Up to this point we have shown that if attention is endogenously shifted away from an invalidly cued location (as in Belopolsky & Theeuwes, 2009a) or is shifted during covert visual search, it is accompanied by preparation of saccade. In both of these situations shifting of attention is under control of the participant. However, attention can also be shifted exogenously, irrespectively of participant’s goals and intentions. To generalize the finding that attention shifts are always accompanied by saccade preparation it is important to demonstrate that this is also the case for the exogenous attention shifts. To examine this issue participants’ attention was manipulated by means of exogenous abrupt onset cue. The location of the cue coincided with the location of the target at a chance level, giving participant no incentive to attend to it. However, it is known that abrupt onset cues automatically activate the oculomotor system (Bisley & Goldberg, 2003; Theeuwes, Kramer, Hahn, & Irwin, 1998). If the exogenous shifting of attention is accompanied by saccade preparation we expected to find facilitation of saccades to a validly cued location despite its low probability of making an eye movement to the attended location. Based on the previous findings, facilitation of saccades was also expected for the invalidly cued trials, when attention had to be shifted away from the exogenous cue. Furthermore, to verify that the attention was captured by the exogenous cue we expected saccades to be initiated faster on validly cued trials than on invalidly cued trials.

Method

Participants

Ten participants (8 females) from the Vrije Universiteit Amsterdam, with normal or corrected-to-normal vision, participated in the experiment. Their age varied between 18 and 23, with a mean age of 20.

Stimuli, Design, and Procedure

The stimuli, design, and procedure used in Experiment 2 were similar to Experiment 1. However, in this experiment the trial started with participants viewing a display with three figure 8 premasks (see Figure 3). After 500 ms, line segments of the figure 8 premasks were removed, revealing the elements. Simultaneously with the offset of the segments a new element was added to the display. This new element that was presented with an abrupt onset could be the target (a number) at a chance level (Yantis & Jonides, 1984). As in Experiment 1, the target could be either number “1,” “2,” “3,” or “4” and distractors could be letters “H,” “P,” “U,” or “F.” The rest of the trial was identical to Experiment 1. The factors of the target location and saccade end point were manipulated orthogonally. This means that the probability that the

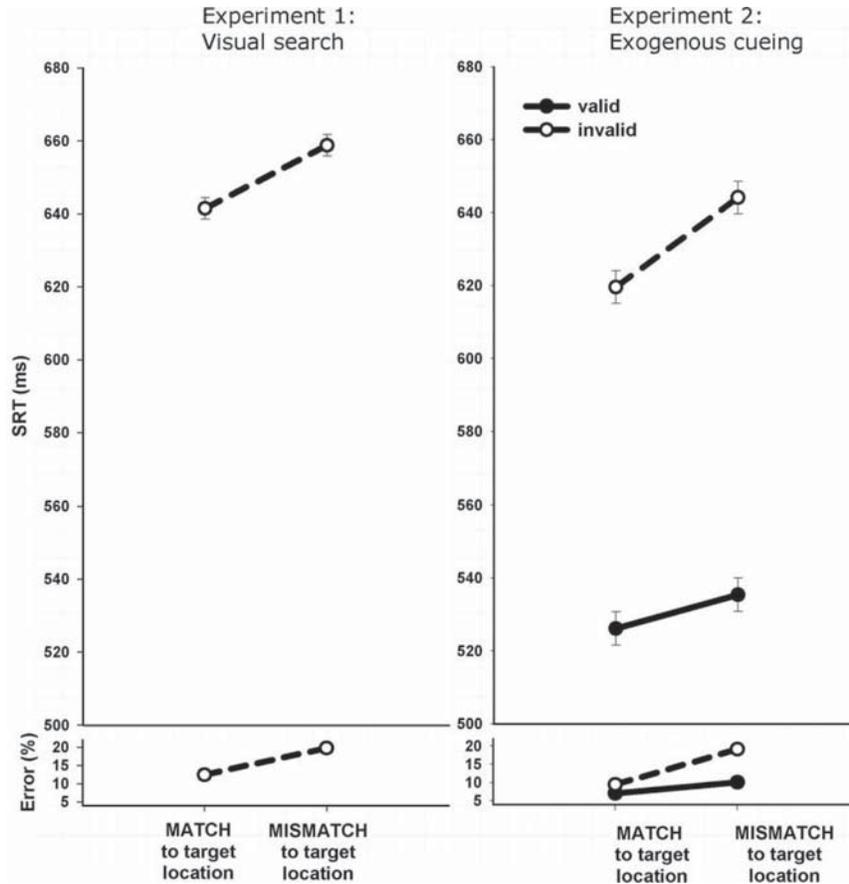


Figure 2. Left: Mean correct saccade reaction time (SRT) in Experiment 1 (visual search) as a function of saccade location. Right: Mean correct saccade reaction time (SRT) in Experiment 2 (exogenous cueing) as a function of saccade location and cueing validity. Error bars show ± 1 SEM normalized for within-subject design (Loftus & Masson, 1994).

target and saccade locations coincided was 25%. Participants completed one practice and six experimental blocks (64 trials each).

