Attention allocation before antisaccades

Anna Klapetek
Allgemeine und Experimentelle Psychologie, Ludwig-Maximilians-Universität München, Munich, Germany
Graduate School of Systemic Neurosciences, Ludwig-Maximilians-Universität München, Planegg-Martinsried, Germany

Donatas Jonikaitis
Department of Neurobiology and Howard Hughes Medical Institute, Stanford University School of Medicine, Stanford, CA, USA

Heiner Deubel
Allgemeine und Experimentelle Psychologie, Ludwig-Maximilians-Universität München, Munich, Germany

In the present study, we investigated the distribution of attention before antisaccades. We used a dual task paradigm, in which participants made prosaccades or antisaccades and discriminated the orientation of a visual probe shown at the saccade goal, the visual cue location (antisaccade condition), or a neutral location. Moreover, participants indicated whether they had made a correct antisaccade or an erroneous prosaccade. We observed that, while spatial attention in the prosaccade task was allocated only to the saccade goal, attention in the antisaccade task was allocated both to the cued location and to the antisaccade goal. This suggests parallel attentional selection of the cued and antisaccade locations. We further observed that in error trials—in which participants made an incorrect prosaccade instead of an antisaccade—spatial attention was biased towards the prosaccade goal. These erroneous prosaccades were mostly unnoticed and were often followed by corrective antisaccades with very short latencies (<100 ms). Data from error trials therefore provide further evidence for the parallel programming of the reflexive prosaccade to the cue and the antisaccade to the intended location. Taken together, our results suggest that attention allocation and saccade goal selection in the antisaccade task are mediated by a common competitive process.

Introduction

The ability of humans to flexibly control their behavior can be studied in the antisaccade paradigm (Hallett, 1978; Hallett & Adams, 1980). In this task, a visual stimulus is presented in one visual hemifield and the observer is asked to make a saccade to its mirror position in the opposite hemifield. Thus, instead of making a reflexive eye movement to a visually salient stimulus location, one has to program an eye movement towards the opposite location. For this reason, the antisaccade task provides a unique situation in which the visual stimulus is dissociated from the final oculomotor command.

Earlier research has focused mainly on motor aspects of performance in the antisaccade task in order to understand the mechanisms underlying antisaccade preparation. It has been suggested that after onset of the visual stimulus, two motor plans are initiated—one towards the stimulus and one towards the antisaccade target (Massen, 2004; Munoz & Everling, 2004; Noorani & Carpenter, 2013). These two plans compete in reaching a threshold at which the winning motor program is executed. The idea of parallel prosaccade and antisaccade programming in the antisaccade task is empirically supported by observations that the intersaccadic interval between an erroneous primary saccade and the secondary corrective saccades directed to the antisaccade goal is often very short (Massen, 2004; Mokler & Fischer, 1999). Moreover, by introducing experimental manipulations that selectively influenced the processing speed of the exogenous prosaccade or the endogenous antisaccade component, Massen (2004) demonstrated that a slowing of the exogenous component (slowing prosaccade preparation) resulted in a reduced error rate, while a slowing of the endogenous

Citation: Klapetek, A., Jonikaitis, D., & Deubel, H. (2016). Attention allocation before antisaccades. *Journal of Vision*, *16*(1):11, 1–16, doi:10.1167/16.1.11.

doi: 10.1167/16.1.11 Received September 23, 2015; accepted November 16, 2015; Published January 20, 2016 ISSN 1534-7362

component (slowing antisaccade preparation) led to more errors.

However, as earlier research has mainly focused on motor performance in the antisaccade task, only little is known about the distribution of attention before antisaccades. This is surprising, especially if we consider that the antisaccade task offers the possibility to investigate competitive interactions between exogenous and endogenous attention. On the one hand, salient visual cues capture attention even if such cues are task-irrelevant (Carrasco, 2011; Carrasco, Ling, & Read, 2004; Müller & Rabbit, 1989; Nakayama & Mackeben, 1989). On the other hand, during the preparation of goal-directed saccades, spatial attention inevitably shifts to the saccade target (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Jonikaitis & Deubel, 2011; Jonikaitis & Theeuwes, 2013; Kowler, Anderson, Dosher, & Blaser, 1995; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). Therefore, there are two potential attentional targets in the antisaccade task—attention is likely to be drawn towards the visual stimulus location and/or towards the antisaccade target. Given that saccade target selection and spatial attention are thought to be closely coupled (Awh, Armstrong, & Moore, 2006; Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995), measuring spatial attention during the antisaccade task should help us to understand covert visual and motor selection during the task even before the eyes move.

Exact attentional effects in the antisaccade task are difficult to predict. Earlier observations contrasting endogenously cued spatial attention and attention at saccade targets found attentional costs either at the attended location (Deubel, 2008; Deubel & Schneider, 1996; Jonikaitis & Theeuwes, 2013; Kowler et al., 1995; Wilder, Kowler, Schnitzer, Gersch, & Dosher, 2009) or at the saccade target (Montagnini & Castet, 2007). Therefore, one could expect attention to be biased either towards the antisaccade target or towards the visual stimulus. The only direct measure of attention allocation before saccades was provided by Mokler, Deubel, and Fischer (2000), who showed that attention shifts in parallel to both locations. However, this study used a spatial precue to increase the percentage of saccade errors, which may have influenced attention in an unforeseeable way.

In order to investigate the relationship between attention and antisaccade programming in as much detail as possible, we completed two experiments that allowed to measure attention at the visual stimulus location as well as at the antisaccade goal. Making use of the fact that probe discrimination at exogenously or endogenously cued locations can be used as a reliable measure of spatial attention (see Carrasco, 2006; Deubel & Schneider, 1996), we employed a dual task, in which observers made prosaccades or antisaccades and simultaneously discriminated visual probes at these locations. Throughout the course of a trial, there were always two (in Experiment 1) or six (in Experiment 2) squares present on the display, one of which was briefly marked by a visual onset cue that signaled to the observer to make a saccade towards this square, or an antisaccade to the diagonally opposite square. At a randomly selected point in time during saccade preparation, a perceptual probe was shown in any of the squares. This allowed us to track spatial attention allocation to different locations during saccade preparation. We were further interested how spatial attention was allocated on error trials—that is when participants made erroneous prosaccades instead of antisaccades. We increased the number of errors by introducing a temporal gap between fixation offset and visual cue appearance (Bell, Everling, & Munoz, 2000; Fischer & Weber, 1997; Forbes & Klein, 1996). Last, we also asked participants to report whether they had made an incorrect saccade or not, as we planned to test whether error awareness would be linked to attention allocation, as was reported by Mokler et al. (2000).

Methods

Participants

Eighteen observers (most of them students) participated in the present study, after giving written informed consent. The participants had normal or corrected-to-normal vision and all except for two of the authors were naive with respect to the goals of the study. Ten observers (five male, five female, ages 21–31) took part in Experiment 1 and 16 observers (four male, 12 female, ages 21–31 participated in Experiment 2). The experiments were carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Apparatus

The observers were seated in a dimly illuminated room in front of a 19-in. CRT monitor (ViewSonic G90fB, screen refresh rate: 120 Hz, spatial resolution: 1024 × 768 pixels), positioned at a viewing distance of 70 cm. Their head position was stabilized by a chin and forehead rest. Eye movements were recorded with an EyeLink 1000 desktop-mounted eye tracker (SR Research, Canada) with a spatial resolution below 0.25°, at a sampling rate of 1000 Hz. The eye tracker was calibrated in the beginning of the experiment, before each new block and whenever it was necessary. Stimulus presentation and response collection were controlled by an Apple Mac Mini, using MATLAB software (MathWorks, Natick, MA) and the Psychophysics and Eyelink Toolbox extensions (Brainard, 1997; Cornelissen, Peters, & Palmer, 2002; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997; see http://psychtoolbox.org). Manual responses were recorded via the arrow keys on the right hand side of a standard computer keyboard.

Stimuli and task

The visual display contained a central black fixation dot (diameter: 0.5° of visual angle) and two (Experiment 1) or six (Experiment 2) green frames (edge length: 2°), positioned symmetrically on the outline of an imaginary circle (radius: 7°) centered on the fixation dot (see Figure 1). The frame objects contained interleaved sequences of vertically oriented Gabor patches (spatial frequency: 2.5 cpd, contrast: 100%, random phase on each presentation) and white noise masks, alternating every three frames (25 ms). The probe, a brief (25-ms) leftward or rightward tilt of the Gabor patch, could appear in any of the squares at different stimulus-onset asynchronies (SOAs) relative to cue onset (the SOA range differed between experiments and is specified later). The angular of the Gabor pattern was chosen for each observer individually, based on the results of a short visual pretest at the beginning of each experimental session (see Pretests section below).

