Visual attention and eye movement control during oculomotor competition

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Saccadic eye movements are typically preceded by selective shifts of visual attention. Recent evidence, however, suggests that oculomotor selection can occur in the absence of attentional selection when saccades erroneously land in between nearby competing objects (saccade averaging). This study combined a saccade task with a visual discrimination task to investigate saccade target selection during episodes of competition between a saccade target and a nearby distractor. We manipulated the spatial predictability of target and distractor locations and asked participants to execute saccades upon variably delayed go-signals. This allowed us to systematically investigate the capacity to exert top-down eye movement control (as reflected in saccade endpoints) based on the spatiotemporal dynamics of visual attention during movement preparation (measured as visual sensitivity). Our data demonstrate that the predictability of target and distractor locations, despite not affecting the deployment of visual attention prior to movement preparation, largely improved the accuracy of short-latency saccades. Under spatial uncertainty, a short go-signal delay likewise enhanced saccade accuracy substantially, which was associated with a more selective deployment of attentional resources to the saccade target. Moreover, we observed a systematic relationship between the deployment of visual attention and saccade accuracy, with visual discrimination performance being significantly enhanced at the saccade target relative to the distractor only before the execution of saccades accurately landing at the saccade target. Our results provide novel insights linking top-down eye movement control to the operation of selective visual attention during movement preparation.

Introduction

Saccadic eye movements play a pivotal role in visual perception. They successively shift our fovea toward objects of interest, allowing us to process their details at high resolution during intermittent fixations. Importantly, to account for the multitude of objects typically competing for in-depth processing within our crowded visual environment, efficient eye movement control is contingent upon top-down selection via attentional mechanisms. Whereas bottom-up (stimulus-driven) processes contribute to visual selection via extraction of the most salient aspects in the visual field, top-down (goal-driven) mechanisms bias selection as a function of the observer's current goals (e.g. Wolfe, 1994; Itti & Koch, 2001). It is generally believed that bottom-up visual selection occurs fast and transiently, whereas top-down control emerges only slower and operates in a more sustained fashion (e.g. Nakayama & Mackeben, 1989; Carrasco, 2011). Crucially, a substantial body of empirical evidence argues for an intriguing coupling between

the mechanisms underlying selective visual attention and the control of saccadic eye movements. For instance, both mechanisms have been found to recruit largely overlapping neuronal circuitries (e.g. Corbetta, 1998). Furthermore, selective perceptual benefits can be evoked via subthreshold microstimulation within oculomotor key structures, such as the frontal eye fields (FEF; Moore & Fallah, 2004) and the superior colliculus (SC; Müller, Philiastides, & Newsome, 2005) of the monkey. In humans, psychophysical dual-task paradigms consistently showed that visual processing is selectively enhanced at the target of an impending saccade during oculomotor preparation (Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Deubel & Schneider, 1996). Some authors even conceptualized visual attention as an obligatory consequence of motor programming (see *Premotor Theory of Attention: Rizzolatti, Riggio, Dascola, & Umiltá, 1987; Rizzolatti, Riggio, & Sheliga, 1994*), or in terms of a common selection mechanism for perceptual processing and motor programming (Schneider, 1995; Deubel & Schneider 1996).

Despite the ability to accurately move our eyes in a voluntary fashion, the oculomotor system is susceptible to systematic inaccuracies when multiple nearby objects compete for selection. Under these circumstances, saccades frequently land at an intermediate location between the competing objects (Coren & Hoenig, 1972; Findlay, 1982; Ottes, Van Gisbergen, & Eggermont, 1984; Van der Stigchel & Nijboer, 2014). This phenomenon – commonly referred to as the global effect or saccade averaging – has been linked to competition in a retinotopically organized saccade map characterized by excitatory connections among proximal neuronal populations (Van Opstal & Van Gisbergen, 1989; Kopecz & Schöner, 1995; Trappenberg, Dorris, Munoz, & Klein, 2001; Godijn & Theeuwes, 2002). It has been proposed that the SC constitutes a likely substrate for the implementation of such a saccade map, representing movement vectors based on the population activity of neurons with large and coarsely tuned movement fields (Schiller & Stryker, 1972; Wurtz & Goldberg, 1972). Indeed, simultaneous microstimulation at two spatially separate sites in the primate SC was shown to elicit averaging saccades landing in between the locations corresponding to each stimulation site (Robinson, 1972; Schiller & Sandell, 1983). However, whether naturally occurring averaging saccades are represented as two separate loci of collicular activity residing at the sites of the competing stimuli (Edelman & Keller, 1998), or a single activity peak located in between the competing stimuli (Glimcher & Sparks, 1993), has not yet been consistently resolved. Due to the observation that saccade averaging is most pronounced at short saccade latencies (Findlay, 1982; Ottes, Van Gisbergen, & Eggermont, 1985; Coëffé & O'Regan, 1987; Edelman