Results and Discussion

Trials with saccades faster than 80 ms and slower than 1000 ms, with saccades that did not start within 1° away from fixation point, and with anticipatory saccades were discarded from further analyses. This resulted in an average loss of 9% of trials.

Mean correct saccade RT data are presented in Figure 2 (right panel). Two-way repeated-measures ANOVA with cue validity (valid, invalid) and saccade location (match to target location, mismatch to target location) showed that participants were faster on the validly cued trials, $F(1, 9) = 106.92, p < .001$, suggesting that observers covertly allocated their attention to the exogenously cued location. Saccades were also initiated faster when the target location and saccade location matched, $F(1, 9) = 5.52, p < .05$. The interaction was not significant, $F(1, 9) = 1.91, p = .2$.¹

On average participants made 11% of errors. They made fewer errors in the validly cued than in the invalidly cued condition (8.5% vs. 14.2%, respectively, $F(1, 9) = 14.87, p < .005$). They made also fewer errors when saccade and target locations matched than when they mismatched (8.2% vs. 14.5%, respectively, $F(1, 9) = 13.65, p <$

.01). The interaction was also significant $F(1, 9) = 8.23, p < .05$, suggesting that the effect of the match between saccade and target locations was larger for the invalidly cued trials (9.4% vs. 19.1%) than for the validly cued trials (7% vs. 10%).

¹ On the invalid trials attention was first drawn to the location of the abrupt onset but then had to be disengaged and through visual search endogenously allocated to the target location. However, on some of the mismatch trials participants had to make an eye movement back to the location previously occupied by the abrupt onset. These saccades should have been especially slow because disengagement from the exogenous cue should have produced inhibition of return (Klein, 2000) and could have exaggerated the facilitation effect. However, the facilitation effect on the invalid trials was still significant, even when we took out the trials on which saccades went to the location previously occupied by a sudden onset, $t(9) = 2.37, p < .05$. Interestingly, there was a marginal IOR observed, meaning that on invalid trials, when saccades mismatched the target location, they were initiated slower to the previous onset location than to other non-onset locations (650 ms vs. 640 ms; $t(9) = 1.88, p = .09$). Because IOR is often taken as a hallmark of exogenous attention, this provides additional support that allocation of attention to the onset cue was in fact exogenous.

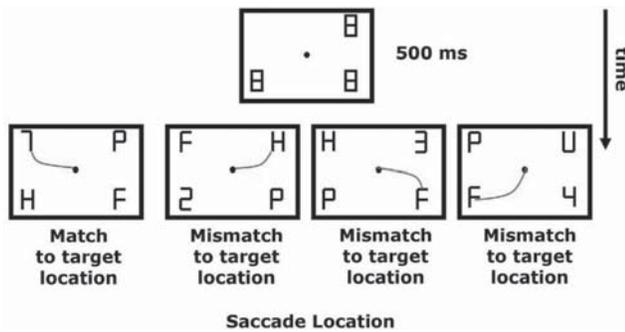


Figure 3. Experiment 2: Illustration of events occurring in a typical trial. Participants had to fixate in the center and after 500 ms, one new character appeared, while simultaneously the rest of the characters were revealed by removing line segments from the figure 8 premasks. Participants had to covertly (without moving their eyes) find the target (“1,” “2,” “3,” or “4”) among letter distractors. Depending on the identity of the target participants had to make a saccade to one of the locations (correct saccade is illustrated by a thin line). The target could be the new character presented with abrupt onset on a chance level.

The results of Experiment 2 clearly indicate that attention was captured by the abrupt onset cue, even though it was irrelevant to the task. Importantly, exogenous shift of attention to the cued location was associated with saccade preparation even though there was no incentive to prepare a saccade to the cued location and the probability of making an eye movement to it was low. This provides further support for shifting component of the premotor theory and is consistent with our shifting and maintenance account. In addition, saccades were facilitated on invalidly cued trials when attention was shifted away from the exogenous cue to find the target. This resembles the performance in the visual search task in Experiment 1, as well as performance on the invalidly cued trials in the previous study (Belopolsky & Theeuwes, 2009a). Interestingly, there was a trend for a greater saccade preparation on invalid cued trials than on validly cued trials, especially evident in accuracy measures. This suggests that after attention was pulled by the exogenous cue there was some build-up of suppression of the oculomotor program to that location. Perhaps, after attention shift suppression of the oculomotor program starts to get applied to a location that is physically marked (i.e., by the abrupt onset cue) as the location to which participants are unlikely to make a saccade. Such mark is absent on the invalidly cued trials, on which there is always more uncertainty about whether suppression should be applied to the currently attended location. In addition, on some validly cued trials (e.g., on trials preceded by trials on which saccades were made away from the attended location) suppression could also be applied faster, resulting in a mixture of facilitation and suppression. This issue is discussed in more detail in the General Discussion.