After a random fixation interval of 800–1200 ms, the fixation dot disappeared and the saccade cue (two 0.2° thick horizontal black lines above and below one of the squares) appeared 180–220 ms later. Depending on the instruction screen at the beginning of each block, observers were asked to make a saccade to the cued square (prosaccade blocks) or to the diagonally opposite square (antisaccade blocks) as quickly as possible. After probe offset, all Gabor patches were replaced by empty squares, so that all objects contained noise-blank masks until the blackening of the display 700 ms after the onset of the saccade cue. Observers had as much time as they needed to indicate the perceived tilt direction by pressing the left arrow key for a leftward tilt or the right arrow key for a rightward tilt. A new trial started 200 ms after their response. In Experiment 2, observers were additionally asked to indicate by a second button press at the very end of each trial whether their initial saccade was correct (up arrow key) or incorrect (down arrow key). They were instructed to use the index and ring fingers of their right hand for the left and right responses and the middle finger for the up and down responses.

Design

Experiment 1

The first experiment consisted of 1,440 trials, divided into 24 blocks of 60 trials. Observers were instructed to make prosaccades in one half of the blocks and antisaccades in the other half. The experiment was divided into four sessions (on separate days), so that each session consisted of three prosaccade and three antisaccade blocks in randomized order. For each trial within a session, the locations of the saccade target and the probe were determined randomly and the cue-to-probe SOA was drawn from 36 time points between −100 and 250 ms.

Experiment 2

Our second experiment consisted of 2,160 trials, divided into 36 blocks of 60 trials each, spread over six sessions. The design was analogous to Experiment 1, but the display now contained six instead of two squares, which made it possible to show the probe at a neutral location in one third of the trials, the remaining two thirds being randomly split between the saccade goal and the diagonally opposite location. The position of the cued square was randomly selected in every trial, so that all six squares were equally likely to be the saccade target. For the first six observers, the cue to probe SOA was randomly drawn from 36 time points between −100 and 250 ms. For the remaining participants, the cue to probe SOA was limited to 11 time points between 100 and 200 ms. The trial number was accordingly reduced to 1,440 trials (24 blocks of 60 trials, divided into four sessions, each consisting of three pro- and three antisaccade blocks in randomized order).

Pretests

The pretests consisted of 60 trials with identical visual stimuli as in the main experiments, except that the probe was always presented at the cued location 100 ms after cue onset. Observers were instructed to covertly attend to the cued square while maintaining central fixation and to discriminate the orientation of the probe at the end of the trial. A modified version of the QUEST procedure (King-Smith, Grigsby, Vingrys, Benes, & Supowit, 1994; Watson & Pelli, 1983) was used to determine the two tilt angles at which observers reached 82% correct probe discrimination in the left and right half of the display. Tilt angles ranged between 4° and 21° in Experiment 1 ($M = 9.7$, $SD = 6.7$) and between 3° and 27° in Experiment 2 ($M = 11.0$, $SD = 4.3$). Angles for the left and right display half were comparable.

Data analyses

All eye movement and behavioral data were analyzed using Matlab software (MathWorks, USA) and the Psychophysics and Eyelink Toolbox extensions (Brainard, 1997; Cornelissen et al., 2002; Kleiner et al., 2007; Pelli, 1997; see http://psychtoolbox.org). Eye movements were recorded online during sessions and evaluated offline using Eyelink's built-in saccade detection algorithm (Experiment1), or our own customized velocity–space algorithm that corrected for glissades (Experiment 2). In a direct comparison, both algorithms detected identical saccade beginning times, but the Eyelink algorithm tended to include glissades at the end of saccades into the saccade duration and thus tended to yield unrealistically short intersaccadic intervals. Primary saccades with latencies below 100 ms or above 600 ms were removed from analysis. In total, we had to reject 5% of all trials due to blinks, missing data, or not clearly separable saccades.

Statistical analyses consisted of repeated-measures analyses of variance (ANOVA) and post hoc comparisons using t tests with a Bonferroni correction. The Greenhouse-Geisser correction was applied whenever sphericity was violated. All analyses were based on a minimum of five trials per participant and condition.

Results

Experiment 1

Saccade latency and direction errors

The initial saccade direction was incorrect in 3% of all prosaccade trials and in 18% of the antisaccade trials. To assess whether saccade latencies differed between prosaccades and antisaccades and whether they were affected by probe location and timing, we performed a repeated-measures ANOVA with saccade type (prosaccade, antisaccade), probe location (at cue, opposite cue) and probe presentation time (six 50-ms wide time bins between −100 and 200 ms) as the within-subjects factors.

We found that antisaccade latencies were longer than prosaccade latencies ($M = 217.5$ ms, $SD = 55.0$ ms for antisaccades vs. $M = 163$ ms, $SD = 45.0$ ms for prosaccades, $F(1, 9) = 138.0$, $p < 0.001$). This latency difference is one of the typical characteristics of antisaccades (Hallett, 1978), that has been robustly replicated in many different versions of the antisaccade task.

Furthermore, we found that neither the location nor the timing of the probe had any effect on saccade latency (no significant main effects of these two factors). This indicates that the probe discrimination task did not alter saccade preparation and can be used as an effective measure of attention allocation during saccade preparation.

Saccade amplitude

In order to assess saccade accuracy, we calculated the gains of primary saccades as the ratio between saccade amplitude and target amplitude. We were mainly interested in whether gains would differ between prosaccades and antisaccades and between correct saccades and erroneous prosaccades. Since saccade gains did not vary as a function of probe presentation time, we decided to exclude this factor from analysis in order to have a sufficient number of trials per participant and condition (before exclusion, many bins had less than five trials, afterwards the minimum was 19). The ANOVA of the gains with saccade type (correct prosaccade, correct antisaccade, erroneous prosaccade) and probe location (at cue, opposite cue) as the between-subjects factors revealed a significant main effect of saccade type, $F(2,18) = 46.1$, $p < 0.001$, and no significant effect of probe location. While amplitudes of correct prosaccades and antisaccades were both very accurate (mean gain = 1.0), erroneous prosaccades tended to undershoot the target (mean gain = 0.86) and thus differed significantly from correct saccades (as revealed by post hoc comparisons).

Discrimination performance

Since we presented the probe at different SOAs with respect to the saccade cue, it was possible to determine the time course of attentional deployment to both probe locations. For this purpose, we sorted all SOAs into 50-ms–wide bins and calculated the proportion of correct probe discriminations for each saccade condition and probe location in each time bin (see Figure 2a). Discrimination performance in the prosaccade condition was clearly superior for probes presented at the cued location (saccade goal) compared to the opposite location, where it was just slightly above chance level. In the antisaccade condition, in contrast, performance was about equally good at the cued and the opposite location (antisaccade goal), but generally worse than at the prosaccade goal in the prosaccade condition, which suggests that attentional resources were split over both locations.

Interestingly, the benefits at the saccade goal in the prosaccade condition and at the cued location and

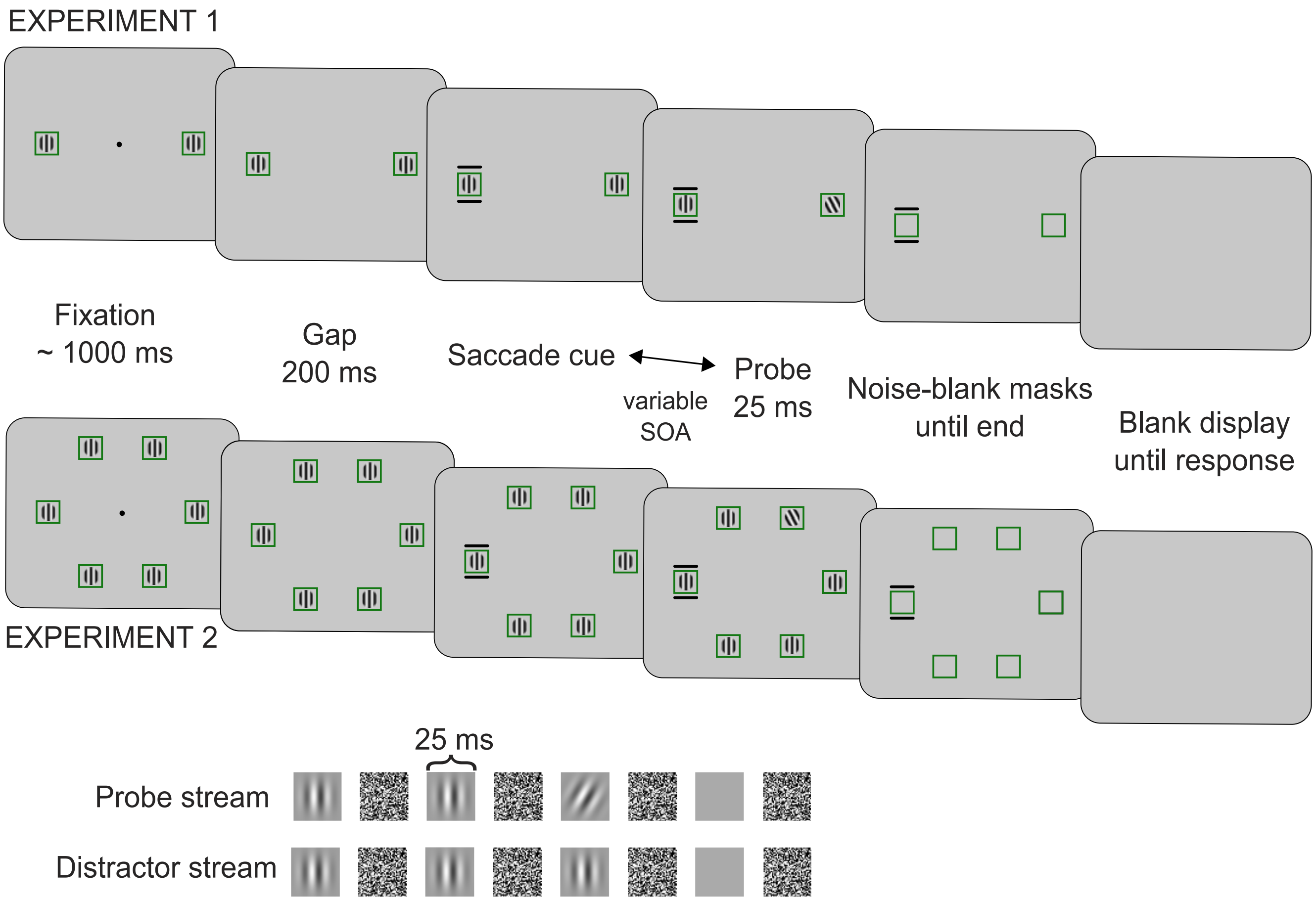

Figure 1. Schematic representation of the stimulus sequences in both experiments and examples for the probe and distractor streams.

