

Spatial and temporal dynamics of presaccadic attentional facilitation before pro- and antisaccades

School of Optometry, University of Montreal,
Montreal, QC, Canada
ImpAct team,
Centre de Recherche en Neurosciences de Lyon (CRNL),
Bron, France

Laura Mikula

Marilyn Jacob

School of Optometry, University of Montreal,
Montreal, QC, Canada

Trang Tran

School of Optometry, University of Montreal,
Montreal, QC, Canada

Laure Pisella

ImpAct team,
Centre de Recherche en Neurosciences de Lyon (CRNL),
Bron, France



Aarlenne Z. Khan

School of Optometry, University of Montreal,
Montreal, QC, Canada



The premotor theory of attention and the visual attention model make different predictions about the temporal and spatial allocation of presaccadic attentional facilitation. The current experiment investigated the spatial and temporal dynamics of presaccadic attentional facilitation during pro- and antisaccade planning; we investigated whether attention shifts only to the saccade goal location or to the target location or elsewhere, and when. Participants performed a dual-task paradigm with blocks of either anti- or prosaccades and also discriminated symbols appearing at different locations before saccade onset (measure of attentional allocation). In prosaccades blocks, correct prosaccade discrimination was best at the target location, while during errors, discrimination was best at the location opposite to the target location. This pattern was inverted in antisaccades blocks, although discrimination remained high opposite to the target location. In addition, we took the benefit of a large range of saccadic landing positions and showed that performance across both types of saccades was best at the actual saccade goal location (where the eye will actually land) rather than at the instructed position. Finally, temporal analyses showed that discrimination remained highest at the saccade goal location, from long before to closer to saccade onset, increasing slightly for antisaccades closer to saccade onset. These findings are

in line with the premises of the premotor theory of attention, showing that attentional allocation is primarily linked both temporally and spatially to the saccade goal location.

Introduction

Saccades refer to rapid eye movements that bring the fovea to the object of interest, thus allowing for visual exploration. In response to a presented target, participants may want to look at the target (prosaccades) or to avoid looking at it and look in the opposite direction (antisaccades), to a location where there may or may not be a visual object. Also, in order to perform antisaccades, participants have to suppress the automatic saccade toward the target location and program a voluntary oculomotor response toward the mirror target location (saccade goal). It is assumed that this latter step is achieved by inverting the *visual* vector (i.e., the distance between the fixation point and the target location) rather than inverting the *motor* vector of the inhibited prosaccade (Collins, Vergilino-Perez, Delisle, & Doré-Mazars, 2008; Lévy-Bencheton, Pisella, Sale-

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mme, Tilikete, & Pélisson, 2013; Munoz & Everling, 2004).

Neuroimaging studies support the notion of overlapping neural networks for attention and eye movements (Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; Corbetta et al., 1998; Nobre, Gitelman, Dias, & Mesulam, 2000) and the idea of a functional link between attention and movements is well established in the literature (McFadden, Khan, & Wallman, 2002). Using dual-task paradigms in which participants perform prosaccades and discriminate symbols at the same time, several studies have confirmed the linkage between attention and saccades. These studies showed that visual perception is facilitated specifically at the future location of the upcoming saccade (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Doshier, & Blaser, 1995), with attention preceding saccade onset by approximately 50 ms (Deubel, 2008; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011; Rolfs & Carrasco, 2012). There are two main explanatory theories for this linkage. The premotor theory of attention posits a strong coupling between goal-directed actions and shifts of attention (Kustov & Robinson, 1996; Rizzolatti, Riggio, Dascola, & Umiltá, 1987; Rizzolatti, Riggio, & Sheliga, 1994; Sheliga, Riggio, & Rizzolatti, 1994) because attention allocation and saccade preparation rely on the same mechanisms of the eye movement system. According to the premotor theory, shifting attention to an object is equivalent to planning a saccade that is not executed. In other words, saccade preparation is responsible for the shift of attention to the location of the planned response. Importantly, this leads to the prediction that if the saccade planned is too long or too short, attention allocation should also show the same offset relative to the target. On the other hand, the visual system is anatomically divided in two streams: The ventral stream is associated with object recognition, whereas the dorsal stream is involved in sensorimotor transformations for visually guided actions toward this object (Goodale & Milner, 1992). The visual attention model assumes the existence of a common object selection mechanism for ventral and dorsal processing (Schneider, 1995) but the dorsal system processes its extrinsic spatial features and especially its location in eye-centered reference frame for saccade planning while the ventral system processes its intrinsic features for perceptual categorization processes. According to this single selection mechanism, attentional resources for perception and for action would be allocated to the same spatial location, but an error in saccade planning should not necessarily be reflected in attentional shifts because attention is directed to the intended rather than to the actual saccadic landing position (Deubel & Schneider, 1996; Schneider, 1995).

Only a fine spatial analysis would be able to distinguish between the predictions of these two theories of attention. Although saccades generally tend to be accurate, there still remains some natural variability in endpoints (Kowler & Blaser, 1995), which reflects errors in the visual-to-motor transformation. Thus, the location where the eyes land (the executed saccade) is sometimes different from the location that was initially targeted. This is especially true for antisaccades that are planned based on the same visual information as prosaccades, but they tend to be more variable (Amador, Schlag-Rey, & Schlag, 1998; Hallett, 1978). Antisaccades thus offer numerous opportunities to distinguish between the target location and the saccade goal location. The premotor theory of attention, postulating a common spatial selection within the eye movement system for both perception and action, would predict greatest attentional allocation to the actual landing position of pro- and antisaccades. The visual attention model, postulating a single object selection for perception and action before saccade planning, would predict that attentional allocation would not end at the actual saccadic landing location but rather at the intended object (target location or saccade goal). In this analysis, it is important to distinguish between selection errors (erroneous antisaccades produced during a prosaccade block or erroneous prosaccades produced during an antisaccade block) and saccadic planning errors due to spatial variability in sensorimotor transformation (resulting in saccade with smaller or larger amplitudes).

Separating the visual target location from the saccade goal of the motor plan is much more straightforward using saccadic adaptation protocols because adaptation results in a clear dissociation between the visual target location and the saccade goal motor plan. However, studies on saccadic adaptation have provided contradictory results (Collins & Doré-Mazars, 2006; Ditterich, Eggert, & Straube, 2000; Doré-Mazars & Collins, 2005; Khan, Heinen, & McPeck, 2010; Lévy-Bencheton et al., 2013; McFadden et al., 2002), which may be due to factors related to multiple possible levels of saccade adaptation (Pélisson, Alahyane, Panouillères, & Tilikete, 2010) rather than attentional-saccade linkage mechanisms. The dissociation between the target location and the saccade goal motor plan and the predictions of the two theories of attention are less straightforward for antisaccades because it is now acknowledged that during antisaccades tasks, there are in fact two motor plans in competition between each other—one is the motor plan to the target location (prosaccade) and the other is the plan to the location opposite to the target location (Massen, 2004; McPeck, Skavenski, & Nakayama, 2000). A successful antisaccade would therefore be one where the neuronal representation of the saccade goal

plan wins over the target location saccade plan. The premotor theory of attention would predict attention at both locations because there are motor plans for both locations, with a diminution of attention toward the target location closer to saccade onset, once the competition is over and the saccadic plan to the target location is aborted. This would be consistent with the finding that attention can be allocated in parallel to perceptually discriminate two visual objects (Awh & Pashler, 2000; Godijn & Theeuwes, 2003). Parallel attentional allocation to the target and the antisaccade goal has been shown in a recent study but in the absence of enhanced attention at the saccade goal, the authors rejected the premotor theory (Klapetek, Jonikaitis, & Deubel, 2016). According to the visual attention model, only information about one object at a time can be attended. However, in the case of antisaccades, the target and saccade goal locations are relevant for visual perception and motor action, respectively. In contrast with the premotor theory of attention, the visual attention model would thus predict inverse temporal patterns of attention allocation for both locations. More specifically, greater attention is expected at the target location long before saccade initiation; it will then decrease as antisaccade onset gets closer so that more attentional resources can be directed to the saccadic goal location.