In Experiment 1 and 2 we have demonstrated that shifting attention involved in covert visual search and shifting attention in exogenous cueing is in both cases accompanied by facilitation of saccades to the attended location. The final way that shifts of attention are typically elicited is by an endogenous cue, in which participants volitionally shifts attention to a location indicated by a symbolic cue (usually an arrow). Such endogenous shifts of attention are often thought to be accomplished through different

mechanisms than exogenous shifts and have a different time-course (e.g., Müller & Rabbitt, 1989; Peelen, Heslenfeld, & Theeuwes, 2004). They are also often considered to be different from shifts of attention during visual search (Duncan et al., 1994; Theeuwes et al., 2004; Wolfe et al., 2000). However, if shifting of attention is always accompanied by an active saccade program, it should not matter in which fashion attention is shifted and saccade preparation should also be present for the endogenous attention shifts. Furthermore, by manipulating the time between the presentation of the endogenous cue and the target display it is possible to examine when attention shift turns into attention maintenance. This was explored in Experiment 3.

Experiment 3: Endogenous Cueing at Three SOAs

The first aim of Experiment 3 was to examine whether shifting attention endogenously also results in saccade preparation. Compared with the exogenous shifts, endogenous shifts of attention are typically slow and take at least 150 ms (Theeuwes, 1991). Therefore, we reasoned that at 200 ms after presentation of the cue attention would just arrive at the cued location and facilitation of saccade should be observed. After attention arrives to the endogenously cued location, it usually is maintained at that location for a period of time. The second goal was to examine at which point facilitation of saccade preparation associated with a shift of attention turns into suppression of saccade preparation associated with maintenance of attention. This was accomplished by manipulating the time between the onset of the endogenous cue and the onset of the target display (200, 500 and 1000 ms SOA). Our previous findings (Belopolsky & Theeuwes, 2009a) showed that attention maintenance is associated with suppression of saccade preparation when the probability of making a saccade to the attended location is low. Therefore, if the maintenance of attention is different from the shifting of attention (as proposed by our account) we expected facilitation of saccades at the shortest SOA, which turns into suppression at later SOAs. Alternatively, the premotor theory would predict that there will be saccade preparation at the attended location at all SOAs.

Method

Participants

Fourteen participants (9 females) from the Vrije Universiteit Amsterdam, with normal or corrected-to-normal vision, participated in the experiment. Their age varied between 19 and 24, with a mean age of 21.

Stimuli, Design, and Procedure

The stimuli, design, and procedure used in Experiment 3 were similar to the previous experiments. As in Experiment 1 the trial started with presentation of a display with four figure 8 premasks. After 500 ms a central arrow cue appeared at the fixation for another 100 ms and indicated the location where the target was going to appear with 100% validity (see Figure 4). The cue then disappeared and after either 100, 400 or 900, ms the line segments of the figure 8 premasks were removed, revealing the target number along with other distractor numbers for 2000 ms. As in the

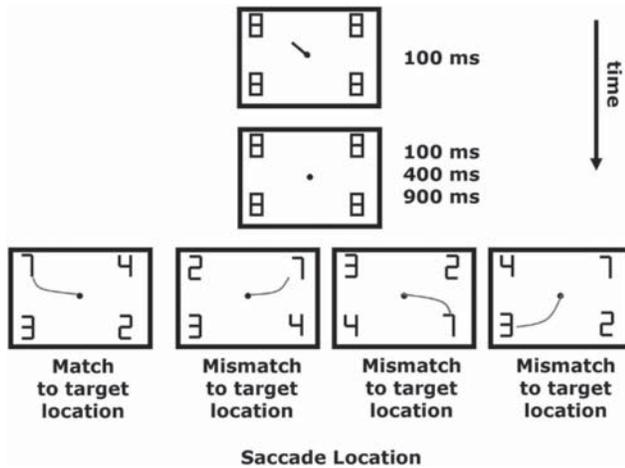


Figure 4. Experiment 3: Participants had to fixate in the center and shift attention to the location pointed to by the central pointer. The cue indicated the target location with 100% probability. After a variable delay the characters were revealed by removing line segments from the figure 8 pre masks. Because all the elements were numbers, participants had to attend to the cued location to know what the target was. Participants had to covertly (without moving their eyes) identify the target digit (“1,” “2,” “3,” or “4”) at the cued location. Depending on the identity of the target digit participants had to make a saccade to one of the locations (correct saccade is illustrated by a thin line).

previous experiments, the target could be either number “1,” “2,” “3,” or “4.” The distractors were also numbers, chosen randomly without replacement from the rest of the numbers. This manipulation ensured that participants had to attend to the cued location because the digit presented at the cued location instructed them to which location they had to execute a saccade. After processing the target digit at the cued location participants made a saccade to the appropriate location. The factors target location and saccade end point were manipulated orthogonally, and the probability that the target and saccade locations coincided was 25%. Participants completed two practice and six experimental blocks (48 trials each).

Results and Discussion

Trials with saccades faster than 80 ms and slower than 1000 ms, with saccades that did not start within 1° away from fixation point, and with anticipatory saccades were discarded from further analyses. This resulted in an average loss of 7% of trials. One participant was replaced because of excessive saccade direction errors (>30%).

Mean correct saccade RT data are presented in Figure 5 (left panel). Two-way repeated-measures ANOVA with SOA (200, 500, 1000 ms) and saccade location (match to target location, mismatch to target location) showed that saccades were initiated slower when the target location and saccade location matched, $F(1, 13) = 8.21, p < .05$. There was no significant effect of SOA or SOA by saccade location interaction (both $F < 1$).