antisaccade goal in the antisaccade condition can already be seen before saccade cue onset. This is likely due to a retroactive attentional effect, which can extend into the precue period (Sergent et al., 2013; Thibault, Cavanagh, & Sergent, 2015). The most likely explanation is that shifts of spatial attention to the cued location or to saccade goals retroactively trigger conscious access to previously unconscious sensory representations. Unfortunately, this effect limits the tracking of the temporal profile of spatial attention. For this reason, we decided to focus in our further analyses on the spatial distribution of attention shortly before the saccade (the last two bins pooled together).

We performed a repeated-measures ANOVA with saccade type (prosaccade, antisaccade) and probe location (at cue, opposite cue) as the within-subjects factors (see Figure 2b for a graphical summary of the results). The results show that probe discrimination performance depended upon probe location (main effect of probe location, $F(1, 9) = 30.0$, $p < 0.001$, and interaction between probe location and saccade type, $F(1, 9) = 32.7$, $p < 0.001$). In the prosaccade task, discrimination performance (% correct) was significantly better at the cued location, which was the saccade goal, ($M = 89.4\%$, $SD = 5.0\%$) than at the task-irrelevant opposite location ($M = 54.7\%$, $SD = 8.7\%$; post hoc comparisons). In contrast to this, in correct trials of the antisaccade task, discrimination at the cued location ($M = 72.0\%$, $SD = 10.7\%$) and at the antisaccade goal ($M = 77.1\%$, $SD = 9.8\%$) were not significantly different.

We were also interested in whether attention allocation to the saccade goal would differ as a function of saccade type. The analysis revealed that discrimination performance at the goal of correct prosaccades ($M = 89.4\%$, $SD = 5.0\%$) was significantly better than at the goal of correct antisaccades ($M = 77.1\%$, $SD = 9.8\%$).

Taken together, the results on discrimination performance demonstrate that during the programming of antisaccades, attention was about equally allocated to the visual cue and to the future saccade goal. Discrimination performance was clearly best at the goal of voluntary prosaccades, which could be explained by the summation of the effects of reflexive

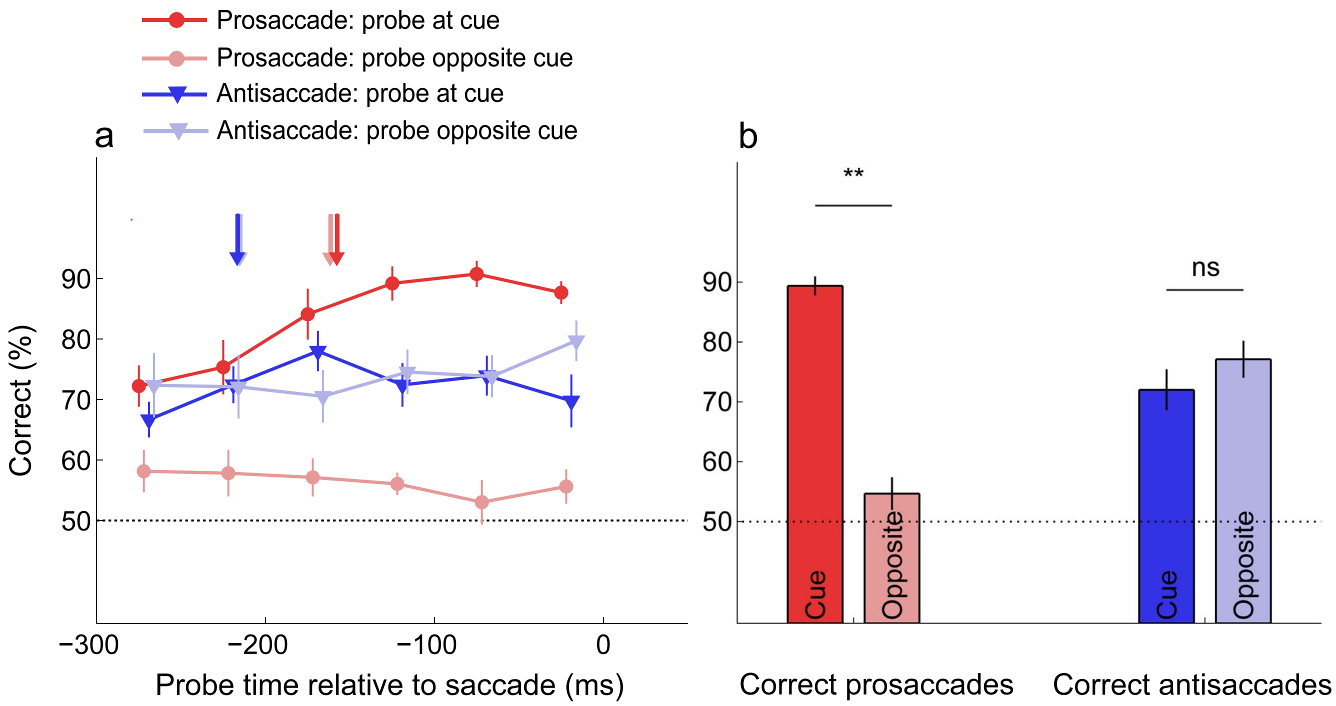

Figure 2. Discrimination performance in Experiment 1. Correct discrimination (in %) is plotted as a function of saccade type (prosaccade or antisaccade) and probe location (at the cued location or opposite from it). Error bars represent standard errors of the mean. The dashed line denotes the chance performance level. (a) Discrimination performance for probes appearing at various times before saccade onset. Only trials with correct saccades were included and each bin contains at least 10 trials per participant and condition ($M = 37$). The vertical arrows indicate the average times when the saccade cues were presented. (b) Discrimination performance for probes presented less than 100 ms before saccade onset as a function of saccade type (prosaccade or antisaccade) and probe location (at the visual cue or opposite from the cue). At least 40 trials per participant and condition were analyzed ($M = 79$ for prosacades and $M = 63$ for antisaccades).

and endogenous attention. An alternative reason for this advantage could be the absence of attentional competition in this condition, as the opposite location was completely irrelevant for the saccade task.

Experiment 2

It is well possible that the parallel allocation of attention in Experiment 1 was, at least in part, a consequence of having only two possible probe locations, which may have allowed observers to split their attention. One of the goals of Experiment 2 therefore was to control for this potential bias by adding four saccade-irrelevant probe locations, thus introducing more visual competition. In addition, we wanted to test whether attention allocation would be related to awareness of direction errors and therefore added a measure of error awareness at the end of each trial. In contrast to Experiment 1, where we were interested in the time course of attention allocation, we decided to focus on the interval between 100 ms postcue and the beginning of the saccade, where we had previously found the strongest attentional cueing effects.

Direction errors and awareness

While saccade accuracy was very high in prosaccade blocks (98% correct), participants made a considerable amount of direction errors in antisaccade blocks. In 16% of all antisaccade trials, the first saccade went to the visual cue (erroneous prosaccade), in 12% it went to one of the squares adjacent to the antisaccade target, and in 3% it went elsewhere. Sixty-one percent of the erroneous prosaccades were not declared by the observers, which is consistent with the 62% reported by Mokler and Fischer (1999).