To address these issues, we asked participants to perform a dual-task paradigm in which they were instructed to produce leftward or rightward saccades of the same amplitude (only two possible saccadic goals) in pro- or antisaccades blocked sessions. At the same time, they were asked to discriminate symbols that appeared momentarily before saccade onset at six possible locations with equal likelihood, including target location, the location opposite to target location (which corresponds to the saccade goal in antisaccade sessions), or four other control locations. In addition, we manipulated the timing of the discrimination symbol presentation relative to saccade onset. The accuracy of symbol discrimination at the different locations was contrasted between correct and erroneous trials. The task design allowed us to perform both a temporal and spatial analysis of attentional allocation for the correct trials, in order to test between the alternative predictions of the two theories. In terms of temporal dynamics, attention was mainly allocated to saccade goal location long before until shortly before saccade onset, for both pro- and antisaccades. For the spatial analysis, we found that attention was predominantly drawn to the actual landing position of the saccade when comparing performance between different saccade landing positions. These results are in favor of the premotor theory. These data have been previously published in abstract form (Mikula, Jacob, Pisella, & Khan, 2016).

Methods

Participants

Thirteen participants (five males, $M = 24.3$ years old, $SD = 5.3$ years) took part in this study. All had normal or corrected-to-normal vision. The experimental protocol was approved by the health research ethics committee at the University of Montreal (Comité d'Éthique de la Recherche En Santé), in agreement with the Declaration of Helsinki. Participants sat in a dimly illuminated room in front of a screen located at a distance of 57 cm from their eyes. Head movements were stabilized using a chin and forehead rest. Eye movements were recorded with an EyeLink 1000 Plus (SR Research, Mississauga, Ontario, Canada) and sampled at 1,000 Hz. The visual stimuli were presented on a black background using Experiment Builder (SR Research, Mississauga, Ontario, Canada) on an LCD screen (size: 10 × 17 in., resolution: 1,680 × 1,050 pixels, 60 Hz).

Task sequence

The sequence of a trial is depicted in Figure 1 and modified from previous experiments (Deubel & Schneider, 1996; Khan, Song, & McPeck, 2011). At the beginning of each trial, a central fixation dot (0.5° diameter) appeared for 1,000 ms. Next, six figure eights (height = 1.5°, width = 0.9°) appeared: three on each side of the fixation dot. The distance of the figure eights was 3°, 5.5°, and 8° away from fixation. The display remained on for 750 ms before two vertical lines appeared randomly at one of the two middle figure eights for 17 ms. The vertical lines served as a saccade target informing the participants where they had to move their eyes; they were asked to perform a saccade either toward the target location (prosaccade blocks) or in the opposite direction (antisaccade blocks). After the extinction of the two vertical lines, there was a variable delay between 17 and 133 ms (in 16.66-ms [one-frame] intervals). This variable delay (stimulus onset asynchrony [SOA]) allowed us to investigate the time course of attention allocation before saccades. As we presumed, antisaccades took significantly longer to initiate than prosaccades (304.3 vs. 267.6 ms; $t[12] = 6.5$, $p = 0.001$); we adjusted the range of SOAs, within the overall range outlined above, differently for the two types of saccades. This allowed us to obtain comparable timings for our analyses (i.e. the timing of the discrimination symbol onset relative to the saccade onset). After the SOA, one of the figure eights changed into one of the four discrimination symbols (P, d, 9, or 6) whereas the five

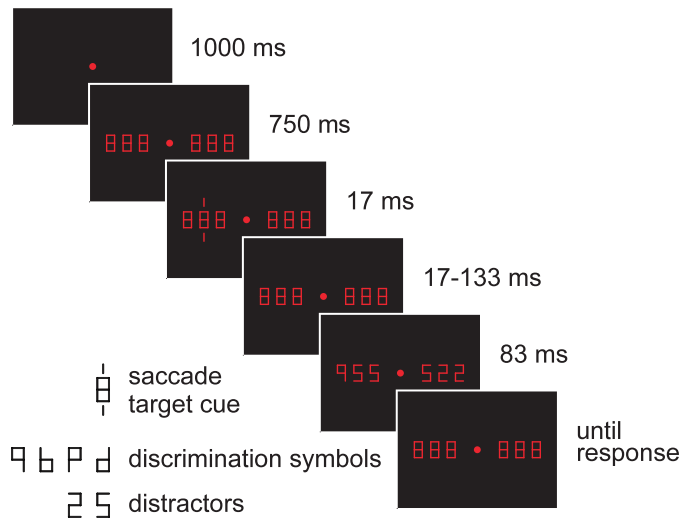


Figure 1. Trial sequence. Each trial began with a central fixation dot. After 1 s, six figure eights appeared for 750 ms and then the saccade target (figure eight with two vertical lines) flashed for 17 ms. When the target disappeared, the frame with the six figure eights was shown again for a duration of 17–133 ms (one to eight frames in one-frame intervals). Thereafter, one figure eight changed into one of the four possible discrimination symbols (P, d, 9, or 6) and the five remaining figure eights changed into distractors (2 and 5). After 83 ms, the discrimination symbol and the distractors became figure eights again until the participants indicated which discrimination symbol they saw after they had completed the saccade. Participants were asked to look either toward the location where the target appeared or in the opposite direction in prosaccade and antisaccade blocks, respectively.

remaining figure eights changed into distractors (2 and 5). The position of the discrimination symbol was unrelated to the target location (left or right) and it randomly appeared at each of the six locations 16.66% of the time. After 83 ms, the discrimination symbol and the distractors changed back to the figure eights until participants' response. At the end of each trial, the participants were asked to indicate which of the four discrimination symbols had been presented, using a four-button gamepad, regardless of where it had appeared.

Design

At the beginning of each block, the participants were informed about whether they were to perform prosaccades (eyes landing on the target location) or antisaccades (eyes landing on the position opposite to the target location). Pro- and antisaccade blocks were performed in a random order. Each block consisted of either 72 or 144 trials and the participants could take a break between the different blocks. Each participant

performed a total of 13 (144 trial blocks) to 43 (72 trial blocks) blocks over the course of several sessions spanning several weeks.

Data processing

We collected a total of 48,663 trials. The parameters of each saccade were calculated offline using custom-written MATLAB programs (MathWorks, Natick, MA). Saccade timing and position were automatically calculated offline using a saccade detection algorithm with a velocity criterion of 50°/s and verified visually. Trials during which the tracker lost eye position, participants made a saccade or a blink around the time of the target onset till the discrimination symbol offset or during which there was incorrect fixation at the central fixation spot at the beginning of each trial were removed from the dataset (6.6% of all trials). Next, start and end positions were shifted, so that within each block the mean horizontal and vertical position of the start positions was at 0. This was done to account for offsets in eye recording; the average absolute shifts were 2.1° horizontally and 0.55° vertical. Thereafter, outliers in the horizontal and vertical start positions were removed (more than 3 *SD* from the mean – 0.8%). Trials were also excluded from further analysis if the saccade amplitude was not between 2° and 9°, if its direction deviated more than 20° from horizontal, and if the saccade reaction time (SRT) was less than 100 ms and more than 1,000 ms (0.4% of all trials). Finally, trials in which saccade offset occurred before discrimination symbol offset were removed (0.5% of the trials). There remained 44,589 trials (91.6%).