& Keller, 1998; Chou, Sommer, & Schiller, 1999), the global effect has originally been interpreted as an automatic oculomotor response originating from bottom-up processing of visual information (Findlay, 1982). More recent accounts, however, hold that the activity profile of the saccade map implements target selection via the integration of bottom-up and top-down signals (Findlay & Walker, 1999; Trappenberg et al., 2001; Meeter, Van der Stigchel, & Theeuwes, 2010), suggesting that higher level information can effectively bias low-level visual competition. In line with this idea, it was shown that the occurrence of averaging saccades can be reduced by increasing target predictability (Coëffé & O'Regan, 1987; He & Kowler, 1989; Aitsebaomo & Bedell, 2000). More recently, the perceptual correlates of saccade averaging were investigated in dual-task paradigms inducing oculomotor competition between nearby objects (Van der Stigchel & de Vries, 2015; Wollenberg, Deubel, & Szinte, 2018; Wollenberg, Deubel, & Szinte, 2019). In our recent work (Wollenberg et al., 2018), we asked participants to move their eyes toward one of two nearby saccade targets at free choice and assessed visuospatial orientation sensitivity during movement preparation. We observed a selective enhancement of visual orientation sensitivity at the endpoint of saccades accurately landing at a saccade target, but – consistent with the results of Van der Stigchel and de Vries (2015) – not at the endpoint of averaging saccades. Instead, visual orientation sensitivity was equally enhanced at the two competing saccade targets prior to the execution of averaging saccades, suggesting that oculomotor competition was not readily resolved at the perceptual level before movement onset. These results emphasize the role of top-down attentional mechanism in resolving bottom-up visual competition for efficient oculomotor control.

The time course of top-down control on saccade averaging was recently investigated in a fixation gap paradigm (Heeman, Theeuwes, & Van der Stigchel, 2014). Without an instruction about the identity of the saccade target, saccades consistently landed in between the saccade target and a nearby distractor. However, when participants received an explicit task instruction specifying the identity of the saccade target, the saccade endpoint deviations linearly decreased with increasing saccade latency. This top-down modulation already emerged at the shortest saccade latencies observed, suggesting an early involvement of top-down mechanisms for the control of saccadic eye movements (see also: Aagten-Murphy & Bays, 2017). Likewise, the proportion of saccades directed to the saccade target rather than to a simultaneously presented distractor was found to increase as a function of saccade latency in visual search tasks (van Zoest, Donk, & Theeuwes, 2004; van Zoest & Donk, 2005). The authors therefore concluded that bottom-up and

top-down control operate at different temporal scales: whereas saccade target selection is susceptible to visual saliency early on during saccade preparation, the influence of stimulus-related top-down control emerges only later. In summary, previous literature suggests that top-down mechanisms play a major role for efficient oculomotor control. Yet, despite the well-documented spatiotemporal coupling between saccade programming and visual attention (Hoffman & Subramaniam, 1995; Kowler et al., 1995; Deubel & Schneider, 1996), the perceptual correlates of top-down eye movement control during oculomotor competition have not yet been systematically investigated.

Here, we asked participants to move their eyes to a saccade target in the presence of a nearby distractor (saccade task), and to report the orientation of a discrimination target presented at different locations and time points during movement preparation (visual discrimination task). Importantly, we systematically manipulated (1) the predictability of the saccade target and the distractor location (via different pre-block instructions) as well as (2) visual processing time prior to saccade onset (via variable saccadic go-signal delays). Consequently, the analysis of presaccadic visual discrimination performance and saccade endpoints allowed us to concurrently evaluate the influence of varying top-down control on saccade target selection at the perceptual and oculomotor level. To our knowledge, this is the first study to directly assess how the spatiotemporal dynamics of visual attention, which affect visual perception during movement preparation, relate to top-down eye movement control.

We reasoned that saccade target selection would be initially challenged by bottom-up competition between the saccade target and the distractor (induced via salient visual onsets at the respective locations). Increasing spatial predictability and visual processing time prior to movement onset should, however, enhance the emergence of top-down control mechanisms (van Zoest et al., 2004; van Zoest & Donk, 2005; Heeman et al., 2014; Aagten-Murphy & Bays, 2017), thereby counteracting bottom-up competition and facilitating efficient saccade target selection.