According to signal detection theory (Green & Swets, 1966), detection performance is a function of the detectability of the signal and the response strategy of the observer. To understand how these two variables influenced our results, we calculated discrimination sensitivity (d') and response bias (C) for each of our participants. Sensitivity ranged between 0.8

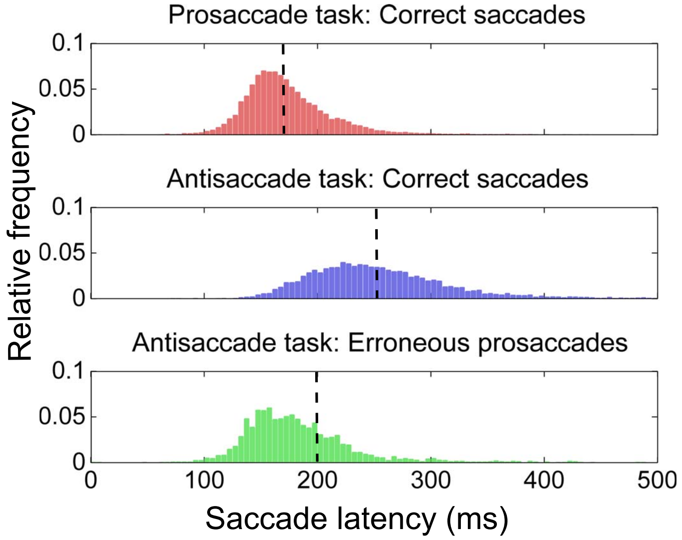

Figure 3. Saccade latencies in Experiment 2. The histograms represent relative frequency distributions of saccade latencies (bin size = 5 ms) of correct prosaccades ($N = 13{,}003$), correct antisaccades ($N = 9{,}665$) and erroneous prosaccades ($N = 2{,}298$). The vertical dotted lines correspond to the means.

and 3.4 ($M = 1.9$), which means that observers could discriminate between trials with correct saccades and those with direction errors way above chance level. C ranged between 0.3 and 1.7 ($M = 1.2$), which indicates that all observers adopted a conservative criterion and tended to prefer "no" responses over "yes" responses. This was most likely a consequence of the low base rate of errors (<10%) and the payoff characteristics (no benefits, but rather expected costs associated with correct error detection) in our experiments. In sum, the analysis of discrimination sensitivity and response bias revealed that observers were reasonably good at detecting errors (some even very good), but they tended to report only errors that they felt certain about.

Saccade latency

Saccade latencies were analyzed in the same way as amplitudes (ANOVA with the factors saccade type and probe location). Figure 3 shows the saccadic latency distributions for correct prosaccades in the prosaccade task and for correct antisaccades and erroneous prosaccades in the antisaccade task.

Saccade latencies for correct antisaccades ($M = 252.8$ ms, $SD = 62.7$ ms) were longer than for correct prosaccades ($M = 170.4$ ms, $SD = 38.8$ ms) and for erroneous prosaccades ($M = 198.6$ ms, $SD = 78.6$ ms), this difference being significant (main effect of saccade type, $F(2, 14) = 16.6$, $p < 0.001$, and post hoc comparisons).

Saccade amplitude

Amplitudes of primary saccades were subjected to a repeated-measures ANOVA with the factors saccade type (prosaccade, antisaccade, erroneous prosaccade) and probe location (at cue, opposite cue). As in Experiment 1, erroneous prosaccades (in the antisaccade task) had significantly shorter amplitudes ($M = 5.7°$, $SD = 1.5°$) than both correct prosaccades ($M = 6.7°$, $SD = 0.8°$) and correct antisaccades ($M = 6.7°$, $SD = 1.1°$). The difference was statistically significant (main effect of saccade type, $F(2, 26) = 63.0$, $p < 0.001$ and post hoc comparisons). Within the group of erroneous prosaccades, amplitudes were significantly shorter for unperceived errors ($M = 5.2°$, $SD = 1.5°$) than for perceived errors ($M = 6.1°$, $SD = 1.2°$), $t(15) = 6.7$, $p < 0.001$.

Corrective saccades

Erroneous prosaccades having wrong direction and shorter amplitudes than the correct saccades were often followed by corrective saccades. Indeed, our analysis revealed that 71% of all prosaccade errors were corrected in the direction of the intended antisaccade goal (only saccades that crossed the midline were counted as corrective saccades). The proportion of corrective saccades was considerably higher after unperceived errors (87%) than after perceived errors (47%).

Figure 4 displays the distributions of primary saccade amplitudes and correction times (intersaccadic intervals) for trials with perceived and unperceived prosaccade errors. About half of the corrective saccades (49%) occurred within less than 100 ms after the end of the erroneous prosaccade. The very short latency suggests that these secondary saccades were programmed partly in parallel with the primary saccade. Correction times were significantly shorter after unperceived ($M = 100.8$ ms, $SD = 48.3$ ms) than after perceived ($M = 138.5$ ms, $SD = 72.6$ ms) errors, $t(15) = 3.5$, $p < 0.01$. There was also a significant correlation between the amplitude of the initial saccade and the correction time of the second saccade, meaning that hypometric errors tended to be corrected faster than errors that landed closer to the target (Spearman correlation: $p < 0.001$ for all but one subject).

Figure 5 illustrates the linear relationship between amplitudes of primary and corrective saccades, which proves that most corrective saccades landed on the target or close to it. The line represents perfect error compensation, where the corrective gain (i.e., the sum of the amplitudes of both saccades, with leftward amplitudes reversed in sign) equals the target distance. This gain was higher following unperceived errors ($M = 7.0°$, $SD = 0.1°$) than following perceived errors ($M = 6.6°$, $SD = 0.1°$) and the difference was statistically

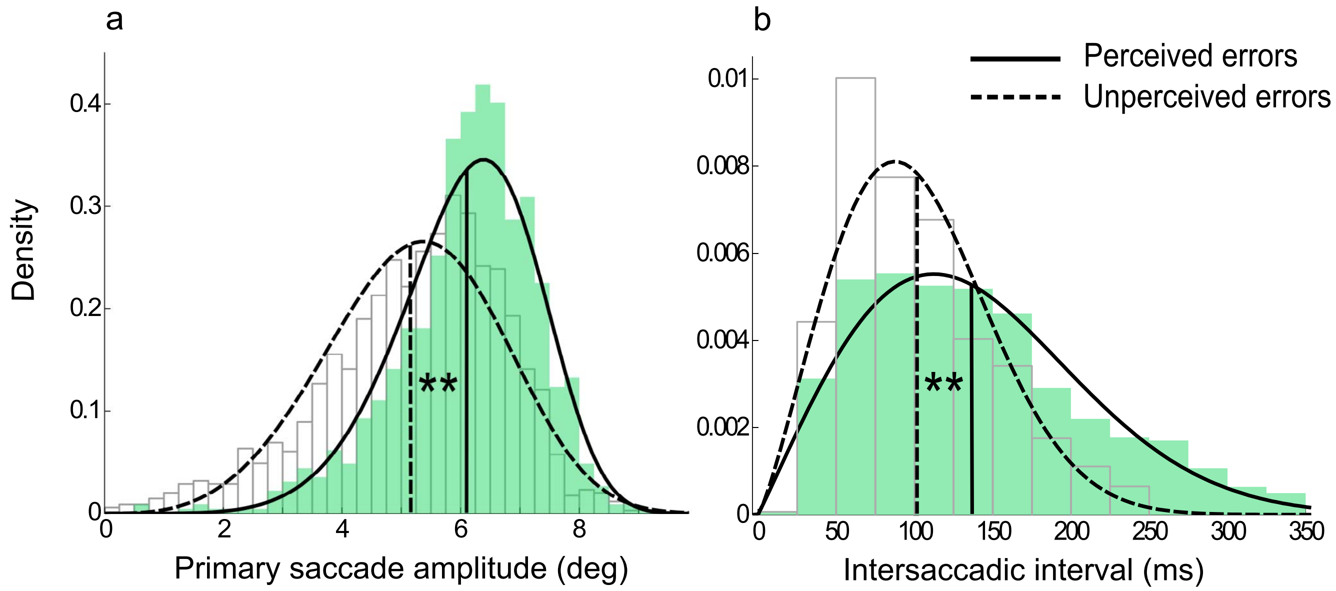

Figure 4. Amplitudes (a) and correction times (b) of perceived versus unperceived erroneous prosaccades. The histograms plot scaled relative frequency, the curves represent Weibull functions fitted to the data, and the vertical lines correspond to the means. (a) Amplitudes of perceived ($N = 907$) compared to unperceived ($N = 1,391$) saccades; bin size = 5°. (b) Correction times of perceived ($N = 563$) compared to unperceived ($N = 1,229$) errors, bin size = 25 ms.

significant, $t(15) = 28.9$, $p < 0.001$. Interestingly, this effect remained present in the subgroup of very quickly corrected saccades, which means that it cannot be explained by differences in correction time.

Discrimination performance

We performed a repeated-measures ANOVA with saccade type (prosaccade, antisaccade, erroneous pro-

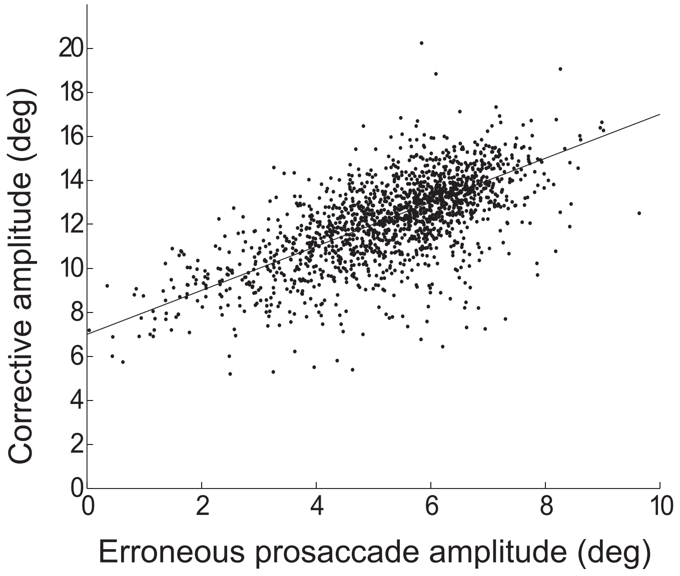

Figure 5. Scatterplot of the amplitudes of erroneous prosaccades and their corrections. The diagonal line represents full correction to the intended antitarget.