The allocation of attention was measured by the performance in the discrimination task. Performance was expressed by the percentage of correct discrimination of the symbol, with chance level at 25% as there were four different discrimination symbols. The discrimination symbols could be presented at any of the six locations—that is, at the target location (corresponding to the saccade goal location for prosaccades) in one out of six of the trials, at the location opposite to target location (corresponding to the saccade goal location for antisaccades) in one of six of the trials, or at one of the four control locations (with equal probability) in two out of three of the trials. The condition in which the discrimination symbol appears at the location opposite to the target location is also relevant for prosaccades since it has been suggested that attentional allocation before a prosaccade differs between the saccade goal (or target location) and the location opposite to it (Klapetek et al., 2016). Because of this design, there were many

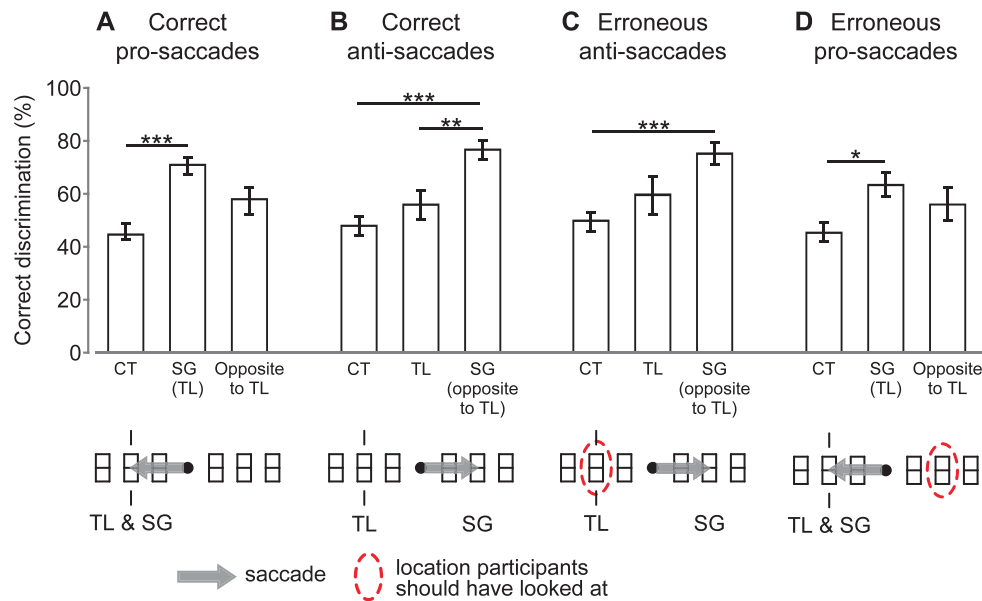


Figure 2. Overall performance for correct and erroneous prosaccade and antisaccades. The percentage of correct discrimination is plotted as a function of the three possible locations of the discrimination symbol (control location, target location, and the position opposite to the saccade target), for the four saccade types. Erroneous antisaccades refer to antisaccades made in the prosaccade blocks while erroneous prosaccades correspond to prosaccades made during antisaccade blocks. The error bars represent the standard error of the mean across participants. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. CT = control location; SG = saccade goal location; TL = saccade target location.

more trials in which the discrimination symbol appeared at a control location, compared to the target location or opposite to the target location condition. For the spatial analysis, we used the horizontal saccade landing position, specifically the x endpoint of the saccade (absolute, to account for saccades leftwards and rightwards). Finally, we separated saccades into correct and erroneous; specifically, we refer to errors during prosaccade trials, where participants made saccades to the location opposite to the target, as erroneous antisaccades. Along the same lines, errors made during antisaccade blocks are referred to as erroneous prosaccades (participants made an automatic prosaccade, but this was incorrect).

For all analyses, we performed linear mixed models using SPSS (IBM SPSS). Participants were set as subjects, for correlated random effects. All other factors were fixed, as outlined in the specific analyses below. We performed a factorial analysis on the fixed factor. Parameter estimation using the default restricted maximum likelihood method was used. Estimated marginal means were calculated for each factor and pairwise comparisons were performed between the estimates using Bonferroni criterion. In terms of covariance structures, we compared multiple structures and chose the one with the smallest Akaike's information criterion; this was either a scaled identity (uncorrelated), unstructured, or a first order factor analytic structure.

Results

Participants performed a total of 21,981 and 22,608 trials during prosaccade and antisaccade blocks, respectively. We defined correct prosaccades as saccades directed toward the target location and correct antisaccades as saccades in the direction opposite to the target location. Erroneous antisaccades were those that went in the direction opposite to the target location, whereas erroneous prosaccades were directed toward the target location. For prosaccade blocks, error rate was 6.4% (93.6% correct trials), while for antisaccade blocks, the error rate was significantly higher at 12.6% (87.4% correct trials, $t[12] = 2.7$, $p < 0.05$), consistent with previous studies using randomized blocked pro- and antisaccades (Ethridge, Brahmabhatt, Gao, McDowell, & Clementz., 2009; Zeligman & Zivotofsky, 2017).

Overall discrimination performance for correct and erroneous saccades trials

Figure 2 depicts the overall discrimination performance at the control location, the target location, and the location opposite to the target location, for correct and erroneous pro- and antisaccades. Note that the location opposite to the target location is the saccade

goal location for both correct and erroneous antisaccades, whereas the target location is the same as the saccade goal location for both correct and erroneous prosaccades (Figure 2, lower panel). Our main observation was that performance tended to be best at the saccade goal location across all types of saccades, consistent with the notion that attention is shifted to the saccade goal location, regardless of the context of the saccade. This was confirmed below.

For correct prosaccades (Figure 2A), a linear mixed-models analysis with discrimination symbol location as a fixed factor revealed a significant main effect, $F(2, 36) = 12.3$, $p < 0.001$. Performance was significantly better at the target location (estimated $M = 70.7\%$, $SE = 3.7\%$) than at the control location (estimated $M = 44.7\%$, $SE = 3.7\%$, $p < 0.001$). In addition, there was a trend toward significance compared to the position opposite to the target location (estimated $M = 57.7\%$, $SE = 3.7\%$, $p = 0.053$). Unexpectedly, there was also a trend toward differences between the position opposite to the target location and the control location ($p = 0.056$). We speculate that this might be due to the fact that the pro- and antisaccade blocks were randomized, resulting in the location opposite to the target location becoming relevant. This may also explain the increase in error rate in the prosaccade blocks compared to other studies (e.g., Peltsch, Hemraj, Garcia, & Munoz, 2011; Zeligman & Zivotofsky, 2017). Consistent with this speculation, we found that for participants who had performed the prosaccade block first, within that block, they showed high performance only at the target location (estimated $M = 62.1\%$, $SE = 5.46\%$) and low performance in the opposite location (estimated $M = 37.8\%$, $F[1, 8] = 9.9$, $p = 0.013$; one participant had performed pilot experiments). This was in contrast to the group that had performed the antisaccade block first, who showed equal performance at the target location (estimated $M = 62.3\%$, $SE = 7.2\%$) and the opposite location (estimated $M = 60.7\%$, $F[1, 12] = 0.24$, $p = 0.88$) during the prosaccade block.