On average participants made 18.8% of errors. There was no significant difference in error rate when saccade and target locations matched than when they mismatched (17.5% vs. 20.2%, respectively,

$F(1, 13) = 1.91, p = .19$). There was no significant effect of SOA or SOA by saccade location interaction (both $F < 1.3$).

The results of Experiment 3 clearly showed that saccade initiation toward the attended location was suppressed at all SOAs. If attention shift is always accompanied by saccade preparation then facilitation and not suppression of saccades should have been observed at the shortest SOA of 200 ms. This is surprising given that activation of saccadic program was observed when attention was shifted by means of visual search or exogenous cue in Experiment 1 and 2. However, one crucial difference is that in those experiments there was no delay between attention shift and presentation of the display, while in the present experiment there was a delay of 200 ms. The most obvious explanation is that suppression occurs very fast with endogenous cues and could be fully established within 200 ms. To test this idea in Experiment 4 we presented the endogenous cue simultaneously with the target display, minimizing the time to apply suppression. If attention shift by means of endogenous cue is accompanied by active saccade program than facilitation and not suppression should be observed.

Experiment 4: Endogenous Cueing at Zero SOA

This experiment was very similar to Experiment 3. The main difference was that the endogenous cue was presented at the same time as the target display, minimizing the time to apply suppression to the oculomotor program to the cued location.

Method

Participants

Ten participants (7 females) from the Vrije Universiteit Amsterdam, with normal or corrected-to-normal vision, participated in the experiment. Their age varied between 18 and 26, with a mean age of 21.

Stimuli, Design, and Procedure

The stimuli, design, and procedure used in Experiment 4 were very similar to Experiment 3, with the main difference that the cue appeared simultaneously with the number display. The trial started with presentation of a display with four figure 8 pre masks. After 800–1300 ms the line segments of the figure 8 pre masks were removed, revealing the target number along with other distractor numbers. Simultaneously with the number display a central arrow cue appeared at the fixation and indicated the location of the target number with 100% validity. As before, participants processed the target number at the cued location and had to make a saccade to the appropriate location. Participants completed one practice and seven experimental blocks (32 trials each).

Results and Discussion

Trials with saccades faster than 80 ms and slower than 1000 ms, with saccades that did not start within 1° away from fixation point, and with anticipatory saccades were discarded from further analyses. This resulted in an average loss of 5% of trials. One participant was replaced because of excessive saccade direction errors (>30%).

Mean correct saccade RT data are presented in Figure 5 (right panel). The effect of the match between the target and saccade

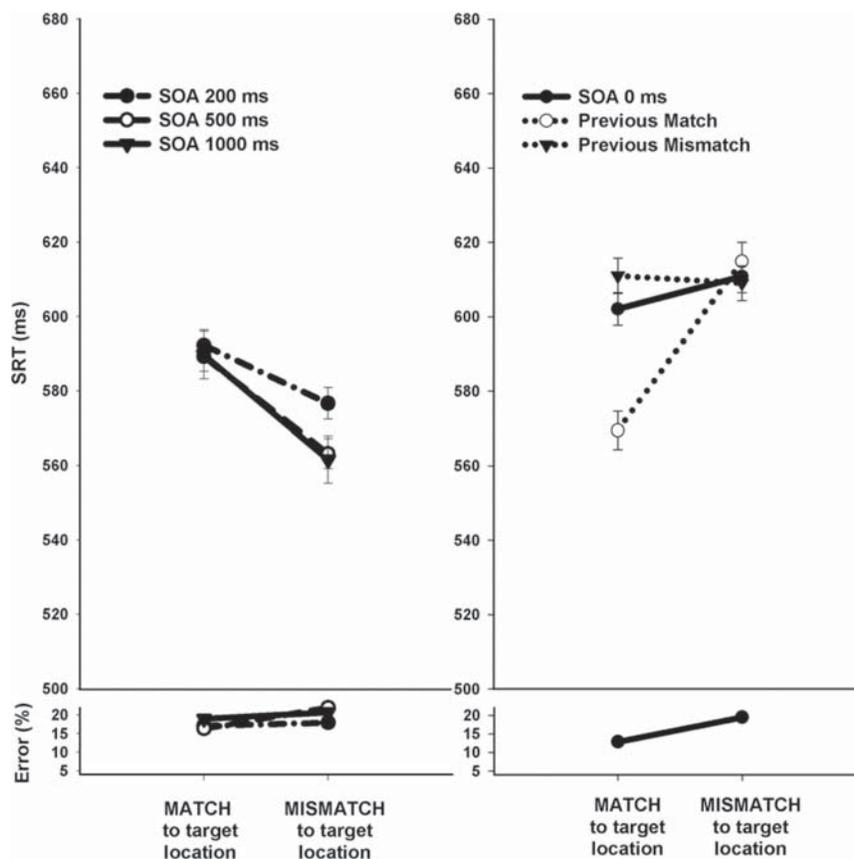


Figure 5. Left: Mean correct saccade reaction time (SRT) in Experiment 3 as a function of saccade location and SOA. Right: Mean correct saccade reaction time (SRT) in Experiment 4 as a function of saccade location. The data are also decomposed as a function of whether on the previous trial there was a match between the target location and the location of saccade target. Error bars show ± 1 SEM normalized for within-subject design (Loftus & Masson, 1994).

location was not significant, $F(1, 9) = 1.00, p = .34$. On average participants made 16.2% of errors. Participants made fewer errors when saccade and target locations matched than when they mismatched (12.9% vs. 19.5%, respectively, $F(1, 9) = 6.15, p < .05$).