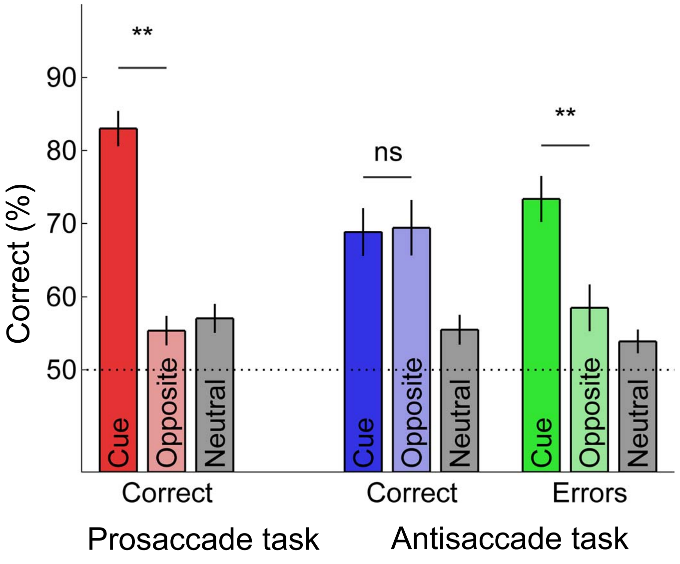

Figure 6. Discrimination performance in Experiment 2. The graph compares discrimination rates for probes presented between 100 and 200 ms after cue onset as a function of saccade type (correct prosaccade, correct antisaccade, erroneous prosaccade) and probe location (at cue, opposite cue, neutral). Error bars represent standard errors of the mean. The dashed line denotes the chance performance level. The analysis was based on at least five trials per participant and condition ($M = 98$ for correct prosaccades, $M = 102$ for correct antisaccades, $M = 19$ for erroneous prosaccades).

saccade) and probe location (at cue, opposite cue, neutral) as the within-subjects factors (see Figure 6 for a graphical summary of the results). The results demonstrate that probe discrimination mainly depended on the location of the probe (main effect of probe location, $F(2, 26) = 28.7$, $p < 0.001$, and revealed a significant interaction between saccade type and probe location, $F(4, 52) = 10.7$, $p < 0.001$). Before correct prosaccades, discrimination performance was significantly better at the cued location, which was the saccade goal, ($M = 83.4\%$, $SD = 8.3\%$) than both at the opposite location ($M = 55.1\%$, $SD = 7.7\%$) and at the neutral location ($M = 57.2\%$, $SD = 7.4\%$), which were task-irrelevant. Before correct antisaccades, discrimination at the cued location ($M = 68.9\%$, $SD = 12.8\%$) and at the antisaccade goal ($M = 69.4\%$, $SD = 15.1\%$) were almost equal and were both significantly better than at the neutral location ($M = 55.3\%$, $SD = 7.9\%$). In contrast to this, probe discrimination before erroneous prosaccades was significantly better at the cued location ($M = 74.4\%$, $SD = 13.9\%$) than at the opposite ($M = 57.5\%$, $SD = 14.8\%$) and neutral ($M = 51.4\%$, $SD = 11.7\%$) locations.

In summary, the results on discrimination performance in Experiment 2 tell the same story as in Experiment 1: Correct antisaccades were associated with presaccadic attention at both locations. We further observed that errors were associated with more attention at the cued location, where the saccade was made to, and less attention at the correct antisaccade goal.

Moreover, the significant difference between performance at the antisaccade goal and at the neutral location before correct antisaccades proves that attention allocation to the antisaccade goal is mediated by oculomotor preparation rather than by some strategy for maximizing discrimination performance.

As we were interested in whether the enhanced attention at the cued location or rather the reduced amount of attention at the correct antisaccade goal was predictive of errors, we performed post hoc comparisons of discrimination performance at the cued and opposite locations before correct antisaccades and before errors. The results revealed that only the error-related decline in performance at the correct antisaccade goal, but not the increase at the cued location, was statistically significant. This suggests that attention at the antisaccade goal is crucial for correct antisaccade programming.

To investigate the question of whether error awareness is related to attention allocation, as has been proposed in previous work (e.g., Deubel, Irwin, & Schneider, 1999; Godijn & Theeuwes, 2003b; Mokler & Fischer, 1999), we compared discrimination performance in trials with perceived and with unperceived errors. The results did not reveal any differences, except for a nonsignificant trend towards better discrimination performance (at all locations) in trials with unperceived errors. To see whether the allocation of attention in trials with corrected errors depended on the latency of the corrective saccade, we compared discrimination performance in trials with very fast ($\leq$90 ms) and longer ($>$90 ms) correction times. The results did not reveal any consistent differences.

Discussion

The goal of this study was to investigate the allocation of spatial attention during the programming of antisaccades. We employed a dual task, in which participants made prosaccades or antisaccades and concurrently discriminated visual probes at the cued location, the opposite location (i.e., the antisaccade goal), or at task-irrelevant locations.

First, we replicated the findings of previous antisaccade studies, such as the substantially longer latency of antisaccades in comparison to prosaccades (Everling, Dorris, & Munoz, 1998; Hallett, 1978) and the higher error rate in the antisaccade condition (Hallett, 1978; Heath, Dunham, Binsted, & Godbolt, 2010). Second, we found that most erroneous prosaccades were not perceived and were rapidly corrected, suggesting that a large proportion of corrective antisaccades was programmed in parallel with the erroneous prosaccades (Massen, 2004; Mokler et al., 2000; Mokler & Fischer, 1999). Our third and most important finding was that before antisaccades, attention was allocated in parallel to the visual cue and the antisaccade goal, rather than being first allocated to the cue and then to the antisaccade goal. Prosaccade errors were associated with an attentional bias towards the prosaccade goal, which has important implications concerning the relationship between attention and saccade programming. In the following sections, we will discuss our results in the context of existing theories and previous findings in this field and propose a model of how attention and saccades could be influenced by a common competitive process.

Parallel programming of prosaccades and antisaccades

Parallel programming of two subsequent saccades can be inferred from very short intersaccadic intervals (Becker & Jürgens, 1979) and has been reported not only in the antisaccade task (Massen, 2004; Mokler & Fischer, 1999), but also in other tasks, such as reading (Morrison, 1984), double-step paradigms (Becker & Jürgens, 1979; Walker & McSorley, 2006), visual search

(McPeek, Skavenski & Nakayama, 2000), and in the oculomotor capture paradigm (Godijn & Theeuwes, 2002, Irwin, Colcombe, Kramer, & Hahn, 2000; Theeuwes, Kramer, Hahn, & Irwin, 1998; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). Recent investigations into this topic have mainly focused on situations where an endogenous saccade is programmed along with an initial involuntary saccade to a visual distractor.

McPeek et al. (2000), for instance, asked their subjects to saccade to a red or green color singleton presented along with two distractors of the opponent color (e.g., green or red). The fact that the same colors were used for target and distractors led to many erroneous saccades towards one of the distractors, especially when the distractors had the same color as the target in the previous trial. These erroneous saccades were often hypometric and many were followed by short-latency corrective saccades to the target. Based on these observations, McPeek et al. (2000) proposed a competition model of saccade programming in which both saccade goals were represented in a common motor map, supposedly located in the superior colliculus. Mutual inhibitory connections between neurons would make sure that any increase in neural activity at one location would result in a decrease in activity at the other.

Investigations using the oculomotor capture paradigm (Godijn & Theeuwes, 2002; Irwin et al., 2000; Theeuwes et al., 1998; Theeuwes et al., 1999), where endogenous saccades to a color-defined target compete with involuntary saccades to an onset distractor, yielded very similar results: A substantial proportion of initial erroneous saccades to the distractor, many of them followed by corrective saccades after less than 100 ms of fixation. After the initial assumption that exogenous and endogenous saccades were programmed in separate brain circuits and simply race towards a threshold (Theeuwes et al., 1998; Theeuwes et al., 1999), Godijn and Theeuwes (2002) formulated their "competitive integration model" (also see Meeter, Van der Stigchel, & Theeuwes, 2010), which also postulates that the rivalry takes place on a common collicular map with lateral inhibitory connections.

