Presaccadic perceptual facilitation effects depend on saccade execution: Evidence from the stop-signal paradigm

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Prior to the onset of a saccadic eye movement, perception is facilitated at the saccade target location. This has been attributed to a shift of attention. To test whether presaccadic attention shifts are strictly dependent on saccade execution, we examined whether they are found when observers are required to cancel the eye movement. We combined a dual task with the stop-signal paradigm: Subjects made saccades as quickly as possible to a cued location while discriminating a stimulus either at the saccade target or at the opposite location. A stop signal was presented on a subset of trials, asking subjects to cancel the eye movement. The delay of the stop signal was adjusted to vield successful inhibition of the saccade in 50% of trials. Results show similar perceptual facilitation at the saccade target for saccades with or without a stop signal, suggesting that presaccadic attention shifts are obligatory for all saccades. However, there was facilitation only when saccades were actually performed, not when observers successfully inhibited them. Thus, preparing an eye movement without subsequently executing it does not result in an attention shift. The results speak to a difference between saccade preparation and saccade programming. In light of the strong dependence on saccade execution, we discuss the functional role and causes of presaccadic attention shifts.

Introduction

Previous research has demonstrated tight links between visual attention and eye movements. For instance, spatial attention is imperatively shifted toward the saccade target just prior to a saccade (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Shepherd, Findlay, & Hockey, 1986). Observers had to prepare a saccade to one display element while simultaneously performing a perceptual-discrimination task at the saccade target location or at another location (see Figure 1 for an example). The typical finding is a spatial congruency effect: Discrimination is substantially better when the perceptual target is presented at the saccade target location compared to when the location of the saccade and the perceptual target do not coincide. Importantly, the spatial congruency effect is already found when the perceptual target is presented slightly before the saccade is launched, suggesting an obligatory presaccadic attention shift occurring at the saccade preparation stage (see Born, Ansorge, & Kerzel, 2012; Zhao, Gersch, Schnitzer, Dosher, & Kowler, 2012 for recent overviews). The idea that preparing a saccade shifts attention to the saccade goal fits well with neurophysiological results showing that stimulating saccade motor neurons in the superior colliculi or the frontal eye fields with a pulse train below the threshold of actually evoking an eye movement improves perception

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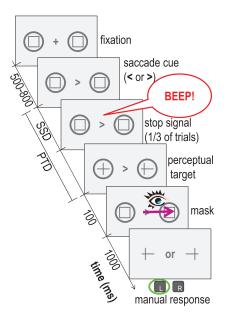


Figure 1. Sequence of events. Participants made a leftward or rightward saccade according to the central arrow cue. Before saccade initiation, a perceptual target was presented either in the circle targeted by the saccade or opposite (50% same location, as shown), and participants were asked to discriminate its asymmetry at the very end of the trial by key press. On one third of trials, an acoustic stop signal instructed participants to withhold their saccade. The SSD and perceptual target delay (PTD) were adjusted individually for each participant (see Methods).

at the corresponding location in the visual field (Cavanaugh, Alvarez, & Wurtz, 2006; Cavanaugh & Wurtz, 2004; Moore & Fallah, 2001, 2004).

However, the results stand in stark contrast to studies demonstrating that saccade preparation and shifts of attention are, to some extent, independent (Hunt & Kingstone, 2003; Klein & Pontefract, 1994). In these studies, participants made an eye movement to the left or right according to an auditory command spoken by a female voice. However, in a small subset of randomly interleaved trials, participants had to respond to a visual target on the left or right by key press while maintaining fixation. In each trial, an auditory cue spoken by a male voice was presented before the target events. The cue indicated the likely direction of the eye movement but did not predict the likely location of the visual target. As an eye movement was required in most trials, it was assumed that observers prepared a saccade to the cued location. The visual task probed whether attention was deployed to the cued location. Results showed faster saccade latencies for validly than invalidly cued trials, indicating that the cue indeed triggered saccade preparation. However, there was no influence of the cue on the visual task, suggesting that saccade preparation without execution does not automatically engage attention. In other words, saccade preparation and shifts of attention are independent because they may dissociate.

Together with the above-mentioned findings of obligatory presaccadic attention shifts when actually executing an eye movement, these results point to a potential difference between what one may call saccade *preparation* and saccade *programming*. While the *programming* of saccades, which is the last step before saccade execution, entails obligatory shifts of attention, saccade *preparation*, which does not necessarily result in a saccade, is relatively independent of attention (a possibility already acknowledged by Klein & Pontefract, 1994).

Even though appealing, differences between studies make it difficult to firmly establish this distinction between effects of preparation (without execution) and programming (with execution). The studies showing obligatory presaccadic attention shifts used a dual-task paradigm (saccade and concurrent perceptual task), visual cues, and short delays between cue and target (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995). In contrast, the preparation studies (Hunt & Kingstone, 2003; Klein & Pontefract, 1994) used auditory speech cues with a rather long cuetarget interval of 1000 ms and a setup more reminiscent of a task-switching paradigm, requiring saccadic or manual responses depending on the target. It is not clear what the exact reasons were, but the different procedures led to some noticeable disparities between studies. For instance, saccadic latencies in the preparation studies were much longer (between 300 and 600 ms) than in the *programming* studies (between 200 and 350 ms).