There was a trend for saccade preparation when the endogenous cue was presented simultaneous with the target display, however it was only significant for the accuracy measures. It is important to investigate whether this trend represents a point at which activation of saccade program turns into suppression of saccade program. To accomplish this, three analyses were conducted. First, saccade preparation was compared across different SOAs between Experiment 3 and 4. If saccade preparation was different among zero SOA in Experiment 4 and longer SOAs in Experiment 3 this should be reflected in a significant interaction between saccade preparation and SOA. Second, we have conducted an intertrial analysis. Our previous findings showed that suppression of the oculomotor program occurs earlier when there is a mismatch between the target and saccade location on the previous trial. Third, to critically show that activation of saccade program was indeed present during endogenous shift of attention but that the program was quickly suppressed we have decomposed the distribution of saccade latencies in Experiment 4 into four quartiles. If endogenous attention shifts are associated with

facilitation of saccade program that can quickly turn into suppression than we expect to find facilitation in the earlier bins and suppression in the later bins.

Comparison of Experiment 3 and Experiment 4

In Experiment 3 endogenous cueing resulted in suppression of saccades to the cued location even for a short SOA of 200 ms. Experiment 4 showed a trend for facilitation of saccades to the cued location when the cue and the target were presented simultaneously. To compare the effects between the two experiments directly we conducted three two-way mixed-effects ANOVA with a between-subjects factor of SOA (0 vs. 200 ms, 0 vs. 500 ms or 0 vs. 1000 ms) and a within-subject saccade location factor (match to target location, mismatch to target location).

There was a significant interaction between the SOA and saccade location for both 500, $F(1, 22) = 8.31, p < .001$ and 1000 ms SOAs, $F(1, 22) = 4.45, p < .05$, and there was a marginal interaction for the 200 ms SOA, $F(1, 22) = 3.84, p = .06$. These results suggest that the dynamics of saccade preparation depends on the time elapsed between the shift of attention to the cued location and the initiation of an eye movement. Consistent with the

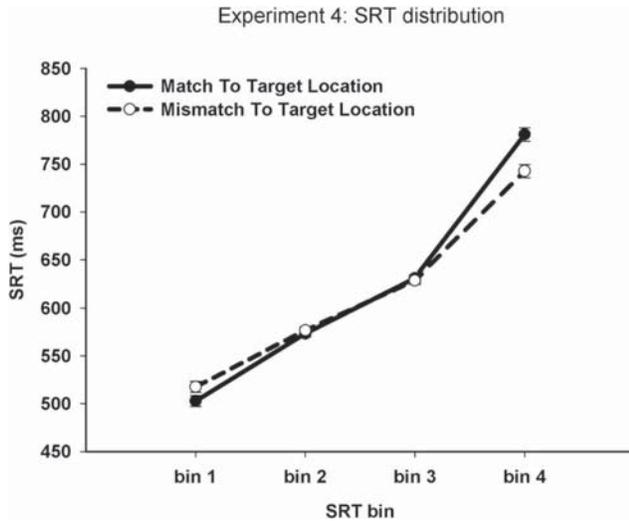


Figure 6. Mean correct saccade reaction time (SRT) in Experiment 4 as a function of saccade location and SRT bin. Only the trials that were preceded by a mismatch between the attended and saccade locations were included in the analysis. Error bars show ± 1 SEM normalized for within-subject design (Loftus & Masson, 1994).

shifting and maintenance hypothesis and the premotor theory, shifting of attention is accomplished by activation of an oculomotor program. However, very shortly after attention is shifted, facilitation starts to get replaced by suppression. Given that in our paradigm identification of the target takes several hundred milliseconds, it appears that suppression partially overlaps in time with target identification (Belopolsky & Theeuwes, 2009a, 2009b). Therefore, under the conditions of low probability of making an eye movement to the attended location, the switch from the shifting attention to maintenance of attention can occur very rapidly.

Our previous findings (Belopolsky & Theeuwes, 2009a) showed that the coupling of attention and eye movement on the previous trial is an important factor in determining the onset of suppression of saccade program. Specifically, suppression occurs earlier when participants repeatedly have to make eye movements away from the attended location. To investigate whether there was activation of the saccade program that was suppressed we have decomposed the data from Experiment 4 based on whether on the previous trial participants had to make an eye movement toward or away from the attended location.