More specifically, we assumed that rendering the saccade target or distractor location predictable would particularly facilitate top-down control when visual processing time is limited before movement onset, leading to an improvement in the accuracy of short-latency saccades. Furthermore, a prolongation of visual processing time should more generally improve top-down control, leading to enhanced saccade accuracy at longer movement latencies. Importantly, based on the tight spatiotemporal coupling between visual attention and oculomotor programming (Hoffman & Subramaniam, 1995; Kowler et al., 1995; Deubel & Schneider, 1996), we assumed that the anticipated top-down improvements in saccade

accuracy would be reflected at the perceptual level during movement preparation. In particular, based on recent evidence demonstrating that attentional resources are split between two proximal stimuli before the execution of averaging saccades (Van der Stigchel & de Vries 2015: page 11, lines 9–14; Wollenberg et al., 2018: page 10, lines 10–13), we hypothesized that the expected improvements in saccade accuracy should be associated with a reduction of presaccadic attentional competition between the saccade target and the distractor. This reduction of attentional competition should affect visual discrimination capabilities during movement preparation and lead to selectively enhanced visual discrimination performance at the saccade target relative to the distractor.

Materials and methods

Ethics statement

This experiment was conducted in accordance with the Declaration of Helsinki and approved by the Ethics Committee of the Faculty for Psychology and Pedagogics of the Ludwig-Maximilians-Universität München (approval number 13_b_2015). All participants gave written informed consent before participation.

Participants

Based on the sample size range of previous studies on presaccadic visual attention (e.g. Deubel & Schneider, 1996; White, Rolfs, & Carrasco, 2013; Wollenberg et al., 2018; Hanning, Szinte, & Deubel, 2019), 9 healthy participants (aged 24–31 years, 5 women, 8 right-eye dominant, and 1 author) with normal or corrected to normal vision completed the experiment over the course of 2 sessions (approximately 150 minutes each, including intermittent breaks) on different days in exchange for 50 €. All participants, except for one author (L.W.), were unaware of the study objectives.

Setup

The experiment was conducted in a dimly illuminated room. Participants were seated at a viewing distance of 60 cm in front of a 19-inch Silicon Graphics CRT screen (resolution: 800 × 600 pixels; vertical refresh rate: 120 Hz), with their head stabilized by a chin and forehead rest. Stimulus presentation and the collection of manual responses and eye data were implemented in Matlab (The MathWorks, Natick, MA) via the
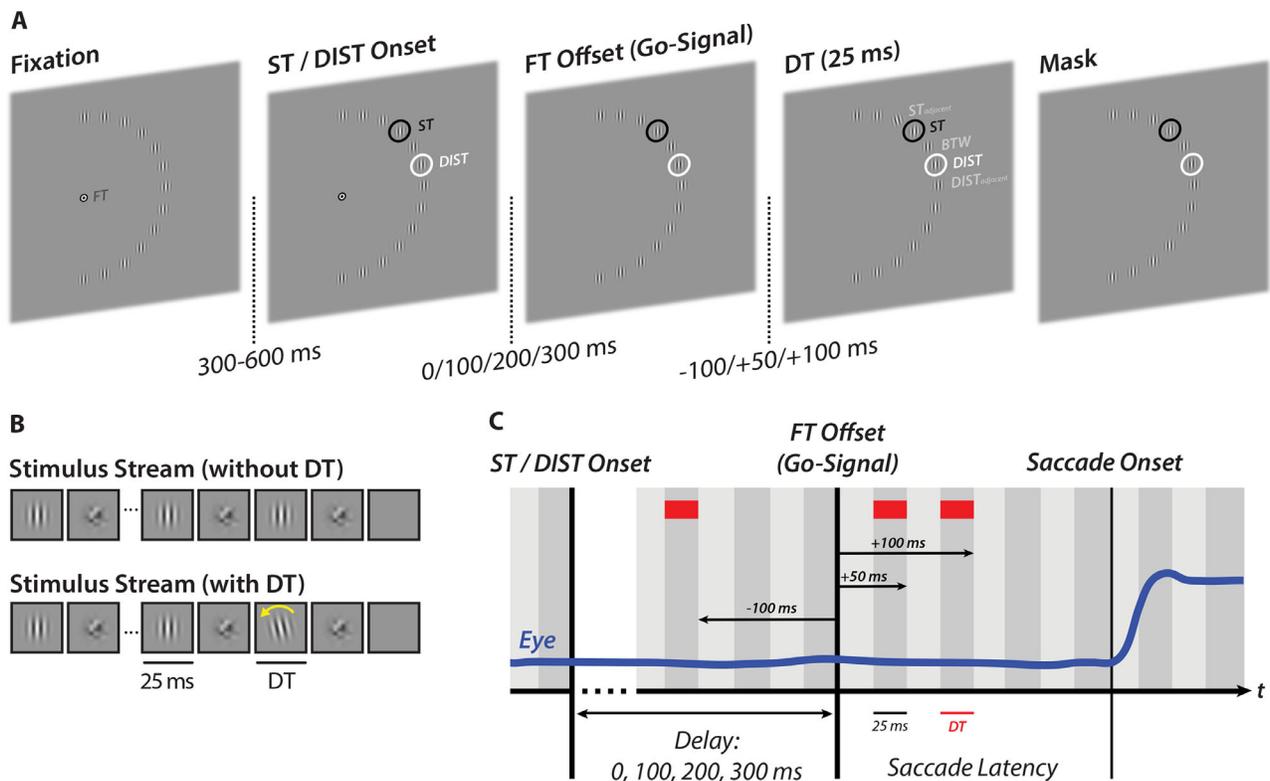
Figure 1. Experimental procedure. Participants performed a dual-task, comprising a saccade task and a visual discrimination task, during episodes of competition between a saccade target (ST) and a nearby distractor (DIST). Experimental blocks varied depending on the predictability of the ST and DIST locations: ST/DIST^{variable}, ST^{fixed}, and DIST^{fixed}. (**A**) Trial chronology. *Fixation:* At the beginning of each trial, 13 flickering stimulus streams (see **B**) appeared on the screen and participants had to maintain fixation at the fixation target (FT). *ST/DIST Onset:* After 300 to 600 ms, a black and a white circle appeared at an angular distance of 30 degrees from each other, surrounding two of the stimulus streams to indicate the ST and DIST locations. *FT Offset (Go-Signal):* Upon a variable delay (0, 100, 200, or 300 ms relative to ST/DIST onset), the FT disappeared and participants had to move their eyes as fast as possible toward ST. *DT (25 ms):* Before saccade onset, a discrimination target (DT, see **B**) – a slightly clockwise or counterclockwise tilted Gabor — was randomly flashed for 25 ms within 1 of 5 predefined stimulus streams (ST, DIST, BTW, ST$_{adjacent}$, and DIST$_{adjacent}$). The DT disappeared at either −100 ms, +50 ms, or +100 ms after the FT offset (see **C**). *Mask:* The DT was subsequently masked by the continuation of the flickering stimulus streams and participants had to report the orientation of the DT via the keyboard at trial end. (**B**) Flickering stimulus streams without (upper depiction) or with (lower depiction) a DT (here, a counterclockwise rotated DT; yellow arrow superimposed for illustration). (**C**) Schematic illustration of stimulus timing (x-axis represents time). The blue line depicts the position of the eye, which is expected to move on average approximately 200 ms after the FT offset (i.e. saccadic go-signal). The dotted line segment of the x-axis indicates the variability of the delay between ST/DIST onset and FT offset. Red squares highlight the 25 ms intervals during which the DT was presented, with arrows indicating the different DTOAs applied. Temporal contingencies were identical in all spatial predictability conditions.