Further, in a related study in which participants switched between manual and saccadic responses (Rafal, Calabresi, Brennan, & Sciolto, 1989), an increase in manual reaction times at the location cued by a central arrow was observed when attention was subsequently summoned back to fixation, a phenomenon known as inhibition of return (IOR) (Posner & Cohen, 1984). As in the aforementioned preparation studies, the initial central arrow cue was validly indicating the target in the saccade task, thus eliciting saccade preparation, which was confirmed in saccadic reaction times. However, it was nonpredictive in the manual task but still influenced manual reaction times. Given that attention is thought to contribute to IOR (see Klein, 2000 for review), this result suggested attentional effects of saccade preparation even in the absence of saccade execution, contradicting the preparation studies. However, the result could not be replicated in a series of more recent experiments (Chica, Klein, Rafal, & Hopfinger, 2010). Instead, positive cuing effects in manual reaction times were observed in some conditions in which IOR was expected. One may thus wonder how the finding of reaction-time differences, their direction (positive or negative cuing effects), or their absence relates to attention and perceptual performance measures (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Hunt & Kingstone, 2003; Kowler et al., 1995). In this context, note that although attention is thought to play a role in IOR, there are other contributing components, for instance, motor preparation (see Klein, 2000).

In the current study, we reexamine the possibility of differential effects of saccade preparation (without execution) and saccade *programming* (with execution) on the allocation of attention. We used a dual-task paradigm (saccade and concurrent perceptual task) in which participants had to withhold their saccadic response occasionally upon presentation of an acoustic stop signal. In those stop-signal trials, two outcomes are possible: (a) Participants manage to inhibit the saccade, which is subsequently referred to as a NO saccade trial. NO saccade trials will show whether the initial preparation of a successfully cancelled saccade has an effect on the perceptual task. In other words, NO saccade trials show whether attention shifts occur following saccade preparation without execution. (b) The second possible outcome is that the stop signal arrives too late for the response to be inhibited and participants make a saccade despite the signal (referred to as STOP saccade trials). Comparing perceptual performance in those trials to the majority of trials without a stop signal (referred to as GO saccade trials) tells us whether trying to cancel a saccade, even if unsuccessful, diminishes the spatial congruency effect typically associated with presaccadic attention shifts. Further, we compared performance to a control block in which no stop signals were presented.

Importantly, our paradigm allows us to study saccade *preparation* and *programming* in the same task, using the same short cue-target interval and the same perceptual measure for assessing attention. To anticipate the results, we found a clear dissociation between preparation and programming: When saccades were successfully inhibited (NO saccade), no spatial congruency effects were found. When a saccade was erroneously made despite a stop signal (STOP saccade), a strong spatial congruency effect was found that did not differ in magnitude from the one found for correct saccades in trials without a stop signal (GO saccade) or from the one found in the control blocks. Thus, we could replicate the results from both lines of previous studies, confirming that merely preparing a saccade is not sufficient to elicit strong attentional and perceptual biases whereas the execution of saccades is imperatively preceded by attention shifts. We complement those previous studies by showing that even error saccades do elicit these shifts. While we were in the process of

running the current experiment, a similar study was presented at an international conference (Khan, Blohm, & Munoz, 2012).

Methods

Participants

Seventeen students (six men) from the University of Geneva aged between 17 and 27 years participated. All had normal or corrected-to-normal vision and gave informed consent. Data of four participants were excluded because discrimination performance never rose above chance level in any condition or their saccade cancellation rate in stop-signal trials was less than 10%, precluding any analysis of residual perceptual advantages at the designated saccade target. The experiments were carried out following the principles laid down in the Declaration of Helsinki.

Apparatus

Experiments were programmed in Matlab (The MathWorks, Inc., Natick, MA) using the Psychophysics and Eyelink Toolbox extensions (Cornelissen, Peters, & Palmer, 2002; Kleiner, Brainard, & Pelli, 2007). Eye movements were recorded at a sampling rate of 1000 Hz using the desktop-mounted EyeLink1000 (SR-Research, Ltd., Mississauga, ON, Canada). Participants were seated in a dimly lit room 67 cm from the screen, a 21-in. CRT (NEC MultiSync FE2111SB) running at 85 Hz with a resolution of 1280 × 1024 pixels. The participant's head was stabilized by a chin and a forehead rest.