Analysis of Coupling on the Previous Trial

To investigate whether the onset of suppression occurred early in Experiment 4, which used an endogenous cueing task at zero SOA, an intertrial analysis was conducted (see Figure 5, right panel). A two-way repeated measures ANOVA with previous saccade target location (match to the previous target location, mismatch to the previous target location) and current saccade target location (match to target location, mismatch to target location) was conducted. There was a marginal main effect of the match on the previous trial $F(1, 9) = 3.97, p = .08$ and a significant main effect of the match on the current trial $F(1, 13) = 7.81, p < .05$, suggesting that there was saccade preparation to the

attended location on the current trial. Importantly, there was a significant interaction between the match on previous and the match on the current trial $F(1, 9) = 14.96, p < .005$, demonstrating that facilitation of saccades on the current trial was much stronger when there was also match on the previous trial. As can clearly be seen from Figure 5 (right panel) the match between the target and saccade location on the previous trial resulted in strong saccade preparation on the current trial, (569 vs. 615 ms; $F(1, 9) = 19.32, p < .005$). However, when the target and saccade locations on the previous trial did not match, saccade preparation was not significant (611 vs. 609 ms; $F < 1$). The intertrial analysis indicates that suppression of saccade program to the attended location develops faster when on the previous trial saccade is made away from the to-be-attended location.

Distribution of Saccade RTs

To demonstrate that endogenous shifts of attention are associated with facilitation of saccade program followed by its suppression we have decomposed the distribution of saccade RTs in each condition and per each participant in Experiment 4 into four quartiles. Crucially, after this decomposition we excluded the trials that were preceded by a match between the attended and saccade locations (see Figure 6).

A two-way repeated measures ANOVA with saccade target location (match to target location, mismatch to target location) and SRT bin (1 to 4) was conducted. There was a significant interaction between bin and match to target location, $F(3, 27) = 12.08, p < .001$, demonstrating a pattern of facilitation of saccade programming in the first bin (15 ms; $t(9) = 1.27, p = .23$) and suppression in the last bin (38 ms; $t(9) = 2.78, p < .05$). This result provides direct support for the idea that the endogenous shift of attention was accomplished through saccade preparation, but the saccade program was quickly suppressed. This suggests that there is an obligatory coupling between endogenous attentional shifts and facilitation of saccade programs that is irrespective of context and probability. This facilitation, however, later turns into suppression.

Together, the results from the between-experiment analysis, the intertrial analyses, and the SRT distribution analysis suggest that consistent with the premotor theory endogenous shift of attention is associated with preparation of saccade to the attended location. However, saccade preparation is quickly replaced by saccade suppression, which is especially evident when saccades are repeatedly made away from the to-be-attended location.

General Discussion

According to the premotor theory (see also “the oculomotor readiness hypothesis” by Klein, 1980) covert attention is oriented by activation of the oculomotor program to the to-be-attended location. The predictions for testing this relationship were first formulated and tested by Klein (1980). He proposed that if covert attention is accomplished by eye movement preparation then (1) covertly attending to a location should facilitate the initiation of an eye movement to the attended location and (2) preparation of an eye movement to a location should result in facilitation of perceptual processing at that location. Klein used a dual-task and found no evidence for either of these predictions, which led him to conclude that endogenous covert orienting was accomplished in-

dependently of the oculomotor system (Klein, 1980; Klein & Pontefract, 1994).

The goal of the present study was to investigate the first prediction—whether allocation of covert spatial attention is always associated with preparation of saccade. Our results are consistent with the premotor theory as far as shifting of attention is concerned. Whenever covert attention had to be shifted to a location, it was always accompanied by activation of a saccade program to the attended location, despite a low probability of the actual execution of an eye movement. In general, this pattern of results was observed under a variety of conditions of attention shifting: when attention was shifted during covert serial visual search (Experiment 1), pulled exogenously to a location (Experiment 2, validly cued trials), shifted away from a location after an exogenous shift of attention (Experiment 2, invalidly cued trials), and shifted in response to an endogenous cue (Experiment 4). However, the present results are inconsistent with the premotor theory for the cases when spatial attention needs to be maintained at a location. When attention had to be maintained at a location for a longer period of time, suppression of the oculomotor program has been observed (Experiment 3), replicating our previous findings (Belopolsky & Theeuwes, 2009a, 2009b).

A similar suppression of overt orienting that coincides with the initial allocation of attention at that location has also been reported in several other studies (Belopolsky & Theeuwes, 2009a, 2009b; Godijn & Theeuwes, 2004). Suppression of saccades to the covertly attended location was evident in both saccade RTs, as well as in saccade accuracy was shown in Experiment 2 by Klein and Pontefract (1994). This was not surprising because in their study saccades were made to the attended location on only 14% of the trials. They interpreted this results as evidence for independence between covert attention and oculomotor preparation. The authors argued that “in shifting attention the subject engages in some degree of suppression of the natural tendency to foveate the cued location” (p. 345). This finding was rightfully taken as the evidence against the premotor theory, which proposes that whenever covert attention is allocated there is an accompanying activation of the oculomotor program to that location. However, it would be wrong to conclude that finding suppression constitutes evidence for the independence account because the relationship between the two systems was not neutral. In light of these findings, we propose that suppression of overt orienting is more in line with the idea of a close relationship between covert attention and saccade preparation, advocated by the premotor theory. The classic version of the premotor theory, however, needs to be updated to include the clause that overt orienting is suppressed during maintenance of spatial attention without an intention to make an eye movement.