For correct antisaccades (Figure 2B), we similarly found a significant main effect of discrimination symbol location, $F(2, 36) = 11.4$, $p < 0.001$; performance was better at the saccade goal location (i.e., the position opposite to the target location; estimated $M = 76.3\%$, $SE = 4.3\%$) compared to the control location (estimated $M = 47.9\%$, $SE = 4.3\%$, $p < 0.001$) and the target location (estimated $M = 55.8\%$, $p = 0.006$). There was no significant difference in performance between the control location and the target location ($p = 0.62$). Since the saccade goal location corresponds to the target location in correct prosaccades and to the position opposite to the target location in correct antisaccades, these results show that discrimination performance was the best when the discrimination

symbol was presented at the saccade goal location, for both correct pro- and antisaccades.

For erroneous saccades, we found a very similar pattern, with the performance once again at the actual saccade goal location, for both pro- and antisaccades. For erroneous antisaccades—that is, errors made during prosaccade blocks (Figure 2C)—there were some missing values due to low error rates. For example, two participants had error rates of only 0.85% (13 trials total) and 0.92% (20 trials total); thus we only included data values in the analysis when there were more than five trials per participant per discrimination symbol location (control = 13 participants, target location = eight participants, opposite location = 11 participants). A linear mixed-model analysis, with discrimination symbol location as a fixed factor, revealed a significant main effect, $F(2, 29) = 8.8$, $p = 0.001$. Pairwise comparisons revealed that discrimination performance was best opposite to the target location (estimated $M = 75.1\%$, $SE = 4.5\%$) and significantly better than at the control location (estimated $M = 49.4\%$, $SE = 4.2\%$, $p < 0.001$, Bonferroni corrected). There was no difference between the target location (estimated $M = 59.4\%$, $SE = 5.3\%$) and either the control ($p > 0.05$) or the opposite location ($p > 0.05$). In sum, the best discrimination performance was observed at the position opposite to the target location, which is the saccade goal location for erroneous antisaccades.

For erroneous prosaccades (Figure 2D), the linear mixed-model analysis also showed a significant effect of discrimination symbol location, $F(2, 36) = 3.4$, $p = 0.043$. Performance was significantly better at the target location (i.e., saccade goal location; estimated $M = 63.4\%$, $SE = 4.8\%$) than at the control location (estimated $M = 45.4\%$, $SE = 4.8\%$, $p < 0.05$). Performance at the position opposite to the target location was in between (estimated $M = 56\%$, $SE = 4.8\%$) and not different from either of the other two positions (both $ps > 0.05$). In sum, for erroneous prosaccades, performance was best at the target location (as for correct prosaccades) but also appeared to be enhanced at the location opposite to the target location, which corresponds to the saccade goal of correct antisaccades, though these differences did not reach significance.

Taken together, these results suggest that for correct pro- and antisaccades as well as erroneous pro- and antisaccades, discrimination was best when the discrimination symbol appeared at the saccade goal location. Considering erroneous saccades, performance also remained high at the location opposite to the saccade goal (the target location for erroneous antisaccades and the position opposite to the target location for erroneous prosaccades). Thus, it seems that attention was mostly allocated to the saccade goal

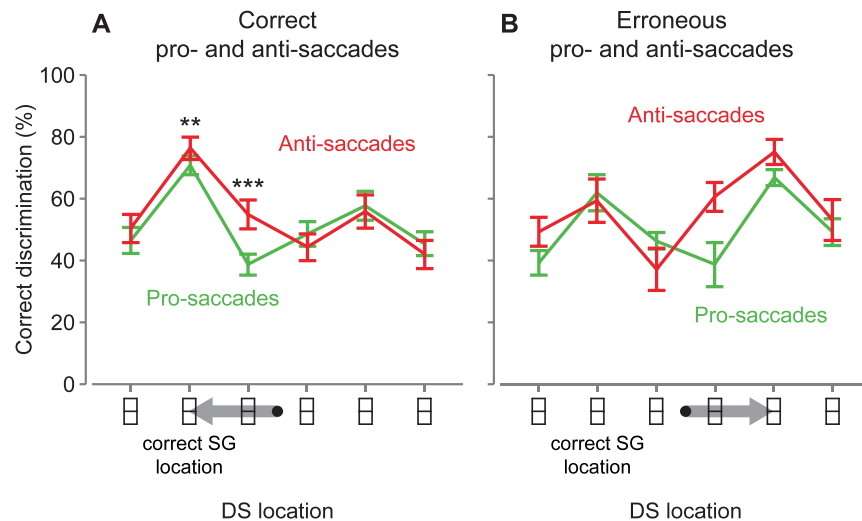


Figure 3. Discrimination performance as a function of discrimination symbol location. (A) Correct pro- and antisaccade trials. The correct discrimination performance (in %) is plotted as a function of the six possible discrimination symbol locations separately for prosaccades (green line) and antisaccades (red line). Saccades toward the left and right have been normalized so that the correct saccade goal location is toward the left (x -axis). For correct prosaccades, this is the target location, and for correct antisaccades, this is the position opposite to the saccade target. (B) Erroneous pro- and antisaccade trials. Erroneous prosaccades are shown in green and erroneous antisaccades are shown in red. The arrow shows that saccades went to the incorrect location (toward the right). For erroneous prosaccades, this is the target location. For erroneous antisaccades, this is the location opposite to the target location. Note that $N = 8$ for this figure. The error bars indicate the standard error of the mean across trials. $**p < 0.01$; $***p < 0.001$. SG = saccade goal location.

location, regardless of the type of saccade that was performed, but that some attention was still distributed to the other relevant location for the saccades tasks.

Discrimination performance over space

We investigated discrimination performance at each of the discrimination symbol locations relative to the saccade goal location for both correct and erroneous trials, to determine whether there were any differences in performance when comparing pro- and antisaccade trials at the different discrimination locations. This comparison was performed to determine whether the spread of attention across space was different for prosaccades compared to antisaccades, considering that during antisaccades there are two highly relevant locations. Figure 3A depicts performance for correct prosaccades (green line) and antisaccades (red line) as a function of discrimination symbol location. We normalized both saccade directions so that the correct or required saccade goal location is the second discrimination symbol location from the left as shown in the icon. For prosaccades, this is the target location, whereas for antisaccades, this is the location opposite to the target. As can be seen, performance was very similar across both types of saccades; performance was best at the saccade goal location and was lower everywhere else, with the exception of higher perfor-

mance at the opposite location. While performance was very consistent between the two types of saccade for discrimination symbol locations on the opposite side to the saccade goal, performance was notably different for the location closest to fixation on the same side as the saccade goal. Consistent with this, a linear mixed-model analysis with two fixed factors found no difference across saccade type ($p > 0.05$), but a significant discrimination symbol location effect, $F(5, 53.3) = 29.8$, $p < 0.001$, and a significant interaction effect, $F(5, 115.4) = 3.7$, $p = 0.004$. We compared whether there were significant differences between the two saccade types at each discrimination symbol location and found significantly better performance for antisaccade trials compared to prosaccade trials at both the saccade goal location (anti: estimated $M = 76.3\%$, pro: estimated $M = 70.7\%$, $F[1, 12] = 12.7$, $p = 0.004$, Bonferroni family-wise corrected) as well as the location between the saccade goal location and fixation (closer; anti: estimated $M = 55\%$, pro: estimated $M = 38.7\%$, $F[1, 12] = 21.6$, $p < 0.001$).