Stimuli, design, and procedure

All stimuli were presented in dark gray (20 cd/m²) on a bright gray background (60 cd/m²). The sequence of events is illustrated in Figure 1. After a variable fixation period, a central arrow cue (< or >) instructed participants to saccade as fast as possible toward the indicated circle (horizontal eccentricity: 5° from central fixation, radius: 1.5°). Approximately 120 ms later, the perceptual target (asymmetric cross; bar length: 1.4°) and a symmetric distractor were shown in the circles. The exact perceptual target delay was adjusted to each participant's median saccade latency to have the perceptual target presented shortly before saccade onset but extinguished before the saccade landed: It was calculated by taking the median saccade latency from all preceding blocks of a participant and

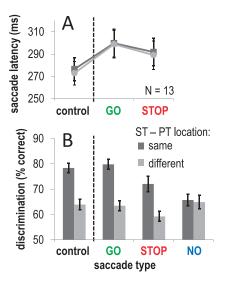


Figure 2. Saccade latency (A) and discrimination performance (B) as a function of spatial location of saccade target (ST) and perceptual target (PT, same vs. different) and saccade type. Control: saccades made in the control blocks without a stop signal; GO: saccades from the experimental blocks in trials without a stop signal; STOP: error saccades made despite a stop signal; NO: correctly cancelled saccades (i.e., participants kept fixation) when a stop signal was presented. Error bars: standard error of the mean.

subtracting 120 ms (one subject), 150 ms (three subjects), or 180 ms (13 subjects). The value was adjusted over the course of running the experiment to better target the presaccadic interval and did not affect the overall pattern of results. The locations of saccade and perceptual target were fully randomized (i.e., 50% same-location trials). After 100 ms, the crosses were masked by squares to avoid postsaccadic foveal vision of the perceptual target. An acoustic stop signal (750-Hz tone, 75-ms duration) was presented in one third of trials (randomly interleaved), requiring participants to cancel the saccade. The stop-signal delay (SSD, time from saccade cue onset) was adjusted individually using a staircase procedure (one-up, one-down rule, step size: 20 ms) to obtain 50% of correctly inhibited saccades and 50% saccades despite the signal. The display with the circles and masking squares remained on screen for 1000 ms before the manual response display was presented showing the two possible perceptual targets of a given trial. Participants judged the asymmetry of the perceptual target (Was the vertical bar slightly shifted to the left or right from the center?) by an unspeeded key press. The distance of the vertical bar from the center was adjusted by a staircase procedure targeting 71% correct responses across all trials according to a two-down, one-up rule, step size: 0.1°. Participants completed 11 blocks of 120 trials in the experimental condition. In addition, a control condition without a stop signal was run (three blocks: two

before and one after the experimental blocks). The first block in each condition was treated as practice and not analyzed.

Results

Excluded trials

Errors led to the exclusion of 7.6% of trials. Errors included anticipatory saccades (latency <80 ms: 0.1%), late saccades (latency >600 ms: 2.4%), breaks of fixation (saccade starting more than 1.5° away from fixation: 1.6%), saccades in the wrong direction (1.4%), participants accidentally hitting one other than the two designated response keys (1%), a combination of the above or technical issues (1.1%). Error analysis was done immediately after each trial, and participants received written feedback on screen in case of an error. Further, another 7.2% of trials were excluded due to saccades being launched before the perceptual target was replaced by the mask.

Stop-signal delay, perceptual target delay, saccade latencies

In stop-signal trials, participants made saccades despite the signal in 51.1% of trials (similar to the error trials described above, these were also followed by an error message). The average SSD across participants, which was individually controlled by staircase, was 106 ms (SE = 12.07). The average delay of the perceptual target was 121 ms in both the control (SE = 9.78) and the experimental conditions (SE = 11.21).

Saccade latencies are illustrated in Figure 2A. A repeated-measures ANOVA revealed a significant main effect of saccade type, F(2, 24) = 29.99, p < 0.001. Subsequent pairwise t tests confirmed that saccade latencies in the control condition (275 ms) were shorter than the latencies of the GO or STOP saccades in the experimental blocks (299 ms and 290 ms, respectively), ts(12) > 4.82, ps < 0.001. This result reflects the wellknown slowing of reaction times in the context of a stop-signal task (Verbruggen & Logan, 2009). The difference between GO saccades and STOP saccades was also significant, t(12) = 4.06, p = 0.002, which is in line with previous research and race-model assumptions postulating independent processes for initiating and inhibiting the saccadic response (Logan & Cowan, 1984). Surprisingly, the ANOVA also revealed a main effect of congruency, F(1, 12) = 16.75, p = 0.001, indicating longer latencies on congruent than incongruent trials (289 ms vs. 287 ms, respectively). Note that, despite being consistently present for a majority of 11 participants and therefore significant, the difference was only 2 ms on average with the largest individual difference being 6 ms. As the effect is so small, we will not interpret it any further. Finally, there was no significant interaction between saccade type and congruency, p = 0.437.