Psychophysics (Brainard, 1997; Pelli, 1997) and EyeLink (Cornelissen, Peters, & Palmer, 2002) toolboxes. Gaze position of the dominant eye was recorded at a sampling rate of 1 kHz by an EyeLink 1000 Desktop Mount eye-tracker (SR Research, Osgoode, Ontario, Canada). Manual responses were recorded via a standard keyboard and auditory feedback (upon incorrect manual responses) was played via external loudspeakers.

Experimental design

Figure 1 illustrates the experimental procedure. On each trial, participants had to initially fixate within a 2.0 degree radius around a central fixation target (FT) – a black (approximately 0 cd/m^2) and white (approximately 44 cd/m^2) bull's eye (radius: 0.4 degrees) – presented on a gray background (approximately 22 cd/m^2). Upon correct fixation for 200 ms,

13 equidistant flickering stimulus streams were presented along an imaginary semicircle (radius: 10°) to the right side of the FT. Stimulus streams alternated every 25 ms (40 Hz) between a vertical Gabor patch (spatial frequency: 2.5 cpd; 100% contrast; random phase selected at each stream refresh; SD of the Gaussian window: 1.1 degrees; mean luminance: approximately 22 cd/m^2) and a Gaussian pixel noise mask (consisting of 0.23 degree width pixels with the same Gaussian envelope as the Gabors; see Wollenberg et al., 2019 for a video demonstration, and Hanning, Deubel, & Szinte, 2019 for a sample code). Between 300 and 600 ms after the onset of the stimulus streams, we presented a saccade target (ST) to which participants had to move their eyes, together with a nearby distractor (DIST), which participants should ignore. ST and DIST were equiluminant relative to the background and appeared in the form of black (approximately 0 cd/m^2) and white (approximately 44 cd/m^2) circles (radius: 1.1 degrees; width: 0.2 degrees) surrounding 2 stimulus streams separated by an angular distance of 30 degrees until trial end. The color configuration of ST and DIST was counterbalanced across participants but constant for each participant across the experiment (5 participants: white ST/black DIST; 4 participants: black ST/white DIST). Importantly, we systematically varied the spatial predictability of the ST and DIST locations via pre-block instructions (8 blocks of each type played in random order). Depending on the block type, participants were either unaware of the ST and DIST locations (ST/DIST^{variable}), informed about the fixed location of ST (ST^{fixed}), or informed about the fixed location of DIST (DIST^{fixed}). Note that, as ST and DIST always appeared at an angular distance of 30 degrees, participants could also predict the DIST location in the ST^{fixed} condition and the ST location in the DIST^{fixed} condition with a probability of 50% (i.e. either two stimulus streams clockwise or counterclockwise to the fixed location). Moreover, to investigate the dynamics of attentional and oculomotor selection as a function of visual processing time prior to saccade onset, we systematically delayed saccades. Participants were instructed to move their eyes as fast and accurately as possible upon the offset of FT (rather than the onset of ST and DIST), which was randomly delayed by 0, 100, 200, or 300 ms (delay^0, delay^{100}, delay^{200}, and delay^{300}) relative to ST and DIST onset. In order to assess the deployment of visual attention during saccade preparation, a discrimination target (DT) was presented shortly before saccade onset. The DT consisted of a slightly tilted Gabor (either clockwise or counterclockwise at a rotation angle of 12 degrees relative to the vertical), which was presented for a duration of 25 ms and disappeared at either −100, +50, or +100 ms relative to the FT offset (saccadic go-signal). Note that, whereas the positive discrimination target offset asynchronies (DTOAs, defined as the duration