We performed the same analysis for the erroneous trials and found similar results (Figure 3B); performance was best at the saccade goal location but also high at the opposite location. For erroneous antisaccades, the eyes landed opposite to the target location. For erroneous prosaccades, the eyes landed at the visual target location rather than the correct saccade goal. For both, this position is the fifth discrimina-

symbol location from the left as shown by the arrow. A linear mixed-model analysis with saccade type and discrimination symbol location as factors revealed a main effect of discrimination location, $F(5, 144) = 6.4$, $p < 0.001$, but no differences between pro- and anti-saccade performance ($p > 0.05$) and no interaction effect ($p > 0.05$). As can be seen (Figure 3B), performance was best opposite to the correct saccade goal location, and was confirmed to be better than all other locations except the opposite location and the closer location ($p < 0.05$, Bonferroni corrected). In summary, we found that the performance was overall very similar for both pro- and antisaccade trials, with the best performance being at the location where the saccades landed, regardless of actual trial type or whether the saccade was erroneous or not, as well as higher performance at the other relevant location (opposite location). In addition, we observed a possible spread of attention during antisaccades (whether correct or erroneous) toward fixation.

The next analysis on saccade landing position was performed in order to determine whether attention was directed to the actual saccade landing position or elsewhere, for both pro- and antisaccades. We first wanted to confirm whether the location of the discrimination symbol had an influence on the saccade landing position at all, and indeed, we found a small significant effect. For this analysis, we used only correct saccades and only the discrimination symbol locations on the same side as the saccade. We found a significant effect of discrimination symbol location, $F(2, 12) = 6.9$, $p = 0.01$, of saccade type, $F(1, 12) = 9.6$, $p = 0.009$, and a significant interaction effect, $F(2, 12) = 7.1$, $p = 0.038$. Across both types of trials, saccades were smallest when the discrimination symbol was located closer to the fixation (pro: estimated $M = 5.18^\circ$, $SE = 0.05^\circ$, anti: estimated $M = 4.65^\circ$, $SE = 0.14^\circ$, $p < 0.05$), followed by the discrimination symbol at the saccade goal (pro: estimated $M = 5.26^\circ$, $SE = 0.05^\circ$, anti: estimated $M = 4.82^\circ$, $SE = 0.13^\circ$) and were biggest when the discrimination symbol was furthest away (pro: estimated $M = 5.36^\circ$, $SE = 0.08^\circ$, anti: estimated $M = 5.05^\circ$, $SE = 0.18^\circ$, $p < 0.05$, Bonferroni-corrected pairwise comparisons). Overall, however, this effect was very small (-0.08° and 0.1° for prosaccades and -0.17° and 0.23° for antisaccades for the closer and further discrimination symbols locations, respectively), and importantly landed at worst very close to the edge of the target location (5.5° eccentricity, with 0.9° diameter) and very far from the other two locations (3° and 8°). Thus, these differences in saccade landing positions cannot explain the previous results of performance differences across the different positions. However, the significantly different overall saccade landing positions for antisaccades (4.84°) compared to prosaccades (5.27°) might explain the better performance at the

closer discrimination location. This assumes that attentional allocation is related to saccade landing position, which was specifically tested in the next analysis below.

Interestingly, these results suggest that the discrimination symbol location influenced saccade planning at least to a slight degree. We presume that this would only be the case when the discrimination symbol was presented well before saccade onset and not just before—that is, early in saccade planning. Indeed, the position of the discrimination symbol might become relevant since its onset is likely to attract top-down attention. There would thus be a competition between the discrimination symbol location and the saccade goal location that biased saccade landing position (again to a very slight degree). Since top-down attention allocation takes time, we hypothesize that this competition would not be immediate. Therefore, if the discrimination symbol appears later in time, the competition would not reach the threshold required to induce a change in saccade landing position, analogous to countermanding saccade tasks (Hanes & Carpenter, 1999; Hanes & Schall, 1995). To investigate this, we binned trials into two groups, long before the saccade (-400 to -200 ms) and shortly before the saccade (-200 to 0 ms). As predicted, saccade landing positions were different when the discrimination symbol was presented long before but not shortly before the saccade. For prosaccades, there was a significant effect of time, $F(1, 12) = 35.6$, $p < 0.001$; of location, $F(1, 12) = 4.6$, $p = 0.032$; and a significant interaction effect, $F(2, 12) = 4.4$, $p = 0.038$. Separated by time, we found a significant effect of discrimination symbol location long before the saccade, $F(2, 12) = 4.7$, $p = 0.03$; pairwise comparisons showed differences across all three locations ($p < 0.05$, Bonferroni-corrected). There were no differences shortly before the saccade ($p > 0.05$). For antisaccades we found a significant effect of time, $F(1, 12) = 5.5$, $p = 0.037$; of location, $F(2, 12) = 9.2$, $p = 0.004$; and a significant interaction effect, $F(2, 12) = 6.3$, $p = 0.013$. Separated by time, we found a significant effect of location long before, $F(2, 12) = 9.4$, $p = 0.003$, showing differences across all three discrimination symbol locations ($p > 0.027$). There were no differences shortly before the saccade ($p > 0.05$). To summarize, the location at which the discrimination symbol was presented had a small biasing effect on saccade landing position for both pro- and antisaccades but only when it appeared long before saccade onset, showing a small influence of discrimination symbol location on saccade planning.

Next, we investigated how discrimination performance varied as a function of saccade landing position, in order to determine whether attention was allocated where the eye movement was planned or where the eyes actually landed, and whether this was different for pro-