Discrimination performance

Discrimination performance is illustrated in Figure 2B. A perceptual advantage at the designated saccade target location (i.e., a spatial congruency effect) was present in all conditions in which a saccade was made (control blocks without stop signal, GO trials without stop signal, and STOP trials in which a saccade was made despite the signal). However, no spatial congruency effect was observed in stop-signal trials in which a saccade was successfully inhibited (NO saccade trials). A repeated-measures ANOVA on the arcsine-transformed percent-correct values revealed a significant main effect of saccade type, F(3, 36) = 6.35, p = 0.001, indicating better performance in control (71.1%) and GO (71.6%) trials than in STOP (65.6%) and NO (65.3%) saccade trials. The effect of spatial congruency was significant (74.0% same vs. 62.9% different location), F(1, 12) = 25.69, p < 0.001, and, importantly, modulated by saccade type, F(3, 36) = 9.51, p < 0.001. Subsequent t tests confirmed that the spatial-congruency effect was significantly different from zero in the control block (14.5%), t(12) = 4.25, p = 0.001; for GO saccades (16.3%), t(12) = 4.84, p < 0.001; and for STOP saccades (12.8%), t(12) = 4.03, p = 0.002, but not for NO saccade trials (0.8%), t(12) = 0.49, p = 0.635. To test whether effects were equivalent across saccade types, we compared congruency effects with pairwise t tests. All saccade types showed significantly larger congruency effects than the NO saccade trials, ts(12) > 3.74, ps < 0.003. However, there were no significant differences between saccade types (control, GO, STOP), ps > 0.303.

Discrimination performance with respect to time to saccade onset

Typically, spatial-congruency effects grow stronger the shorter in time the perceptual target is presented before saccade onset, reflecting the progressive allocation of attention toward the saccade target location (e.g., Deubel, 2008; Doré-Mazars, Pouget, & Beauvillain, 2004; Harrison, Mattingley, & Remington, 2013; Jonikaitis & Deubel, 2011; Rolfs & Carrasco, 2012). Accordingly, we performed a median split of the data individually for each participant based on how long before the saccade the perceptual target was

presented in each trial (lead time = time from perceptual target offset/mask onset to saccade onset). As before, we excluded all trials in which the perceptual target was still visible during or after the saccade. The average median for the split was 65 ms (SE = 4.39) before saccade onset, resulting in mean lead times of 40 ms (SE = 2.97) and 123 ms (SE = 8.37) for the two bins. Figure 3A shows that the difference between the same and different location trials was greater with short lead times (median > lead time, plotted on the right of each graph in Figure 3A) than with long lead times (median < lead time, plotted on the left of each graph in Figure 3A). A repeated-measures ANOVA on the arcsinetransformed percent-correct values revealed a significant interaction between lead time and spatial congruency, F(1, 12) = 10.44, p = 0.007, confirming that the congruency effect was larger with shorter lead times. The main effects of lead time (67.5% long vs. 70.9% short), F(1, 12) = 9.85, p = 0.009, and spatial congruency (76.2% same vs. 62.3% different), F(1, 12) =26.32, p < 0.001, were likewise significant. Further, there was a significant main effect of saccade type, F(2, 24) = 5.79, p = 0.009, indicating that overall discrimination performance was lower in STOP saccade trials (65.5%) compared to the control condition (70.6%) or GO trials (71.7%). However, there was no significant interaction between saccade type and congruency, p = 0.289, and no three-way interaction saccade type \times lead time \times congruency, p = 0.964. Thus, the spatial-congruency effect and its time course were comparable for the three saccade types. The interaction between saccade type and lead time likewise did not reach significance, p = 0.467.

Discrimination performance with respect to stop-signal delay

Next, to examine the relationship between the spatial-congruency effects and the state of the saccadecancellation process, we performed a median split of the stop-signal trials based on each participant's individually adjusted SSDs. Although our staircase procedure was meant to keep the SSDs for each participant close to a value yielding 50% saccades despite the stop signal, the one up—one down rule made the trial-by-trial SSDs vary around that value sufficiently to perform such a split (see difference in the average SSD for the two bins reported below). According to race model assumptions, the earlier the stop signal is presented, the more time there is available to cancel the saccade before the perceptual target is presented. Thus, even though we did not find any decrease in spatial-congruency effects for STOP saccades compared to GO and control saccades, we might still find reduced congruency effects in STOP saccade

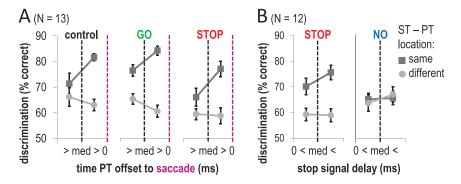


Figure 3. Time course analysis of discrimination performance as a function of spatial location of ST and PT (same vs. different). (A) Median (med) split based on the time from PT offset (mask onset) to saccade initiation (lead time). Zero on the x-axis denotes saccade onset (i.e., long lead times are depicted to the left, short lead times to the right in each graph). (B) Median (med) split based on SSD. Zero on the x-axis denotes saccade cue onset (i.e., short delays to the left, long delays to the right). Error bars: standard error of the mean.