Another important question of the present study was the time point at which shifting of attention turns into maintenance of attention. The present experiments allowed us to distinguish between these two processes in their relationship to the oculomotor system. Given that in all of the experiments the probability of making a saccade to the attended location was low, based on the previous findings (Belopolsky & Theeuwes, 2009a) we expected that maintenance of attention would be associated with suppression of the oculomotor program. Therefore, the change from facilitation to suppression of the oculomotor program served as a marker at which shifting of attention switches to attention main-

tenance. Experiment 4 showed that for endogenous cues this point occurs very fast: even when the attentional cue is presented simultaneously with the target display, a mixture of facilitation and suppression was observed. The time-course of early facilitation and later suppression of saccade program for endogenous attention shifts was clearly demonstrated by the SRT distribution analysis. It seems likely that the process of suppressing the saccade program can partially overlap in time with covert target processing.

Saccade preparation seemed to be somewhat weaker when the attended location was cued (exogenously or endogenously) compared with when attention was shifted from one location to another location without any external cues (i.e., in visual search). This suggests that suppression might operate faster when location can be marked in some external way, whether it is marked by an exogenous or endogenous cue. Perhaps, in all cases when the probability of execution of saccade is low, after the attention shift is completed the oculomotor program starts to get suppressed, whether covert attention needs to be maintained at the cued location as in the case of endogenous cues or when attention does not need to be maintained as in the case of exogenous cues. Suppression of the oculomotor program can directly be applied to the location, which could be marked as the location to which eye movement is unlikely to be made. During visual search or on the invalidly cued trials, there is more uncertainty about whether suppression should be applied to the currently attended location. Perhaps, implicit learning of the probability of making a saccade to the attended location occurs faster when the location is cued. Some evidence for this observation comes from the intertrial analysis. Intertrial effects are often considered to be automatic and not under voluntarily control (Maljkovic & Nakayama, 1996; Theeuwes & Van der Burg, 2011). Confirming our previous findings (Belopolsky & Theeuwes, 2009a) the association formed between attention and saccade program during the previous trial significantly affected saccade preparation on the current trial. If during the previous trial saccades were made to the attended location, there was greater saccade preparation to the attended location on the current trial (Experiment 4). However, preparation was on average absent when on the previous trial saccade was made away from the attended location.

Importantly, the second prediction about saccade preparation leading to a covert shift of attention (Klein, 1980; Klein & Pontefract, 1994) has been extensively examined in the literature, and a significant amount of evidence supporting this prediction has been accumulated (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995; Shepherd et al., 1986). For example, Deubel and Schneider (1996) have elegantly showed that right before the execution of an eye movement there is facilitation of perceptual processing that is confined to the location of saccade target. Furthermore, in follow-up experiments they showed that this facilitation was independent of the time available to the participant for preparing an eye movement (Deubel & Schneider, 2003). This means that saccades could not be preprogrammed and the same amount of attention is required whether participants had 1200 ms or 100 ms to prepare an eye movement (Chelazzi et al., 1995).

The main difference of these studies and studies of Klein and colleagues (1980, 1994) is that preparation of an eye movement was always followed by its execution, whereas in the latter studies the probability of execution was much lower. For example, in Klein and Pontefract (1994) the cue to prepare a saccade was followed by a

saccade in its direction only on 58% of trials and on 70% of trials in the study by Hunt and Kingstone (2003). The fact that prepared eye movement was not actually executed on such a large proportion of trials leaves a possibility that participants were either not sufficiently preparing a saccade or might have adopted a specific strategy to suppress the oculomotor program upon presentation of a covert attention probe (Chelazzi et al., 1995). Alternatively, one could argue that attention is only shifted to the saccade goal right before saccade is actually executed (Klein & Pontefract, 1994).

One study has clearly demonstrated that saccade preparation not only results in sustained activity in lateral intraparietal area (LIP), but that it is also correlated with enhanced perceptual sensitivity at the future saccade goal (Bisley & Goldberg, 2003). Furthermore, a study by Wauschkuhn and colleagues (Wauschkuhn, Wascher, & Verleger, 1997) provided interesting insights on dynamics of saccade preparation using ERPs. They presented participants with two cues, first of which (S1) instructed participants to prepare an eye movement, but withhold its execution until the presentation of the second cue (S2), which always occurred 700 ms later. It was demonstrated that instruction to prepare a saccade to a location elicited an early temporal-parietal lateralization in the event-related potential observed 200–450 ms after S1. This lateralization resembled the N2pc component, which is commonly associated with shifts of visual-spatial attention and reflects activity in the posterior parietal cortex (Woodman & Luck, 1999). Interestingly, no such lateralization was observed after the presentation of the S2, suggesting that because attention was already allocated at the saccade goal no additional shift of attention was required before the actual execution of an eye movement. This study clearly shows that saccade preparation results in a shift of spatial attention.

The Shifting and Maintenance Account

Consistent with the premotor theory, we claim that attention shift always obligatory precedes the planning of saccade (i.e., the first prediction of Klein, 1980). However, allocation of covert attention without an intention to make a saccade is not always associated with an active saccade program (i.e., the second prediction of Klein, 1980). Consistent with the premotor theory, attention shift is indeed achieved through activation of saccade program and is observed independently of the probability of executing the eye movement or whether attention and saccades were coupled on the previous trial. Therefore, the coupling between covert attention and the oculomotor preparation for attention shifts is obligatory. However, the fate of saccade program after attention is shifted depends on the probability of execution of that motor program. The oculomotor program often remains active (as in Experiment 1 in Belopolsky & Theeuwes, 2009a) and only when there is a strong bias against making an eye movement to the attended location can the suppression of the oculomotor program start to develop. It is simply not economical to maintain a saccade program that has only a small chance of being executed.