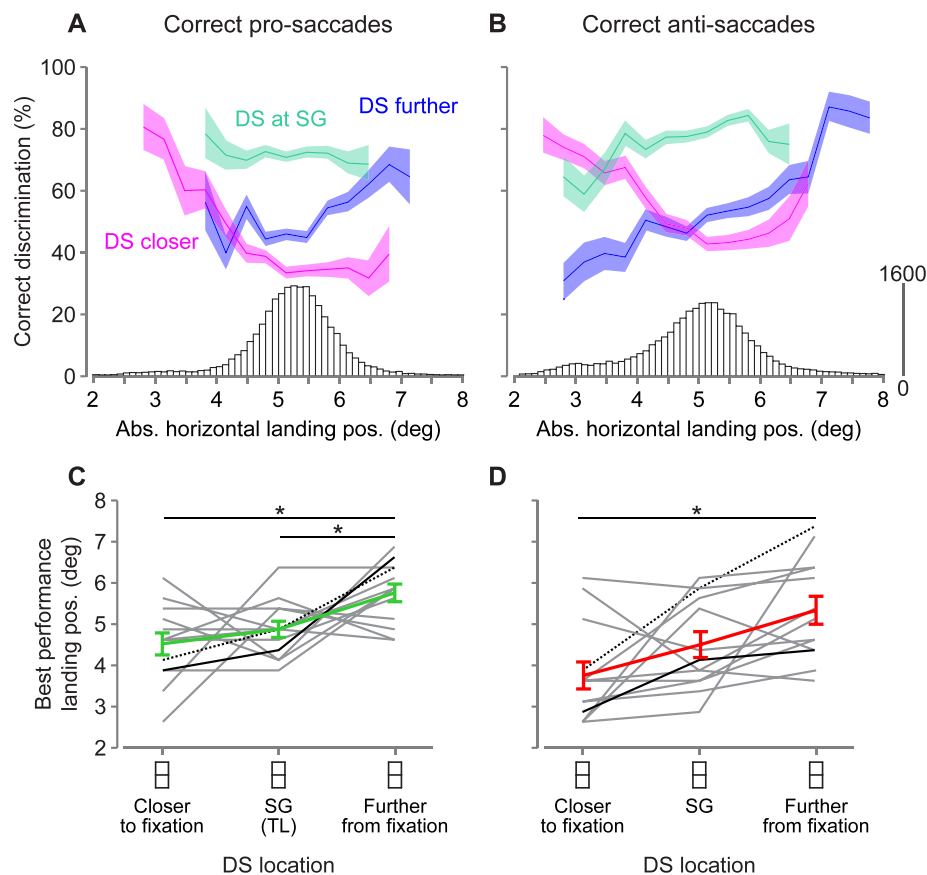


Figure 4. Discrimination performance over space for correct pro- and antisaccades. (A–B) Performance across all participants. Correct discrimination performance is plotted as a function of the absolute horizontal saccade landing position (in degrees) for the three discrimination symbol locations on the same side as the saccade goal location. The discrimination symbol could be located at the saccade goal location (green), closer to fixation (pink), or further from fixation (blue). For each discrimination symbol location, trials were sorted into 0.33° saccade landing position bins and means and standard errors were calculated. Only bins with more than 25 data points are shown. Histograms at the bottom of the plots represent the number of trials for each bin of horizontal saccade landing position. (C–D) Horizontal landing position of best performance. For each participant, performance was calculated for each 0.25° horizontal landing position bin, separately for each discrimination symbol location, then the horizontal saccadic landing position with the best performance was selected and plotted. Mean performance (with standard errors across participants) is plotted for prosaccades (green, [C]) and antisaccades (red, [D]). Individual performance is also shown as gray lines. * $p < 0.05$. DS = discrimination symbol; SG = saccade goal location; TL = saccade target location.

and antisaccades. We investigated specifically the three locations on the same side of the saccade (closer to fixation, at the saccade goal or further away) and the entire range of saccade landing positions from 2° to 8° (distributions of landing positions are shown in Figure 4A and B for pro- and antisaccades, respectively). Thus, the slight bias of discrimination symbol location on saccade landing position has been taken into account. In Figure 4A and B are plotted correct discrimination performance for each of the three locations as a function of saccade landing positions for correct saccades, separately for pro- and antisaccades. Saccade landing positions were pooled into 0.33° bins and means were calculated across all participants; only bins with more than 25 data points were used for the figures. As can be seen, for shorter saccades, perfor-

mance was high at the close location and performance at this location gradually decreased with increasing saccade landing positions. The opposite pattern was observed for the further location. This was the case for both pro- and antisaccades. For the saccade goal location, performance remained high across multiple saccade landing positions locations, though it did drop for smaller saccades in the antisaccade condition. Thus, it appears that discrimination performance is best at the position where the saccades actually land, suggesting that attention is driven to the saccade endpoint for both pro- and antisaccades, but also at the saccade goal location, as demonstrated by the high performance across a larger range of saccade landing positions when the discrimination symbol was presented at the saccade goal location (Figure 4A and B). In addition, the

improved discrimination performance for antisaccades at the closer location (Figure 3) can be simply explained by the greater variability in landing positions for antisaccades, with more saccades landing near the closer discrimination symbol location.

Because of the variability of saccade landing positions for different participants and across different saccade trial types, we were unable to perform a repeated-measures comparison of the above data due to missing values. Therefore, we performed a different analysis, in which, for each participant, saccade trial type, and discrimination symbol location, we extracted the landing position bin in which the participant had the best performance. For this analysis, we pooled landing position into 0.25° bins, allowing a reasonable number of trials within each bin for an appropriate discrimination performance calculation (i.e., five trials or more). For each bin, we calculated the mean performance. We then selected the landing position bin with the best performance within the set of landing position bins for each participant. This is shown in Figure 4C and D, separately for pro- and antisaccades, with both mean landing positions (thick lines with standard error bars) as well as the landing positions for individual participants (thin gray lines). As examples, two participants' data are highlighted (dotted black: Participant 8, solid black: Participant 9). For example, in prosaccades, both participants had the best performance when the discrimination symbol was presented at the closer location for saccade landing positions within 3.75° – 4.25° . Their saccade landing positions similarly increased for the best performance when the discrimination symbol was presented at the saccade goal location and again larger for the further location. The pattern was similar but more divergent for antisaccades.

We performed a linear mixed-model analysis on best performance landing position (bin center) with saccade type and discrimination symbol location as fixed factors, revealing a significant main effect of location, $F(2, 72) = 12.7, p < 0.001$, as well as saccade type, $F(1, 72) = 5.1, p = 0.027$, but no significant interaction effect ($p > 0.05$). We then performed mixed-model analyses with discrimination symbol location as a fixed factor separately for pro- and antisaccades, both of which were significant (pro: $F[2, 36] = 8.06, p = 0.001$; anti: $F[2, 36] = 5.8, p = 0.007$). Bonferroni-corrected pairwise comparisons on prosaccades revealed significant differences between the further discrimination symbol and the other two locations ($p < 0.05$), while the further and closer locations were significantly different for antisaccades ($p < 0.05$). In summary, the saccade landing position was linked to the location of best performance in discrimination for both pro- and antisaccades.

Taken together, these findings suggest that attention is allocated to the location closest to the saccade landing point, for both pro- and antisaccades.

Discrimination performance over time

Because of the variability of SRTs and the different timings of the onset of the discrimination symbol after target onset, we were able to explore dynamic attentional allocation before the execution of the saccade. For this analysis, we kept only correct saccades that landed less than 1° away from the saccade goal in either direction (87.6% of all prosaccades and 68.9% of all antisaccades), since performance also varied as a function of saccade landing position relative to the saccade goal location as shown above.

Figure 5A and B plots discrimination performance collapsed across all participants for trials where the discrimination symbol appeared either at a control location (gray), the saccade goal location (i.e., target location for prosaccades and opposite to the target for antisaccades; green), and the opposite or the target location (i.e., opposite to the target for prosaccades and at the target location for antisaccades; brown). Performance is plotted as a function of time (discrimination symbol onset relative to saccade onset). The data were pooled in 25-ms bins of time from -500 to -100 ms, the time between discrimination symbol onset and saccade onset. Only bins with at least 25 data points are shown. The figures show that discrimination performance is best at the saccade goal location, followed by the opposite location/saccade target location and lowest at the control locations. There also appears to be a slight decrease in performance overall the closer one gets to saccade onset. We quantify these observations below.

Because different participants had different SRTs (and therefore, different discrimination symbol onset to saccade onset times), we could not perform a simple binning as there was insufficient data from all participants in all bins, particularly for bins long before and shortly before the saccade. We therefore split each participant's times (separately for each saccade type and discrimination symbol location) into five quantiles and calculated the mean performance within each quantile (0%–100% in 20% quantiles). Figure 5C (correct prosaccades) and 5D (correct antisaccades) plot the mean discrimination performance for each quantile for each discrimination symbol location as a function of the mean times for each quantile across participants (first, third, and fifth mean quantile is shown in the x -axis). Participants' mean performance and mean quantile time is also shown as colored squares.