trials with short SSDs (which allow for advanced saccade cancellation at the onset of the perceptual target) compared with long SSDs (which provide little time to cancel the saccade before the onset of the perceptual target). Similarly, for NO saccade trials, small congruency effects might emerge when only looking at the trials with long SSDs. One more participant had to be excluded for this analysis as the staircase procedure for the SSD converged to 0 ms with almost no variability; hence, a median split was not possible. Figure 3B illustrates the results for the remaining 12 participants. The average median for the split was a SSD of 111 ms (SE = 12.01), resulting in average delays of 79 ms (SE = 10.64) and 147 ms (SE =9.78) for the two SSD bins. A repeated-measures ANOVA on the arcsine-transformed percent-correct values revealed a significant main effect of spatial congruency (69.2% same vs. 62.3% different location), F(1, 11) = 14.11, p = 0.003, that was modulated by saccade type, F(1, 11) = 16.73, p = 0.002, confirming differences in congruency effects between STOP and NO saccade trials. There was a trend for a three-way interaction of saccade type, SSD bin, and spatial congruency, F(1, 11) = 3.43, p = 0.091. No further effect or interaction approached significance, Fs < 1.62, ps >0.229. Separate ANOVAs for STOP and NO saccade trials confirmed a significant main effect of spatial congruency for STOP saccade trials (72.8% same vs. 59.0% different location), F(1, 11) = 22.79, p = 0.001. Although Figure 3B suggests that the congruency effect for STOP saccades was indeed slightly larger with longer SSDs, the interaction SSD bin \times spatial congruency did not reach significance, p = 0.150. Likewise, there was no significant main effect of SSD bin, p = 0.353. The repeated-measures ANOVA for the NO saccade trials did not reveal any significant effects or interactions (SSD bin: p = 0.386, spatial congruency: p = 0.982, SSD bin × spatial congruency: p = 0.389).

Discussion

We examined the dependence of presaccadic attention shifts on the execution of eye movement. It had previously been suggested that presaccadic attention shifts might occur only when the saccade is subsequently executed but not when the saccade was prepared but then cancelled (Klein & Pontefract, 1994). However, evidence for presaccadic attention shifts and the lack of those effects without actual saccade execution came from studies using very different experimental setups and different measures for attentional deployment. Using the stop-signal paradigm allowed us to study both saccade preparation (without execution) and *programming* (with execution) in the same task and using the same attentional marker: a spatial-congruency effect in a concurrent perceptualdiscrimination task (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995). Our results show that presaccadic attention shifts produce substantial perceptual facilitation at the saccade target location even for saccades that were meant to be inhibited (STOP saccades). Further, the congruency effect was equivalent for erroneous saccades in stopsignal trials (STOP saccades), correct saccades in GO trials, and control saccades in experimental blocks in which we never presented any stop signal. In sum, whenever a saccade was made, a strong spatialcongruency effect was found, no matter in which trial context the saccade had been executed or whether the saccade was meant to be cancelled. Further, spatialcongruency effects grew stronger the closer the perceptual target was presented before saccade onset (see also Deubel, 2008; Doré-Mazars et al., 2004; Harrison et al., 2013; Jonikaitis & Deubel, 2011; Rolfs & Carrasco, 2012), and this time course was similar for the three types of saccades. However, spatial-congruency effects did not vary substantially with SSD. Thus, presaccadic attention shifts were tightly linked to the actual point in time the saccade was executed but largely independent of the progress of the saccade-cancellation process.

In contrast, there was no perceptual advantage at the designated saccade target location (i.e., no spatial-congruency effect) when the saccade was successfully cancelled. Thus, in line with previous work, we found no evidence for attention shifts induced by saccade *preparation* without execution (Hunt & Kingstone, 2003; Klein & Pontefract, 1994). This was even true for trials with long SSDs (i.e., long delays between the saccade cue and the stop signal) for which the saccade preparation process should have been slightly more advanced at the time the saccade was cancelled.

One may wonder whether there was any saccade preparation at all in NO saccade trials. In this context, recall that stop signals were presented only in a minority of one third of randomly interleaved trials and that our staircase procedure was successful in keeping the percentage of saccades, despite the signal, around 50%. In race-model terms, these settings should (despite some variability on a trial-by-trial basis) result in tight races between the execution and the cancellation process, each equally likely to win (e.g., Logan, Schachar, & Tannock, 1997). Thus, even in saccade trials with a stop signal, the cancellation process should have advanced substantially. Similarly, there should have been some saccade preparation in successfully cancelled trials. Note that although the magnitude of the congruency effect remained unaffected, the overall discrimination performance was slightly lower in STOP and NO saccade trials compared to the other saccade-type conditions. This result may reflect the ongoing cancellation efforts. Note further that another prediction of the race model is met in our experiment: Average saccade latencies were faster in STOP saccade trials compared to GO saccade trials, reflecting that in stop-signal trials, the GO process can only win the race when it progresses quickly (Logan & Cowan, 1984). Thus, we think the race model is an adequate approximation of the processes involved in our experiment, and we are confident that some saccade preparation has occurred even in cancelled trials.

If saccade preparation has occurred but did not result in an attention shift, how else might performance be affected? One possibility is that saccade preparation reflects a state of motor readiness or response preparation, affecting reaction times or response choices. Note, for instance, that the studies by Klein and Pontefract (1994) and Hunt and Kingstone (2003), despite a null effect on manual responses, did find effects of their speech cue in saccade reaction times. Whether this motor readiness is specific to saccades or a more general phenomenon (as, for instance, in the

reaction-time differences reported by Chica et al., 2010; Rafal et al., 1989) remains to be clarified. However, our experiment confirms that it does not seem to entail any perceptual enhancement at the likely saccade location (Hunt & Kingstone, 2003).