The idea of a parallel competition between erroneous prosaccades and subsequent corrective saccades in the antisaccade task was first addressed by Mokler and Fischer (1999) and further elaborated by Massen (2004). Although Massen assumed mutual inhibition between the pro- and antisaccade programs, her findings (see Introduction) could not rule out an independent race model (the only evidence for mutual inhibition between prosaccades and antisaccades came from her observation that slower and faster corrected erroneous prosaccades tended to have shorter amplitudes, which could be due to interference from the second saccade program). Kristjánsson and colleagues (Kristjánsson, Chen, & Nakayama, 2001; Kristjánsson, Vandenbroucke, & Driver, 2004) showed that manipulations that slow down the prosaccade component can lead to faster antisaccades, which is more compatible with a model that assumes competitive interactions between both. The results of the present study confirm many of the above-mentioned findings, such as the shorter amplitudes of erroneous saccades and the significant proportion of very short correction times. In agreement with McPeek et al. (2000), we found a significant correlation between the amplitudes of initial erroneous saccades and their correction times: The faster a saccade was corrected, the smaller tended to be its amplitude. This suggests that the first saccade was influenced or even disrupted by the programming of the second saccade. Slower errors also tended to have shorter amplitudes (although this relationship was less consistent). Taken together, our findings provide further evidence that reflexive and endogenous saccades compete within the same or overlapping neural networks.

Parallel attentional selection

The results of our experiments revealed that antisaccades are preceded by attentional allocation to both the visual cue and the antisaccade goal, thus suggesting that both locations compete for attentional resources. Our findings are consistent with previous evidence that visuospatial attention can be divided when this is beneficial for the task (Awh & Pashler, 2000; Baldauf & Deubel, 2008a, 2008b, 2009; Baldauf, Wolf, & Deubel, 2006; Deubel, 2014; Godijn & Theeuwes, 2003a; Jefferies, Enns, & Di Lollo, 2014; Jonikaitis & Deubel, 2011). Moreover, our data rule out the serial hypothesis, according to which attention first needs to be disengaged from the visual target before it can shift to the antisaccade goal (e.g., Crawford, Kean, Klein, & Hamm, 2006; Olk & Kingstone, 2003). If the serial hypothesis was true, we would have observed improved performance at the antisaccade target and poor performance at the cued location shortly before saccade onset. Instead, we found comparable performance at both locations.

The link between attention and (anti)saccades

Our findings on attention allocation before correct antisaccades and before prosaccade errors have some important implications concerning the link between attention and saccade programming. The fact that attention before correct antisaccades was equally distributed among the cued location and the antisaccade goal is in conflict with the premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Rizzolatti, Riggio, & Sheliga, 1994), which regards attention as functionally equivalent to saccade preparation. If this theory was correct, correct antisaccades would be associated with more attention at the antisaccade goal than at the cued location, which was clearly not the case. Nevertheless, our results suggest that attention and saccade programming are closely linked, as attentional distribution was predictive of prosaccade errors.

Current views of visual attention are tied to the concept of priority maps (Fecteau & Munoz, 2006; Serences & Yantis, 2006), which are thought to integrate information about bottom-up saliency with top-down influences into a single real-time representation of behavioral relevance. In agreement with this concept, we believe that during the preparation of antisaccades, cue-related and antisaccade-related activity compete on such a map (or several related maps) and that the resulting priority signal influences both saccade programming (through modulatory influences on the oculomotor system) and visual perception (through feedback to early visual areas). Our findings are compatible with such a model, as discrimination performance was clearly modulated by the saccade task and the ratio between cue-related and antisaccade-related attention was predictive of erroneous prosaccades.

Research indicates that such a priority map could be represented in the posterior parietal cortex. Single-cell recording studies in monkeys have shown that neurons in the lateral intraparietal (LIP) area combine visual, cognitive, and saccadic signals—and possibly others, such as information about reward—into a topographic representation of behavioral priority, which can be used to guide eye movements and attention (Bisley & Goldberg, 2010; Bisley, Ipata, Krishna, Gee, & Goldberg, 2009; Ipata, Gee, Bisley, & Goldberg, 2009). Gottlieb and Goldberg (1999) investigated LIP activity while monkeys performed antisaccades and found that most neurons strongly responded to the visual stimulus, when it fell in their receptive field, and some also fired in response to the antisaccade target. Recently, LIP has been shown to implement center-surround suppression mechanisms that can account for the type of competitive interactions between an endogenous saccade plan and a visually salient distractor, as we assume are happening in the antisaccade task. In humans, researchers have identified topographically organized areas within the intraparietal sulcus (IPS) that most likely are the human homologues to monkey LIP (Schluppeck, Glimcher, & Heeger, 2005; Sereno, Pitzalis, & Martinez, 2001; Silver, Ress, & Heeger, 2005). Corbetta and Shulman (2002) identified IPS as a central part of the brain's network for endogenous attention. At the same time, IPS seems to play a role in selection for perception, as it has been shown to modulate activity in primary visual cortex via top-down attentional signals (Lauritzen, D'Esposito, Heeger, & Silver, 2009). A recent study by Khan et al. (2009) established a link between these two roles by showing that the well-documented facilitation of visual perception at the goal of a planned saccade crucially depends on the parietal cortex. IPS lesions lead to prolonged antisaccade latencies (Machado & Rafal, 2004), and a number of fMRI studies have found enhanced IPS activation in antisaccades as compared to prosaccades (see a recent meta-analysis by Jamadar, Fielding, & Egan, 2013). Of particular interest are the results of a study by Anderson, Husain, and Sumner (2008), which suggest that human IPS importantly contributes to the resolution of competition in the antisaccade task.

The idea that we try to convey here, namely that competitive integration can be generalized beyond the eye movement system and could occur on a parietal priority map, is not new, as it was already suggested by Hunt, von Mühlenen, and Kingstone (2007), based on their results on parallels between attentional and oculomotor capture. We would like to emphasize that this proposal does not contradict the idea that saccade programs compete on a common collicular motor map (e.g., Findlay & Walker, 1999; Godijn & Theeuwes, 2002, McPeek et al., 2000; Trappenberg, Dorris, Munoz, & Klein, 2001), since we do not assume that our putative priority signal can directly drive eye movements. It rather seems that the motor map in the superior colliculus (SC) consists of a further competitive stage, even more specialized on oculomotor selection. Interestingly, findings from neurophysiological studies in monkeys revealed that stimulus-related activity bursts can be larger than antisaccade-related bursts even in the frontal eye fields (FEF) and SC, which are known to directly trigger eye movements (Everling, Dorris, Klein, & Munoz, 1999; Everling & Munoz, 2000). This indicates that the final threshold for saccade generation is not localized in SC or FEF, but rather in the brainstem saccade generator, where outputs from the whole oculomotor network are integrated (see Jantz, Watanabe, Everling, & Munoz, 2013, for further evidence). The brain employs several strategies to downweight target-related activity and upweight antisaccade-related activity, both at the level of the SC and downstream from it. Examples are the increase in fixation-related and decrease in visual SC activity in the preparation of an antisaccade (Everling, Dorris, & Munoz, 1998) or the transient increase in omnipause neuron activity following the appearance of the visual stimulus (Everling, Paré, Dorris, & Munoz, 1998). It has also been suggested that input from other oculomotor areas, such as the supplementary eye field, could boost the relatively weak antisaccade-related activity downstream from the SC (Jantz et al., 2013; Munoz & Everling, 2004). The question whether the antisaccade target is also favorized by signals from a parietal priority map remains to be clarified by further research.

Taken together, our results, as well as the research reviewed here, suggest that attention and saccade programming are both inherently parallel processes in which different spatial locations are selected along each other, rather than one after the other. Although attentional and oculomotor selection seem to be linked, they are not identical, as perceptual benefits are not limited to the goal of the upcoming saccade. In terms of brain economy, such a distinction makes sense: While it may often be beneficial to attend to several objects or locations at the same time, the eyes cannot go to more than one target. This constraint, along with the relatively high costs associated with an erroneous eye movement, entails a greater need to favorize task demands over bottom-up salience for saccade programming. Nevertheless, a parallel accumulation of information until a very late stage of oculomotor programming is still advantageous, as it allows the system to act fast and flexibly and dramatically reduces planning costs—for example, when several eye movements are made in sequence.

Error awareness and attention

Some authors (Deubel et al., 1999; Mokler & Fischer, 1999) have proposed that error recognition in the antisaccade task is mediated by visuospatial attention, in the sense that our mind falsely attributes eye position to the current locus of attention. If, according to this hypothesis, attention first moved to the visual cue, the participant would recognize the saccade direction error. If, however, attention first shifted to the antisaccade goal and only the eyes initially made a reflexive saccade in the wrong direction, the error would not reach awareness and could be corrected faster, as attention would not need to move to the correct location anymore. Mokler et al. (2000) observed that unperceived erroneous prosaccades were associated with better visual discrimination performance at the antisaccade goal than at the visual target, while the opposite was true for perceived errors. From this they concluded that reflexive prosaccades can occur without a prior attention shift to the target. In our study, discrimination performance in error trials was always best at the cue location and error perception was associated with slightly worse performance in the discrimination task. One attempt to explain these contradictory findings could be through the exact comparison of the experimental designs used in their study and in ours. Notably, Mokler and her collaborators did not present probes at a neutral location, which makes it impossible to judge the amount of task-related attention at the antisaccade goal. Second, the 100% valid exogenous precue shown 100–200 ms before the probe, which was intended to increase the rate of erroneous prosaccades (see Fischer & Weber, 1996), may have led to better discrimination performance at the cued location. Alternatively, the process of error monitoring may have drawn attentional resources away from the discrimination task. Such an account could explain both the better discrimination performance in association with unperceived errors and the shorter latencies of subsequent corrective saccades observed in the present study. The results of a study by Taylor and Hutton (2011) support this hypothesis by showing that error perception in the antisaccade task may require top-down attentional control. The lower frequency and reduced gain of corrective saccades that we observed following perceived errors would also be consistent with such an explanation.