Furthermore, our results show that suppression of oculomotor program does not take much time and can be instantiated very quickly. The time point at which suppression emerges mainly depends on the prior history of making an eye movement away from the attended location: suppression emerges earlier if participants had been repeatedly making eye movements away from the attended location.

As discussed above, adding shifting and maintenance component to the premotor theory can explain the dissociation between covert attention and saccade preparation observed in behavioral studies (Hunt & Kingstone, 2003; Klein, 1980; Klein & Pontefract, 1994). In addition, it can also help explain why the dissociation is sometimes observed at the neural level (Ignashchenkova et al., 2004; Juan et al., 2004; Thompson et al., 2005). For example, in a study by Juan et al. (2004) monkeys were engaged in the antisaccade task while saccade preparation was probed by microstimulation in the FEF. The results showed that saccades that were evoked tended to deviate toward the saccade goal and not toward the attended location. Similarly, in a study by Thompson and colleagues (2005) during a covert feature search task, spatially selective activity was only present in the visually responsive neurons in FEF, while the motor responsive neurons were nonspatially suppressed (i.e., significant decrease was observed after the presentation of the search array, but there was no difference in whether a target or distractor was present in the receptive field). Furthermore, a similar dissociation between the visual, visuomotor, and motor responsive neurons and their relationship to the covert attention has been demonstrated in SC (Ignashchenkova et al., 2004). On the basis of these results it has been suggested that “spatial attention corresponds to the visual selection stage of saccade production . . . , but is not by itself a saccade plan” (Thompson et al., 2005, p. 9486). According to the shifting and maintenance account in the tasks described above saccade preparation could have been suppressed because the probability of actually executing a saccade plan was either null (Ignashchenkova et al., 2004; Thompson et al., 2005) or small (Juan et al., 2004). There remains a possibility that consistent with the premotor theory the whole network responsible for preparing and executing a saccade is active during attention shifts, but that some parts of the network can be dissociated (such as dissociation in modulation of visual, visuomotor and motor neurons) when maintenance of attention without saccade execution is required by the task. We propose that such dissociation is accomplished through suppression of saccade preparation.

Godijn & Theeuwes (2004; Theeuwes & Godijn, 2004) have proposed a theoretical framework for understanding inhibition of saccades that can be used to explain suppression of saccades during maintenance of attention. This framework was developed on the basis of comparison of the time-courses of two inhibitory phenomena: the saccade curvature away from a distractor location (Van der Stigchel, Meeter, & Theeuwes, 2006) and the inhibition of return (IOR)—slowed initiation of saccades to the previously attended locations (Klein, 2000). It was suggested that saccade curvature reflected inhibition within the saccade map located in the intermediate layers of SC, whereas IOR reflected inhibition applied to the preoculomotor attentional map in the lateral intraparietal area (LIP), located in the intraparietal sulcus (IPS). This conclusion was supported by the neurophysiological data of Dorris et al. (Dorris, Klein, Everling, & Munoz, 2002), who showed that there was no evidence for active inhibition of neural activity within the SC, but that it probably received reduced input from other areas, such as PPC. According to this framework, the inhibition of saccade initiation during maintenance of attention might originate from FEF and/or dorsolateral prefrontal cortex (dlPFC) and is applied to the preoculomotor attentional map located in PPC, which in turn reduces the input into saccade map in SC and leads to slowed initiation of saccades to the attended location.

In support of this view, some recent studies have shown a dissociation in posterior parietal cortex regarding the operations of shifting and maintenance of attention (Kelley, Serences, Giesbrecht, & Yantis, 2007; Yantis et al., 2002). Specifically, it was demonstrated that medial regions of FEF and SPL are involved in shifting of attention, while more lateral regions of FEF and IPS are associated with the maintenance of attention. Therefore, it is plausible that when the probability of executing a saccade to the location where attention is maintained is low, suppression is applied from FEF to IPS, which delays initiation of saccades to the attended location.

To summarize, the premotor theory can provide a convincing and elegant explanation for the origin of attention shifts. Our results are generally consistent with the premotor theory but suggest that it needs to be updated because allocation of attention is not always accompanied by saccade preparation. The premotor theory should include the shifting and maintenance component for cases when covert shifts of attention are made without the intention to execute a saccade. Here we have shown that any attentional shift, whether it occurs during visual search or by means of exogenous or endogenous cueing, is always associated with activation of saccade program. After attention is shifted, saccade program can be quickly suppressed while perceptual processing at that location is still enhanced. However, the point of suppression seems to depend on how attention is shifted. Specifically, suppression seems to emerge faster when location can be marked as an unlikely one for a saccade in some external way, such as by an exogenous or endogenous cue. Therefore, to go back to the example given in the introduction, when you want to attend to someone covertly your first shift of attention is equivalent to planning a saccade to their location. However, if you want to keep attending covertly without making eye contact, you need to soon thereafter suppress the eye movement to the location of that person.

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