We conclude that presaccadic perceptual facilitation effects do occur at a saccade-preparation stage at which the decision that an eye movement will be launched has already been made, a stage one may call saccade programming. It has been suggested that presaccadic perceptual facilitation plays a role in setting the spatial coordinates or selecting a specific target object for the desired eye movement (Kowler et al., 1995). Their tight link to actual saccade execution and the current finding of their robustness against ongoing cancellation processes might also speak for the involvement of presaccadic facilitation in processes for maintaining visual stability across eye movements. Although already debated for centuries, the question of how we perceive the visual world as stable despite large retinal image shifts caused by each eye movement has recently seen a considerable increase in research interest in neuroscience and psychology (see e.g., Bays & Husain, 2007; Cavanagh, Hunt, Afraz, & Rolfs, 2010; Melcher, 2011 for overviews). It has been argued that, to be related to visual stability, an effect must meet two preconditions: On the one hand, it should only be seen when an eye movement is actually executed as spatial updating is only necessary when the eye movement actually shifts the image on the retina (Colby, 1996; Sommer & Wurtz, 2008). On the other hand, the effect should be uniformly seen for every eye movement, irrespective of trial context or cancellation attempts as, in the end, all eye movements will cause retinal image shifts that need to be compensated. The current study confirms both preconditions for presaccadic attention shifts toward the saccade target. Going one step further, several authors have proposed that the role of presaccadic attention shifts in visual stability is to provide a preview template of the saccade target. This template may then be compared to the postsaccadic visual input (Currie, McConkie, Carlson-Radvansky, & Irwin, 2000; Deubel, Schneider, & Bridgeman, 1996; McConkie & Currie, 1996; see Mathôt & Theeuwes, 2011 for review). Further, the behavioral-congruency effects may be related to systematic presaccadic receptive field shifts toward the saccade endpoint observed in some cortical areas (V4, FEF; Tolias et al., 2001; Zirnsak, Lappe, & Hamker, 2010; Zirnsak, Xu, Noudoost, & Moore, 2011). However, if and how exactly presaccadic attention shifts are involved in visual stability remains speculative.

Given the tight link to actual saccade execution, one may wonder whether presaccadic attention shifts are distinct from covert attentional allocation without saccades. Blangero et al. (2010) tested a patient with right posterior parietal damage in a variant of the dualtask paradigm. They report presaccadic facilitation when a centrally presented arrow cue validly indicated the location of the perceptual target but no attentional facilitation for the same cue when the patient had to keep fixation. Interestingly, performance in the control group was also significantly better in the saccade than in the covert-attention condition. The authors argue for a saccade-specific or action-specific attentional mechanism that can be dissociated from covert attention. In line with this proposition, other recent studies have shown that some mechanisms guiding attention, for instance, based on color or known location, can act independently of the presaccadic perceptual facilitation effects (Born et al., 2012; Born, Ansorge, & Kerzel, 2013; Gersch, Kowler, Schnitzer, & Dosher, 2008, 2009; Jonikaitis & Theeuwes, 2013; Montagnini & Castet, 2007). However, repeated motion congruency (White, Rolfs, & Carrasco, 2013), irregular letter configurations at the beginning of words (Doré-Mazars et al., 2004), and salient onsets (Deubel, 2008) were found to attract attention only early in the saccade latency period. They were no longer effective close in time to the saccade when attentional facilitation was confined to the saccade target. These results suggest that presaccadic attention is not completely independent of other attentional resources. The three mentioned findings may suggest interactions with exogenous attention (onsets, salient irregularities) or dorsal stream processes (motion congruency). This idea also fits well with reports that, on the flip side of the coin, exogenous orienting is impaired when eye movements cannot be executed (Smith, Rorden, & Jackson, 2004; Smith, Schenk, & Rorden, 2012), but future research is necessary to further pinpoint the exact overlaps.