Based on their findings from the oculomotor capture paradigm, Godijn and Theeuwes (2003b) proposed a weaker form of Mokler's hypothesis, which states that involuntary saccades to distractors may not be perceived when attention remains on the distractor for too little time. Our results do not support any of the two accounts, since we found neither a proof for attention being disengaged from the cued location nor for less cue-related attention before unperceived errors. Rather, the main problem associated with both hypotheses may be that they presume that attentional processes are strictly serial, which reflects the persistent influence of the attentional spotlight metaphor. Only recently, the notion of a single attentional focus that needs to be shifted in space has been replaced by newer theories, in which activations corresponding to spatial locations can be enhanced or suppressed through mutual interactions or through external modulatory influences, leading to dynamic attentional landscapes that are adapted to the current sensory-motor task (Baldauf & Deubel, 2010).

Keywords: antisaccades, attention, parallel programming, oculomotor selection

Acknowledgments

This work was funded by the Deutsche Forschungsgemeinschaft Research Training Group GRK

1091 and a grant by the Deutsche Forschungsgemeinschaft (DE 336/5-1).

Commercial relationships: none.
anna.klapetek@psy.lmu.de
Corresponding author: Anna Klapetek.
Email: anna.klapetek@psy.lmu.de.
Address: Allgemeine und Experimentelle Psychologie, Ludwig-Maximilians-Universität München, Munich, Germany.

References

Anderson, E. J., Husain, M., & Sumner, P. (2008). Human intraparietal sulcus (IPS) and competition between endogenous and exogenous saccade plans. *NeuroImage*, *40*, 838–851. [PubMed]

Awh, E., Armstrong, K. M., & Moore, T. (2006). Visual and oculomotor selection: Links, causes and implications for spatial attention. *Trends in Cognitive Science*, *10*(3), 124–130. [PubMed]

Awh, E., & Pashler, H. (2000). Evidence for split attentional foci. *Journal of Experimental Psychology: Human Perception and Performance*, *26*, 834–846. [PubMed]

Baldauf, D., & Deubel, H. (2008a). Properties of attentional selection during the preparation of sequential saccades. *Experimental Brain Research*, *184*(3), 411–425. [PubMed]

Baldauf, D., & Deubel, H. (2008b). Visual attention during the preparation of bimanual movements. *Vision Research*, *48*, 549–563. [PubMed]

Baldauf, D., & Deubel, H. (2009). Attentional selection of multiple movement goal positions before rapid hand movement sequences: An event-related potential study. *Journal of Cognitive Neuroscience*, *21*(1), 18–29. [PubMed]

Baldauf, D., & Deubel, H. (2010). Attentional landscapes in reaching and grasping: Mini review. *Vision Research*, *50*, 999–1013. [PubMed]

Baldauf, D., Wolf, M., & Deubel, H. (2006). Deployment of visual attention before sequences of goal-directed hand movements. *Vision Research*, *46*, 4355–4374. [PubMed]

Becker, W., & Jürgens, R. (1979). An analysis of the saccadic system by means of double-step stimuli. *Vision Research*, *19*, 967–983. [PubMed]

Bell, A. H., Everling, S., & Munoz, D. P. (2000). Influence of stimulus eccentricity and direction on characteristics of pro- and antisaccades in non-human primates. *Journal of Neurophysiology*, *84*(5), 2595–2604. [Article]

Bisley, J. W., & Goldberg, M. (2010). Attention, intention, and priority in the parietal lobe. *Annual Reviews in Neuroscience*, *33*, 1–21. [PubMed]

Bisley, J. W., Ipata, A. E., Krishna, B. S., Gee, A. L., & Goldberg, M. E. (2009). The lateral intraparietal area: A priority map in posterior parietal cortex. In M. Jenkin & L. Harris (Eds.), *Cortical mechanisms of vision* (pp. 9–34). Cambridge: Cambridge University Press.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10*, 433–436. [PubMed]

Carrasco, M. (2006). Covert attention increases contrast sensitivity: Psychophysical, neurophysiological, and neuroimaging studies. In S. Martinez-Conde, S. L. Macknik, L. M. Martinez, J. M. Alonso, & P. U. Tse (Eds.), *Progress in brain research* (Vol. 154, pp. 33–70). Amsterdam: Elsevier.

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*, 1484–1525. [PubMed]

Carrasco, M., Ling, S., & Read, S. (2004). Attention alters appearance. *Nature Neuroscience*, *7*, 308–313. [Article]

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*, 201–215. [PubMed]

Cornelissen, F. W., Peters., E., & Palmer, J. (2002). The Eyelink Toolbox. *Behavior Research Methods, Instruments & Computers*, *34*, 613–617. [PubMed]

Crawford, T. J., Kean, M., Klein, R. M., & Hamm, J. P. (2006). The effects of illusory line motion on incongruent saccades: Implications for saccadic eye movements and visual attention. *Experimental Brain Research*, *173*, 498–506. [PubMed]

Deubel, H. (2008). The time course of presaccadic attention shifts. *Psychological Research*, *72*, 630–640. [PubMed]

Deubel, H. (2014). Attention in action. In A. C. Nobre & S. Kastner (Eds.), *The Oxford handbook of attention* (pp 865–889). Oxford: Oxford University Press.

Deubel, H., Irwin, D. E., & Schneider, W. X. (1999). The subjective direction of gaze shifts long before the saccade. In W. Becker, H. Deubel, & T. Mergner (Eds.), *Current oculomotor research: Physiological and psychological aspects* (pp. 65–70). New York: Plenum.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827–1837. [Article]

Everling, S., Dorris, M. C., Klein, R. M., & Munoz, D. P. (1999). Role of primate superior colliculus in preparation and execution of anti-saccades and pro-saccades. *Journal of Neuroscience*, *19*, 2740–2754. [Article]

Everling, S., Dorris, M. C., & Munoz, D. P. (1998). Reflex suppression in the anti-saccade task is dependent on prestimulus neural processes. *Journal of Neurophysiology*, *80*, 1584–1589. [Article]

Everling, S., & Munoz, D. P. (2000). Neuronal correlates for preparatory set associated with saccade generation in the frontal eye field. *Journal of Neuroscience*, *20*, 387–400. [Article]

Everling, S., Paré, M., Dorris, M. C., & Munoz, D. P. (1998). Comparison of the discharge characteristics of brain stem omnipause neurons and superior colliculus fixation neurons in monkey: Implications for control of fixation and saccade behavior. *Journal of Neurophysiology*, *79*, 511–528. [Article]

Fecteau, J. H., & Munoz, D. P. (2006). Salience, relevance, and firing: A priority map for target selection. *Trends in Cognitive Science*, *10*(8), 382–390. [PubMed]

Findlay, J. M., & Walker, R. (1999). A model of saccade generation based on parallel processing and competitive inhibition. *Behavioral and Brain Sciences*, *22*(4), 661–721. [PubMed]

Fischer, B., & Weber, H. (1996). Effects of procues on error rate and reaction time of antisaccades in human subjects. *Experimental Brain Research*, *109*, 507–512. [PubMed]

Fischer, B., & Weber, H. (1997). Effects of stimulus conditions on the performance of antisaccades in man. *Experimental Brain Research*, *116*(2), 191–200. [PubMed]

Forbes, K., & Klein, R. M. (1996). The magnitude of the fixation offset effect with endogenously and exogenously controlled saccades. *Journal of Cognitive Neuroscience*, *8*(4), 344–352. [PubMed]

Godijn, R., & Theeuwes, J. (2002). Programming of exogenous and endogenous saccades: Evidence for a competitive integration model. *Journal of Experimental Psychology: Human Perception and Performance*, *28*(5), 1039–1054. [PubMed]

Godijn, R., & Theeuwes, J. (2003a). Parallel allocation of attention prior to the execution of saccade sequences. *Journal of Experimental Psychology: Human Perception and Performance*, *29*, 882–896. [PubMed]

Godijn, R., & Theeuwes, J. (2003b). The relationship between exogenous and endogenous saccades and attention. In J. Hyönä, R. Radach, & H. Deubel (Eds), *The mind's eyes: Cognitive and applied aspects of eye movements* (pp. 3–26). Amsterdam: Elsevier.

Gottlieb, J., & Goldberg, M. E. (1999). Activity of neurons in the lateral intraparietal area of the monkey during an antisaccade task. *Nature Neuroscience*, *2*(10), 906–912. [PubMed]

Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: Wiley.