between FT offset and DT offset) of +50 and +100 ms were used across all saccadic go-signal delays (delay^0, delay^{100}, delay^{200}, and delay^{300}), the negative DTOA of −100 ms was only introduced in half of the trials without a saccadic go-signal delay (i.e. delay^0). These trials were used to evaluate potential effects of spatial predictability on the endogenous deployment of visual attention prior to the actual presentation of ST and DIST. The DT location was randomly selected among five possible stimulus streams at: the saccade target (ST), the distractor (DIST), in between the saccade target and the distractor (BTW), adjacent to the saccade target (ST$_{adjacent}$), or adjacent to the distractor (DIST$_{adjacent}$). Discrimination performance was averaged across the latter two locations to derive a robust baseline measure (CTRL) of visual orientation sensitivity. On approximately 2% of trials, no DT was presented in order to evaluate potential influences of the DT appearance on saccade latencies. Eight hundred ms after the onset of ST and DIST, all stimuli were erased from the screen. At the end of each trial, participants reported the DT orientation (two alternative forced choice: clockwise versus counterclockwise) via button press on the keyboard (right versus left arrow). A feedback sound was played upon incorrect manual responses and the next trial was launched once the manual discrimination response was registered.

Overall, participants completed 24 blocks, each consisting of 230 trials. Incorrect trials, in which online saccade onset was not detected between 50 and 350 ms relative to the FT offset (saccadic go-signal) upon correct fixation (within a 2.0 degree radius around the FT) were repeated at the end of each block.

Data preprocessing

Saccades were detected based on the velocity distribution of the sampled eye data (Engbert & Mergenthaler, 2006). We registered saccade onsets/offsets whenever the eye's velocity was greater/smaller than the median of a moving average across 20 subsequent eye-position samples by 3 SDs for at least 20 ms. For further analyses, we only included trials without intermittent eye blinks, in which (1) initial fixation was maintained within a radius of 2.0 degrees around FT, (2) saccade onset fell between 50 ms and 350 ms relative to the saccadic go-signal, and (3) a saccade landed between 7 degrees and 13 degrees from FT. Moreover, to base our measures of visual orientation sensitivity on the deployment of visual processing resources before saccade onset, only trials in which the DT offset occurred before the eyes started to move were further considered. After preprocessing the data as described, a total number of 46,400 trials were included in the final analyses, corresponding to 81.74%

of all trials played and an average of 5156 ± 59 (mean ± SEM) trials per participant.

Data analysis

Our analyses focused on the evaluation of saccade endpoints and presaccadic visual discrimination performance obtained under conditions varying with regard to the predictability of the saccade target and distractor locations (ST/DIST^{variable}, ST^{fixed}, and DIST^{fixed}) and movement preparation time (delay^0, delay^{100}, delay^{200}, and delay^{300}).

For the analysis of saccade endpoints, we first divided the stimulus stream semicircle into 13 even angular sectors of 15 degrees (±7.5 degrees from each stimulus stream center angle) and computed the percentage of saccade endpoints recorded within a given sector. This allowed us to derive saccade endpoint distributions reflecting the proportion of target saccades (landing closest to the saccade target), distractor saccades (landing closest to the distractor), and averaging saccades (landing in the sector between the saccade target and the distractor).

Presaccadic visual discrimination performance was computed as the percentage of correct orientation discrimination responses observed for the stimulus streams located at ST, DIST, and BTW (between ST and DIST), respectively. Data obtained at the streams surrounding ST and DIST were collapsed into a baseline measure of visual discrimination performance (CTRL).

All results are reported as M ± SEM (mean ± standard error of mean). Reported effect sizes represent the standardized mean difference Cohen's d_z among the compared groups (Lakens, 2013).