Keywords: eye movements, presaccadic attention, stop-signal paradigm

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References

- Bays, P. M., & Husain, M. (2007). Spatial remapping of the visual world across saccades. *Neuroreport*, *18*(12), 1207–1213, doi:10.1097/WNR. 0b013e328244e6c3.
- Blangero, A., Khan, A. Z., Salemme, R., Deubel, H., Schneider, W. X., Rode, G., & Pisella, L. (2010). Pre-saccadic perceptual facilitation can occur without covert orienting of attention. *Cortex*, 46(9), 1132–1137, doi:10.1016/j.cortex.2009.06.014.
- Born, S., Ansorge, U., & Kerzel, D. (2012). Feature-based effects in the coupling between attention and saccades. *Journal of Vision*, *12*(11):27, 1–17, http://www.journalofvision.org/content/12/11/27, doi:10. 1167/12.11.27. [PubMed] [Article]
- Born, S., Ansorge, U., & Kerzel, D. (2013). Predictability of spatial and non-spatial target properties improves perception in the pre-saccadic interval. *Vision Research*, *91*, 93–101, doi:10.1016/j.visres. 2013.08.003.
- Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in Cognitive Sciences*, 14(4), 147–153, doi:10.1016/j.tics.2010.01.007.
- Cavanaugh, J., Alvarez, B. D., & Wurtz, R. H. (2006). Enhanced performance with brain stimulation: Attentional shift or visual cue? *Journal of Neuroscience*, *26*(44), 11347–11358, doi:10.1523/JNEUROSCI.2376-06.2006.
- Cavanaugh, J., & Wurtz, R. H. (2004). Subcortical modulation of attention counters change blindness. *Journal of Neuroscience*, *24*(50), 11236–11243, doi: 10.1523/JNEUROSCI.3724-04.2004.
- Chica, A. B., Klein, R. M., Rafal, R. D., & Hopfinger, J. B. (2010). Endogenous saccade preparation does not produce inhibition of return: Failure to replicate Rafal, Calabresi, Brennan, & Sciolto (1989). *Journal of Experimental Psychology: Human Perception and Performance*, 36(5), 1193–1206, doi: 10.1037/a0019951.
- Colby, C. L. (1996). A neurophysiological distinction between attention and intention. In T. Inui & J. L. McClelland (Eds.), *Attention and performance XVI: Information integration in perception and communication* (pp. 157–176). Cambridge, MA: MIT Press.
- Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments and Computers*, *34*(4), 613–617, doi:10.3758/BF03195489.
- Currie, C. B., McConkie, G. W., Carlson-Radvansky,

- L. A., & Irwin, D. E. (2000). The role of the saccade target object in the perception of a visually stable world. *Perception and Psychophysics*, 62(4), 673–683, doi:10.3758/BF03206914.
- Deubel, H. (2008). The time course of presaccadic attention shifts. *Psychological Research*, 72(6), 630–640, doi:10.1007/s00426-008-0165-3.
- Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827–1837, doi:10.1016/0042-6989(95)00294-4.
- Deubel, H., Schneider, W. X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Research*, *36*(7), 985–996, doi:10.1016/0042-6989(95)00203-0.
- Doré-Mazars, K., Pouget, P., & Beauvillain, C. (2004). Attentional selection during preparation of eye movements. *Psychological Research*, 69(1–2), 67–76, doi:10.1007/s00426-003-0166-1.
- Gersch, T. M., Kowler, E., Schnitzer, B. S., & Dosher, B. A. (2008). Visual memory during pauses between successive saccades. *Journal of Vision*, 8(16):15, 1–18, http://www.journalofvision.org/content/8/16/15, doi:10.1167/8.16.15.
- Gersch, T. M., Kowler, E., Schnitzer, B. S., & Dosher, B. A. (2009). Attention during sequences of saccades along marked and memorized paths. *Vision Research*, *49*(10), 1256–1266, doi:10.1016/j. visres.2007.10.030.
- Harrison, W. J., Mattingley, J. B., & Remington, R.W. (2013). Eye movement targets are released from visual crowding. *Journal of Neuroscience*, *33*(7), 2927–2933, doi:10.1523/JNEUROSCI.4172-12. 2013.
- Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception and Psychophysics*, *57*(6), 787–795, doi:10. 3758/BF03206794.
- Hunt, A. R., & Kingstone, A. (2003). Covert and overt voluntary attention: Linked or independent? *Cognitive Brain Research*, *18*(1), 102–105, doi:10.1016/j. cogbrainres.2003.08.006.
- Jonikaitis, D., & Deubel, H. (2011). Independent allocation of attention to eye and hand targets in coordinated eye-hand movements. *Psychological Science*, 22(3), 339–347, doi:10.1177/0956797610397666.
- Jonikaitis, D., & Theeuwes, J. (2013). Dissociating oculomotor contributions to spatial and feature-based selection. *Journal of Neurophysiology*, *110*(7), 1525–1534, doi:10.1152/jn.00275.2013.