Hallett, P. E. (1978). Primary and secondary saccades to goals defined by instructions. *Vision Research*, *18*, 1279–1296. [PubMed]

Hallett, P. E., & Adams, B. D. (1980). The predictability of saccadic latency in a novel voluntary oculomotor task. *Vision Research*, *20*, 329–339. [PubMed]

Heath, M., Dunham, K., Binsted, G., & Godbolt, B. (2010). Antisaccades exhibit diminished online control relative to prosaccades. *Experimental Brain* Research, *203*(4), 743–752. [PubMed]

Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception and Psychophysics*, *57*(6), 787–795. [PubMed]

Hunt, A. R., von Mühlenen, A., & Kingstone, A. (2007). The time course of attentional and oculomotor capture reveals a common cause. *Journal of Experimental Psychology: Human Perception & Performance*, *33*, 271–284. [PubMed]

Ipata, A. E., Gee, A. L., Bisley, J. W., & Goldberg, M. E. (2009). Neurons in the lateral intraparietal area create a priority map by the combination of disparate signals. *Experimental Brain Research*, *192*, 479–488. [PubMed]

Irwin, D. E., Colcombe, A. M., Kramer, A. F., & Hahn, S. (2000). Attentional and oculomotor capture by onset, luminance, and color singletons. *Vision Research*, *40*, 1443–1458. [PubMed]

Jamadar, S. D., Fielding, J., & Egan, G. F. (2013). Quantitative meta-analysis of fMRI and PET studies reveals consistent activation in fronto-striatal-parietal regions and cerebellum during antisaccades and prosaccades. *Frontiers in Psychology*, *4*:749. [PubMed]

Jantz, J. J., Watanabe, M., Everling, S., & Munoz, D. P. (2013). Threshold mechanism for saccade initiation in frontal eye field and superior colliculus. *Journal of Neurophysiology*, *109*(11), 2767–2780. [Article]

Jefferies, L. N., Enns, J. T., & Di Lollo, V. (2014). The flexible focus: Whether spatial attention is unitary or divided depends on observer goals. *Journal of Experimental Psychology: Human Perception and Performance*, *40*, 465–470. [PubMed]

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. [PubMed]

Jonikaitis, D., & Theeuwes, J. (2013). Dissociating oculomotor contributions to spatial and feature-based selection. *Journal of Neurophysiology*, *110*(7), 1525–1534. [Article]

Khan, A. Z., Blangero, A., Rossetti, Y., Salemme, R., Luauté, J., Deubel, H., … Pisella, L. (2009). Parietal damage dissociates saccade planning from presaccadic perceptual facilitation. *Cerebral Cortex*, *19*, 383–387. [PubMed]

King-Smith, P. E., Grigsby, S. S., Vingrys, A. J., Benes, S. C., & Supowit, A. (1994). Efficient and unbiased modifications of the QUEST threshold method: Theory, simulations, experimental evaluation and practical implementation. *Vision Research*, *34*(7), 885–912. [PubMed]

Kleiner, M., Brainard, D., and 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. [PubMed]

Kristjánsson, Á., Chen, Y., & Nakayama, K. (2001). Less attention is more in the preparation of antisaccades, but not prosaccades. *Nature Neuroscience*, *4*(10), 1037–1042. [PubMed]

Kristjánsson, Á., Vandenbroucke, M. W., & Driver, J. (2004). When pros become cons for anti-versus prosaccades: Factors with opposite or common effects on different saccade types. *Experimental Brain Research*, *155*, 231–244. [PubMed]

Lauritzen, T. Z., D'Esposito, M., Heeger, D. J., & Silver, M. A. (2009). Top-down flow of visual spatial attention signals from parietal to occipital cortex. *Journal of Vision*, *9*(13):18, 1–14, doi:10.1167/9.13.18. [PubMed] [Article]

Machado, L., & Rafal, R. D. (2004). Control of fixation and saccades during an anti-saccade task: An investigation in humans with chronic lesions of oculomotor cortex. *Experimental Brain Research*, *156*, 55–63. [PubMed]

Massen, C. (2004). Parallel programming of exogenous and endogenous components in the antisaccade task. *The Quarterly Journal of Experimental Psychology, Section A: Human Experimental Psychology*, *57*(3), 475–498. [PubMed]

McPeek, R. M., Skavenski, A. A., & Nakayama, K. (2000). Concurrent processing of saccades in visual search. *Vision Research*, *40*, 2499–2516. [PubMed]

Meeter, M., Van der Stigchel, S., & Theeuwes, J. (2010). A competitive integration model of exogenous and endogenous eye movements. *Biological Cybernetics*, *102*(4), 271–291. [PubMed]

Mokler, A., Deubel, H., & Fischer, B. (2000, August). Unintended saccades can be executed without presaccadic attention shifts. Poster presented at the European Conference on Visual Perception (ECVP), Groningen, The Netherlands.

Mokler, A., & Fischer, B. (1999). The recognition and correction of involuntary prosaccades in an antisaccade task. *Experimental Brain Research*, *125*, 511–516. [PubMed]

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, doi:10.1167/7.14.8. [PubMed] [Article]

Morrison, R. E. (1984). Manipulation of stimulus onset delay in reading: Evidence for parallel programming of saccades. *Journal of Experimental Psychology: Human Perception and Performance*, *10*, 667–682. [PubMed]

Müller, H. J., & Rabbit, P. M. (1989). Reflexive and voluntary orienting of visual attention: Time course of activation and resistance to interruption. *Journal of Experimental Psychology: Human Perception and Performance*, *15*(2), 315–330.

Munoz, D. P., & Everling, S. (2004). Look away: The anti-saccade task and the voluntary control of eye movement. *Nature Reviews Neuroscience*, *5*(3), 218–228. [PubMed]

Nakayama, K., & Mackeben, M. (1989). Sustained and transient components of focal visual attention. *Vision Research*, *29*, 1631–1647. [PubMed]

Noorani, I., & Carpenter, R. H. (2013). Antisaccades as decisions: LATER model predicts latency distributions and error responses. *European Journal of Neuroscience*, *37*(2), 330–338. [PubMed]

Olk, B., & Kingstone, A. (2003). Why are antisaccades slower than prosaccades? A novel finding using a new paradigm. *NeuroReport*, *14*, 151–155. [PubMed]

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442. [PubMed]

Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, *25*, 31–40. [PubMed]

Rizzolatti, G., Riggio, L., & Sheliga, B. M. (1994). Space and selective attention. In C. Umiltà & M. Moscovitch (Eds.), *Attention and performance XV* (pp. 231–265). Cambridge, MA: MIT Press.

Rolfs, M., Jonikaitis, D., Deubel, H., & Cavanagh, P. (2011). Predictive remapping of attention across eye movements. *Nature Neuroscience*, *14*, 252–256. [PubMed]

Schluppeck, D., Glimcher, P., & Heeger, D. J. (2005). Topographic organization for delayed saccades in human posterior parietal cortex. *Journal of Neurophysiology*, *94*(2), 1372–1384. [PubMed]

Serences, J. T., & Yantis, S. (2006). Selective visual attention and perceptual coherence. *Trends in Cognitive Science*, *10*, 38–45. [PubMed]

Sereno, M. I., Pitzalis, S., & Martinez, A. (2001). Mapping of contralateral space in retinotopic coordinates by a parietal cortical area in humans. *Science*, *294*, 1350–1354. [PubMed]

Sergent, C., Wyart, V., Babo-Rebelo, M., Cohen, L., Naccache, L., & Tallon-Baudry, C. (2013). Cueing attention after the stimulus is gone can retrospectively trigger conscious perception. *Current Biology*, *23*(2), 150–155. [Article]

Silver, M. A., Ress, D., & Heeger, D. J. (2005). Topographic maps of visual spatial attention in human parietal cortex. *Journal of Neurophysiology*, *94*(2), 1358–1371. [Article]

Taylor, A. J. G., & Hutton, S. B. (2011). Error awareness and antisaccade performance. *Experimental Brain Research*, *213*, 27–34. [PubMed]

Theeuwes, J., Kramer, A. F., Hahn, S., & Irwin, D. E. (1998). Our eyes do not always go where we want them to go: Capture of the eyes by new objects. *Psychological Science*, *9*, 379–385.

Theeuwes, J., Kramer, A. F., Hahn, S., Irwin, D. E., & Zelinsky, G. J. (1999). Influence of attentional capture on oculomotor control. *Journal of Experimental Psychology: Human Perception & Performance*, *25*, 1595–1608. [PubMed]

Thibault, L., Cavanagh, P., & Sergent, C. (2015). Retroactive attention can trigger all-or-none conscious access to past sensory stimulus. *Journal of Vision*, *15*(12): 547, doi:10.1167/15.12.547. [Abstract]

Trappenberg, T. P., Dorris, M. D., Munoz, D. P., & Klein, R. M. (2001). A model of saccade initiation based on the competitive integration of exogenous and endogenous signals in the superior colliculus. *Journal of Cognitive Neuroscience*, *13*, 256–271. [PubMed]

Walker, R., & McSorley, E. (2006). The parallel programming of voluntary and reflexive saccades. *Vision Research*, *46*, 2082–2093. [PubMed]

Watson, A. B., & Pelli, D. G. (1983). QUEST: a Bayesian adaptive psychometric method. *Perception & Psychophysics*, *33*(2), 113–120.

Wilder, J. D., Kowler, E., Schnitzer, B. S., Gersch, T. M., & Dosher, B. A. (2009). Attention during active visual tasks: counting, pointing, or simply looking. *Vision Research*, *49*(9), 1017–1031. [PubMed]