Results

Basic analyses

Before focusing on the analyses of saccade endpoints and visual discrimination performance, we first verified central assumptions underlying the interpretation of our data.

Figure 2 shows mean saccade latencies separately for each spatial predictability condition and saccadic go-signal delay. In order to validate the effectiveness of our saccadic delay manipulation, we collapsed data across the different spatial predictability conditions and subjected the mean saccade latency (measured relative to saccade target and distractor onset) of each saccadic go-signal delay to a 1-way repeated measures ANOVA. We observed that saccade latencies significantly increased as a function of the saccadic go-signal delay
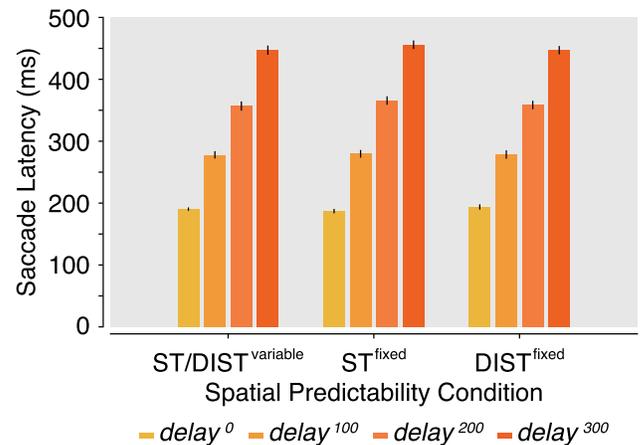

Figure 2. Saccade latencies. Mean saccade latencies relative to saccade target and distractor onset observed in the different spatial predictability conditions for each saccadic go-signal delay (0 - 300 ms; light to dark orange). Error bars represent SEM ($n = 9$).

(delay^0: 190.34 ± 3.28 ms, delay^{100}: 278.68 ± 6.11 ms, delay^{200}: 360.39 ± 6.96 ms, and delay^{300}: 450.18 ± 6.75; F(1.85, 14.77) = 964.52, $p < 0.001$, Greenhouse Geisser corrected). Thus, as expected, our saccadic delay manipulation led to a systematic prolongation of visual processing time prior to saccade onset. Saccadic go-signal delays did, however, not increase saccade latencies exactly proportional to their duration, which becomes evident when computing the mean saccade latency increase relative to the corresponding saccadic go-signal delay duration (delay^{100}: −11.66 ms, delay^{200}: −29.95 ms, and delay^{300}: −40.16 ms). This effect likely indicates that oculomotor processing already started (to some degree) with the onset of the oculomotor cues rather than strictly contingent upon the go-signal. Importantly, despite this relative acceleration of movement execution, the observed saccade latencies clearly indicate that the DT offset (at −100, +50, or +100 ms relative to the go-signal) consistently occurred before movement onset.

Next, we verified that the mere presence of the discrimination target did not inherently capture attention, which would be reflected in saccade latency modulations. We collapsed data across all spatial predictability conditions and saccadic go-signal delays, and subsequently compared the mean saccade latency between trials in which DT was presented (DT^{present}; approximately 98% of trials) and trials without DT (DT^{absent}; approximately 2% of trials). We only included trials in which DT occurred after the go-signal (i.e. DT offset at either +50 or +100 ms relative to FT offset) to ensure that this comparison was based on the presence of the discrimination target shortly before saccade onset. A paired *t*-test did not reveal a significant saccade latency difference (DT^{present}: 319.91 ± 5.03
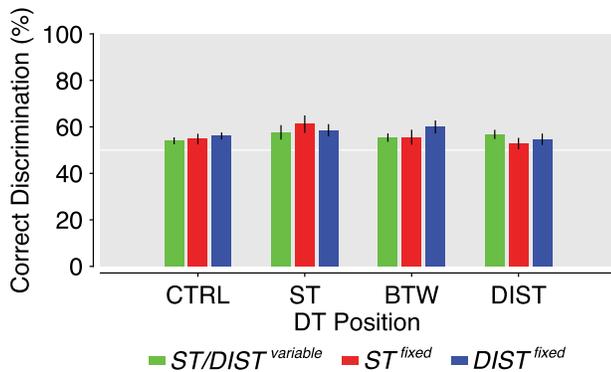
Figure 3. Visual discrimination performance before cue onset. Mean percentage of correct orientation discrimination at the CTRL, ST, BTW, and DIST location observed in the different spatial predictability conditions (ST/DIST^{variable}: green; ST^{fixed}: red; and DIST^{fixed}: blue) prior to the visual onset of saccade target and distractor. Error bars represent SEM ($n = 9$).

ms versus DT^{absent}: 316.28 ± 5.18 ms; t(8) = 1.48, $p > 0.05$, $d_z = 0.49$). Accordingly, our discrimination target signal allowed to probe visual attention during the presaccadic interval without interfering with oculomotor preparation.