- Khan, A., Blohm, G., & Munoz, D. (2012). Successful countermanding affects presaccadic attention at the saccade goal. *Journal of Vision*, 12(9): 393, http://www.journalofvision.org/content/12/9/393, doi: 10.1167/12.9.393. [Abstract]
- Klein, R. M. (2000). Inhibition of return. *Trends in Cognitive Sciences*, *4*(4), 138–147, doi:10.1016/S1364-6613(00)01452-2.
- Klein, R. M., & Pontefract, A. (1994). Does oculomotor readiness mediate cognitive control of visual attention? Revisited! In C. Umilta & M. Moscovitch (Eds.), *Attention & performance XV: Conscious and unconscious processing* (pp. 333–350). Cambridge, MA: MIT Press.
- Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychtoolbox-3? Perception, 36, ECVP Abstract Supplement.
- Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, *35*(13), 1897–1916, doi: 10.1016/0042-6989(94)00279-U.
- Logan, G. D., & Cowan, W. B. (1984). On the ability to inhibit thought and action: A theory of an act of control. *Psychological Review*, *91*(3), 295–327, doi: 10.1037/0033-295X.91.3.295.
- Logan, G. D., Schachar, R. J., & Tannock, R. (1997). Impulsivity and inhibitory control. *Psychological Science*, 8(1), 60–64, doi:10.1111/j.1467-9280.1997. tb00545.x.
- Mathôt, S., & Theeuwes, J. (2011). Visual attention and stability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1564), 516–527, doi:10.1098/rstb.2010.0187.
- McConkie, G. W., & Currie, C. B. (1996). Visual stability across saccades while viewing complex pictures. *Journal of Experimental Psychology: Human Perception and Performance*, 22(3), 563–581, doi:10.1037/0096-1523.22.3.563.
- Melcher, D. (2011). Visual stability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1564), 468–475, doi:10.1098/rstb. 2010.0277.
- Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *Journal of Vision*, 7(14):8, 1–16, http://www.journalofvision.org/content/7/14/8, doi:10.1167/7.14.8. [PubMed] [Article]
- Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. *Proceedings of the National Academy of Sciences*, USA, 98(3), 1273–1276, doi:10.1073/pnas.021549498.

- Moore, T., & Fallah, M. (2004). Microstimulation of the frontal eye field and its effects on covert spatial attention. *Journal of Neurophysiology*, *91*(1), 152–162, doi:10.1152/jn.00741.2002.
- Posner, M. I., & Cohen, Y. (1984). Components of visual orienting. In H. Bouma & D. G. Bouwhuis (Eds.), *Attention and performance X* (pp. 531–556). Hillsdale, NJ: Erlbaum.
- Rafal, R. D., Calabresi, P. A., Brennan, C. W., & Sciolto, T. K. (1989). Saccade preparation inhibits reorienting to recently attended locations. *Journal of Experimental Psychology: Human Perception and Performance*, *15*(4), 673–685, doi:10.1037/0096-1523.15.4.673.
- Rolfs, M., & Carrasco, M. (2012). Rapid simultaneous enhancement of visual sensitivity and perceived contrast during saccade preparation. *Journal of Neuroscience*, *32*(40), 13744–13752a, doi:10.1523/JNEUROSCI.2676-12.2012.
- Shepherd, M., Findlay, J. M., & Hockey, R. J. (1986). The relationship between eye movements and spatial attention. *The Quarterly Journal of Experimental Psychology Section A*, 38(3), 475–491, doi: 10.1080/14640748608401609.
- Smith, D. T., Rorden, C., & Jackson, S. R. (2004). Exogenous orienting of attention depends upon the ability to execute eye movements. *Current Biology*, 14(9), 792–795, doi:10.1016/j.cub.2004.04.035.
- Smith, D. T., Schenk, T., & Rorden, C. (2012). Saccade preparation is required for exogenous attention but not endogenous attention or IOR. *Journal of Experimental Psychology: Human Perception and Performance*, 38(6), 1438–1447, doi:10.1037/a0027794.
- Sommer, M. A., & Wurtz, R. H. (2008). Brain circuits

- for the internal monitoring of movements. *Annual Review of Neuroscience*, *31*, 317–338, doi:10.1146/annurev.neuro.31.060407.125627.
- Tolias, A. S., Moore, T., Smirnakis, S. M., Tehovnik, E. J., Siapas, A. G., & Schiller, P. H. (2001). Eye movements modulate visual receptive fields of V4 neurons. *Neuron*, *29*(3), 757–767, doi:10.1016/S0896-6273(01)00250-1.
- Verbruggen, F., & Logan, G. D. (2009). Proactive adjustments of response strategies in the stop-signal paradigm. *Journal of Experimental Psychology: Human Perception and Performance*, *35*(3), 835–854, doi:10.1037/a0012726.
- White, A. L., Rolfs, M., & Carrasco, M. (2013). Adaptive deployment of spatial and feature-based attention before saccades. *Vision Research*, 85, 26–35, doi:10.1016/j.visres.2012.10.017.
- Zhao, M., Gersch, T. M., Schnitzer, B. S., Dosher, B. A., & Kowler, E. (2012). Eye movements and attention: The role of pre-saccadic shifts of attention in perception, memory and the control of saccades. *Vision Research*, 74, 40–60, doi:10.1016/j. visres.2012.06.017.
- Zirnsak, M., Lappe, M., & Hamker, F. H. (2010). The spatial distribution of receptive field changes in a model of peri-saccadic perception: Predictive remapping and shifts towards the saccade target. *Vision Research*, *50*(14), 1328–1337, doi:10.1016/j. visres.2010.02.002.
- Zirnsak, M., Xu, K. Z., Noudoost, B., & Moore, T. (2011). Mapping of presaccadic receptive field profiles in the macaque frontal eye field. *Journal of Vision*, *11*(11): 539, http://www.journalofvision.org/content/11/11/539, doi:10.1167/11.11.539. [Abstract]