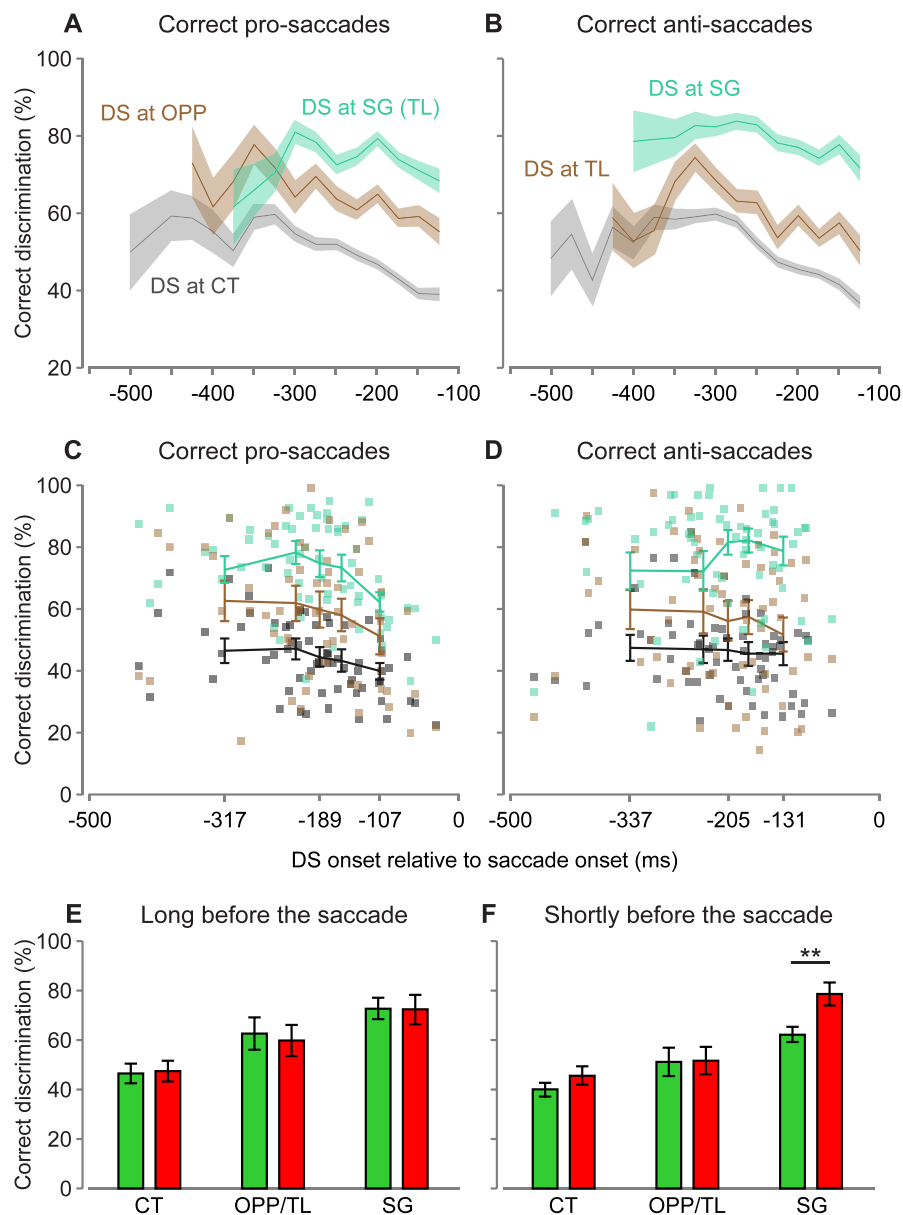


Figure 5. Discrimination performance over time for correct pro- and antisaccades. (A–B) Performance across all participants. Correct discrimination performance is plotted as a function of time (discrimination symbol onset relative to saccade onset) for the three possible discrimination symbol locations. The discrimination symbol was located at the saccade goal (green), at or opposite to target location (brown), or at a control location (gray). Data were pooled into 25-ms bins of time from -500 to -100 ms, the time between DS onset and saccade onset, and means and standard errors at each bin were calculated. Only bins with at least 25 data points are shown. For prosaccades (A), the saccade goal is the target location. For antisaccades (B), the saccade goal corresponds to the location opposite to the saccade target. (C–D) Performance sorted into time quantiles. For each participant, time was sorted into five quantiles (0% to 100% in 20% quantiles), then discrimination performance was calculated for each discrimination symbol location at each quantile. Mean discrimination performance (with standard errors across participants) is plotted against mean quantile time for each discrimination symbol location. In addition, individual performance as individual mean quantile times are also plotted as squares, to provide an estimate of the ranges of timings across participants. The first, third, and fifth mean quantile times are shown in the x-axis. (E–F) Performance comparing pro- and antisaccades across time. Mean discrimination performance is shown for pro- (green) and anti- (red) saccades for the first quantile (long before the saccade [E]) and for the fifth quantile (shortly before the saccade [F]) separately for each discrimination symbol location. $**p < 0.01$. CT = control location; DS = discrimination symbol; OPP = location opposite to saccade target; SG = saccade goal location; TL = saccade target location.

We compared performance long before the saccade (first quantile) versus shortly before the saccade (fifth quantile) with a linear mixed-model analysis, with three fixed factors: saccade type, time (long vs. shortly before), and discrimination symbol location. We found a significant main effect of saccade type, $F(1, 12.8) = 7.9, p = 0.015$; of discrimination symbol location, $F(2, 64.8) = 20.2, p < 0.001$; and of time, $F(1, 91.5) = 4, p = 0.048$. There was also a significant interaction effect between time and saccade type, $F(1, 20.9) = 10.4, p = 0.004$, and between saccade type and discrimination symbol location, $F(2, 38) = 12.7, p < 0.001$. These results confirm the best performance was observed when the discrimination symbol was located at the saccade goal location, followed by the opposite or target location, and finally the control location, and that this pattern remained similar long before and shortly before the saccade for both prosaccades and antisaccades. To investigate the significant interaction between time and saccade type, we ran separate linear mixed-model analyses for pro- and antisaccades with time as the fixed factor. We observed that overall performance decreased significantly for prosaccades, $F(1, 2.7) = 467.8, p < 0.001$, but not for antisaccades ($p = 0.47$), as can be seen in the figures.

Based on the significant interaction effect between saccade type and time and between discrimination symbol and time, we compared performance between the two saccade types for each discrimination symbol location separately long before the saccade (Figure 5E) and shortly before the saccade (Figure 5F). Only the significant difference between pro- and antisaccade discrimination performance at the saccade goal location shortly before the saccade survived the family-wise correction, $F(1, 12) = 18.9, p = 0.001$, reflecting enhanced attentional allocation at the saccade goal just before the eye movement for antisaccade trials.

In summary, we observed both similar and different dynamics in attentional allocation for the pro- and antisaccade trials over time. For both types of saccade, discrimination performance was similar with most attention allocated to the saccade goal location even long before the saccade. However, performance decreased for all discrimination symbol locations shortly before the saccade for prosaccades, which was not the case for antisaccades. For prosaccades the relative attentional allocation remained steady over time, while for antisaccades, attentional allocation tended to be shifted more toward the saccade goal location the closer in time to saccade onset.

Discussion

The aim of this study was to further investigate the link between attention and saccades and to test

different predictions in the context of the premotor theory versus the visual attention model. To these aims, we performed both temporal and spatial analyses of the deployment of attention during the latency of pro- and antisaccades cued by the flash of a peripheral placeholder in the left or the right visual field. Pro- and antisaccade blocks were performed in random order in a within-subjects design and differed by the instruction given to the subject at the start to direct their saccade to the target location or to the opposite location. Each block consisted of a dual-task paradigm requiring participants not only to perform leftward or rightward saccades (toward the central placeholder location in either visual field) but also to discriminate symbols that briefly appeared at one of the six placeholder locations at different time points before saccade onset. Discrimination performance was used as a behavioral measure of attention allocation and was measured for different timings and for the six potential locations where the discrimination symbol appeared, including the target location, the location opposite to the target, and four control target locations. In accordance with the premotor theory, we found that attention was preferentially allocated to the saccade goal—that is, the location where the saccade actually landed, regardless of correct or erroneous trials and also when saccades were inaccurate. Moreover, we found that attentional allocation was allocated to the saccade goal location over time, more so closer to the saccade goal during antisaccade trials.