Last, we examined whether spatial predictability systematically affected the endogenous deployment of visual attention. To this end, we combined all trials in which the discrimination target appeared before the onset of the saccade target and the distractor (i.e. only trials associated with a DTOA of −100 ms at delay^0) and computed visual discrimination performance at the CTRL, ST, BTW, and DIST location separately for each spatial predictability condition (see Figure 3). Subsequently, visual discrimination performance at ST and DIST in the ST^{fixed} and DIST^{fixed} conditions was compared to the ST/DIST^{variable} condition using paired *t*-tests (at a Bonferroni-corrected alpha of 0.025 for both the ST and DIST comparisons). Interestingly, visual discrimination performance at ST in both the ST^{fixed} (61.18 ± 3.75%) and DIST^{fixed} (58.56 ± 2.62%) condition did not significantly differ from the ST/DIST^{variable} condition (57.64 ± 3.10%; both *p* values > 0.05). Similarly, no significant modulation of visual discrimination performance at DIST was observed in the ST^{fixed} (52.84 ± 2.45%) and DIST^{fixed} (54.68 ± 2.44%) relative to the ST/DIST^{variable} condition (56.77 ± 1.96%; both *p* values > 0.05). Thus, being able to predict the upcoming location of the saccade target or the distractor did not systematically affect the endogenous deployment of visual attention prior to saccade target and distractor onset at the respective locations. Consequently, any top-down effects on saccade accuracy and visual discrimination performance emerging after the visual onsets of saccade target and distractor did not result from a predictive deployment of attention.

Main analyses

Saccade accuracy

To investigate the influence of our experimental manipulations on the accuracy of saccades, we computed the distribution of saccade endpoints across the angular sectors surrounding the ST, BTW, and DIST location (see saccade endpoint binning procedure described in Data analysis) separately for each spatial predictability condition and saccadic go-signal delay (see Figure 4A). These data were subjected to a 2-way repeated measures ANOVA (spatial predictability × saccadic go-signal delay) taking the proportion of target saccades landing closest to ST as the dependent measure. Interestingly, even though spatial predictability tended to increase the proportion of target saccades (ST/DIST^{variable}: 80.48 ± 1.70, ST^{fixed}: 85.96 ± 3.50, and DIST^{fixed}: 86.34 ± 1.67), the main effect of spatial predictability only approached statistical significance (F(2,16) = 3.48, $p = 0.06$). There was, however, a highly significant main effect of the saccadic go-signal delay duration (F(1.29,10.30) = 38.07, $p < 0.001$, Greenhouse Geisser corrected), demonstrating that the proportion of target saccades generally increased with prolonged movement preparation time. Yet, as revealed by the average proportion of target saccades observed for the different go-signal delays (delay^0: 75.19 ± 2.42, delay^{100}: 86.26 ± 2.03, delay^{200}: 88.01 ± 1.96, and delay^{300}: 87.58 ± 2.20), movement accuracy did not linearly increase with movement preparation time but rather reached a plateau after a 100 ms go-signal delay. Moreover, we found a highly significant interaction effect of spatial predictability and saccadic-go signal delay (F(6,48) = 18.79, $p < 0.001$). The distribution of saccade endpoints (see Figure 4A) suggests that this interaction is driven by the sharp increase in target directed saccades in the ST/DIST^{variable} condition from delay^0 to delay^{100}. A more detailed insight into the distribution of saccade endpoints can be obtained from Supplementary Figure S1, which depicts saccade endpoint data at a finer resolution.