We first compared attention allocation between correct versus erroneous trials, with correct saccades defined as those that were directed according to the instruction toward the target location in prosaccade blocks and toward the location opposite to the target in antisaccade blocks. We found that attention was generally the highest at the saccade goal, which is presumably the location that won the motor competition between the leftward and the rightward saccadic plans, but this was not the entire story. In correct prosaccades, discrimination performance at the location opposite to the target was intermediate—that is, statistically different from both that at saccade goal and that at the control location. Similar intermediate discrimination performance was observed at the target location in correct antisaccades, even though the comparison between the control and the target location did not reach significance. These three levels of performance were also observed during erroneous trials, as if the wrong location was suppressed. Indeed, the temporal analysis suggests that at an early stage in processing, both the target location and the location opposite to target location are selected (two levels of performance) and then later on, all locations distinct from the saccade goal are inhibited leading to the observed three levels of performance. In antisaccades,

attention at the saccade goal (opposite to target location) is further enhanced and attention at target location is more actively suppressed (than at the control location) the closest in time relative to saccade onset. This significant decrease in discrimination performance at nonsaccade locations has been shown in previous studies and is thought to be reflective of a suppression of distractor locations related to saccade execution (Harrison, Mattingley, & Remington, 2013; Khan, Blohm, Pisella, & Munoz, 2015; Rolfs et al., 2011). Together with attentional facilitation at the saccade goal, suppression at other locations allows enhanced visual discrimination as well as improved saccade accuracy at the goal of the intended saccade.

In contrast to previous studies (Deubel, 2008; Deubel & Schneider, 1996; Doré-Mazars, Pouget, & Beauvillain, 2004; Rolfs et al., 2011; Rolfs & Carrasco, 2012), we did not observe attentional enhancement at the saccade goal around 50–100 ms before saccade onset. This may be due to task difficulty. For example, some studies have utilized discrimination tasks in which participants reported the orientation of Gabor patches while performing saccades, usually with two alternatives (Castet et al., 2006; Klapetek et al., 2016; Montagnini & Castet, 2007; Rolfs et al., 2011; Rolfs & Carrasco, 2012), that may be easier and faster, or at least different from symbol discrimination. Further, while other studies have used symbols (on which the current study was based), only two different symbols were presented (Deubel, 2008; Deubel & Schneider, 1996). In contrast, our participants were asked to discriminate between four possible symbols. Therefore, the overall increased difficulty of our task might have led to different temporal dynamics of presaccadic attentional shifts compared to anterior studies. Indeed, the current results are consistent with a previous study in which the same discrimination symbols were used (Khan et al., 2015). Future investigations comparing task difficulty and context are necessary to determine the underlying processes leading to these observed findings.

To investigate whether attention was driven where the eyes are aiming for or where they are actually landing, we conducted a spatial analysis. Our results provide evidence for the latter hypothesis. In accordance with the predictions of the premotor theory, we found that attention was predominantly allocated to the actual landing position of the saccade. For pro- and antisaccades, the discrimination symbol location with the best performance depended on the landing position of the saccade. Attention allocation at the actual eye position is also suggested by relatively high discrimination performance at the saccade goal location following erroneous pro- and antisaccades. During erroneous saccades, participants appeared to redirect their attentional resources from where they should have

looked to where they ended up looking (Figures 2 and 3). These findings are in line with a previous study showing that the best perceptual discrimination performance was found at the actual saccade endpoint (Doré-Mazars et al., 2004). In their study, they did not provide any explicit instruction with respect to the required saccade landing position, in a word reading task. Similar to our results, they found that discrimination was best at the actual saccade landing position. This strong coupling between saccade programming and the orienting of attention may be a consequence of the ability of some areas of the saccadic system, specifically the frontal eye fields, to orient attention when they are activated (Moore & Fallah, 2001, 2004).

Overall, we found that even though saccades were performed correctly and relatively accurately toward the expected direction, attention was automatically drawn toward the two central placeholders where the saccades could be directed. Attention was thus deployed early and preferentially to both the target location and the location opposite to target location, for both pro- and antisaccades, similar to what was recently reported for antisaccades (Klapetek et al., 2016). Accordingly, it has been shown that attention can be divided when it is beneficial for the task (Awh & Pashler, 2000; Godijn & Theeuwes, 2003). Thus, our findings could be interpreted as a strategic deployment of attention toward the two most important locations of the pro- and antisaccades tasks. Indeed, even though the discrimination symbol could equally appear at six possible locations, only the target location and the location opposite to target location could be both saccadic goals and placeholders for the discrimination symbol. According to the premotor theory, we can speculate that this early attentional allocation both at target location and at the opposite location may be reflective of two parallel underlying saccadic plans. This suggests that the motor plan for the saccade goal location was established very early, even for antisaccades, probably due to the task requirements. Because only two saccade directions were possible in our paradigm, it is possible that both saccade directions were preplanned due to anticipatory strategies from the participants. However, in contrast to attention, which can be maintained covertly at two locations, only one saccade plan must be selected for motor execution. The observation of a progressive enhancement of attentional allocation at the saccade goal location for antisaccades, where there is presumably more competition (Figure 5), is in favor of the premotor theory.

While we found higher discrimination performance at the saccade goal location for correct antisaccades, Klapetek et al. (2016) found similar performances between the saccade goal location and the target location. It is likely that this discrepancy is due to the saccade target presentation in the two studies. In our

study, we used a cue that flashed before the discrimination symbol appeared, whereas Klapetek et al. (2016) presented a cue that appeared before the discrimination symbol onset and remained even after it had disappeared. This could have maintained attention at the target location. This could also explain why performances are consistently higher at the target location in their study compared to ours. In the present paradigm, two vertical lines that appeared for 17 ms served as a saccade cue to instruct participants where to make pro- and antisaccades. Due to its abrupt onset, our cue elicited and captured exogenous attention (Theeuwes, 1991). Exogenous orienting refers to the automatic shorter lasting shift of attention induced by the intrinsic salience of a peripheral stimulus. One could argue that our results would have been different if we had used endogenous cueing by presenting a central arrow with different colors for pro- and antisaccades instead of a peripheral stimulus. This remains to be investigated.

Conclusions

Our results show that overall attentional allocation (reflected by discrimination performance) during both pro- and antisaccades was best at the saccade goal location. This was reflected in both correct and erroneous trials for both saccade types. Performance was also best when the discrimination symbol was presented at the actual saccade landing position, rather than the instructed position. Attentional allocation toward the saccade goal position was highest both because it was selected (together with the opposite location) and because all other locations were progressively inhibited as saccade execution became imminent. These findings are consistent with the premises of the premotor theory of attention with respect to the relationship between attentional allocation and saccade planning.

Keywords: discrimination, spatial attention, saccade reaction times

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Corresponding author: Aarlenne Zein Khan.

E-mail: aarlenne.khan@umontreal.ca.

Address: School of Optometry, University of Montreal, Montreal, QC, Canada.

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