Based on the assumption that spatial predictability would lead to a fast improvement in saccade accuracy, we subsequently used paired *t*-tests (at a Bonferroni-corrected alpha of 0.0167) to compare the proportion of undelayed target saccades (delay^0) between the different spatial predictability conditions (see leftmost plot in Figure 4A). Indeed, relative to the ST/DIST^{variable} condition (63.64 ± 3.15%), the proportion of target saccades was significantly larger in the ST^{fixed} (82.79 ± 4.05%; t(8) = 4.14, $p < 0.01$, $d_z = 1.38$) and DIST^{fixed} condition (79.15 ± 2.26%;
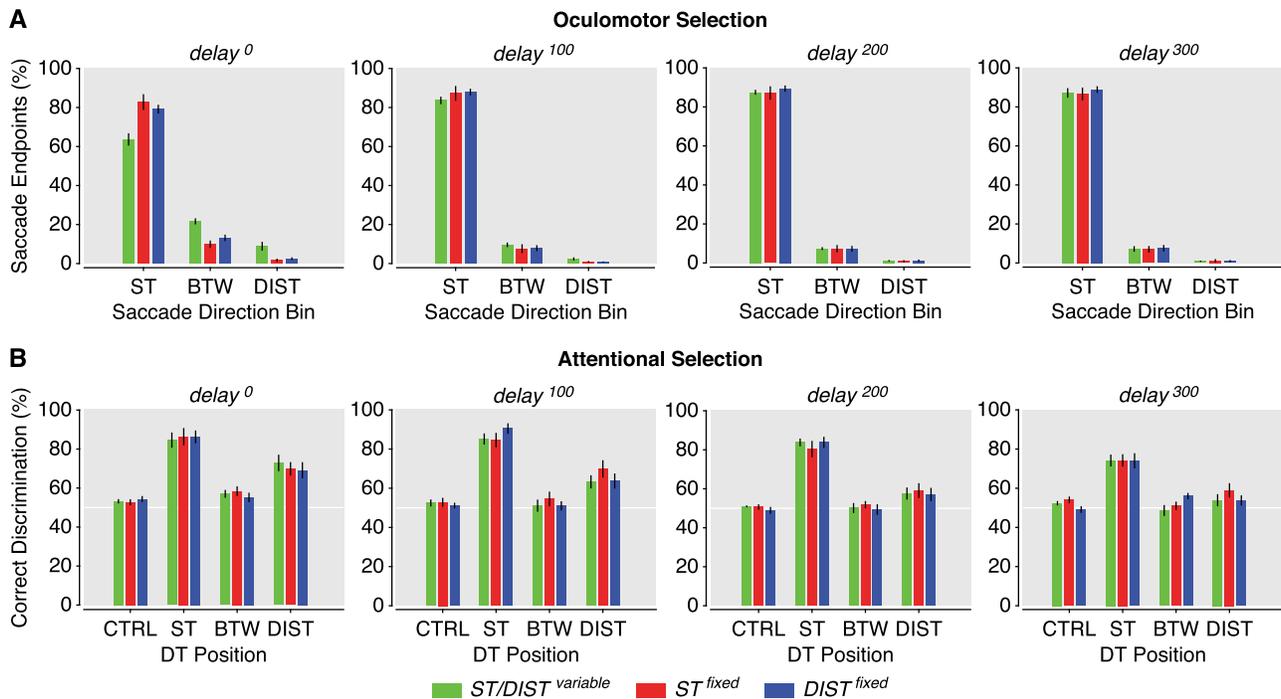
Figure 4. Saccade endpoints and visual discrimination performance during movement preparation. (**A**) *Oculomotor Selection*. Mean proportion of saccades landing around the ST, BTW, and DIST location for each spatial predictability condition (ST/DIST^{variable}: green; ST^{fixed}: red; and DIST^{fixed}: blue) for a given saccadic go-signal delay (0 - 300 ms; from left to right). (**B**) *Attentional Selection*. Mean percentage of correct orientation discrimination at CTRL, ST, BTW, and DIST for the respective conditions. Note that only trials in which the DT appeared after ST/DIST onset were included. Error bars represent SEM ($n = 9$).

t(8) = 4.45, $p < 0.01$, $d_z = 1.48$), but did not differ between the ST^{fixed} and DIST^{fixed} conditions (t(8) = 1.27, $p > 0.05$, $d_z = 0.42$). Thus, when either the saccade target or the distractor location was predictable, eye movements were more frequently directed to the instructed target location as compared to when saccade target and distractor locations were unpredictable.

We further investigated the observed interaction effect by comparing the proportion of target saccades within each spatial predictability condition between delay^0 and delay^{100} using paired *t*-tests (at a Bonferroni-corrected alpha of 0.0167). Here, we found that the proportion of target saccades significantly increased by approximately 20% to 83.61 $\pm$ 1.93% in the ST/DIST^{variable} condition (t(8) = 7.69, $p < 0.001$, $d_z = 2.56$). Similarly, the proportion of target saccades significantly increased by approximately 9% to 87.91 $\pm$ 1.73% in the DIST^{fixed} condition (t(8) = 6.49, $p < 0.001$, $d_z = 2.16$). Although the proportion of target saccades increased by approximately 4% to 87.25 $\pm$ 3.79% in the ST^{fixed} condition, this improvement in saccade accuracy did not reach statistical significance at corrected alpha (t(8) = 2.81, $p > 0.0167$, $d_z = 0.94$).

Taken together, these data show that a saccadic go-signal delay of 100 ms systematically improved voluntary eye movement control such that saccades more frequently landed at the instructed target location (whereas conversely reducing saccade averaging as well as the occurrence of distractor saccades). Importantly, as reflected by the differential increase in the proportion of target saccades across the spatial predictability conditions (ST/DIST^{variable}: 19.97%, ST^{fixed}: 4.46%, and DIST^{fixed}: 8.76%), this facilitatory effect of additional visual processing time was most pronounced when the saccade target and distractor locations were unpredictable.

Before proceeding with the analysis of visual discrimination performance, we evaluated whether the latency of saccades had a systematic effect on movement accuracy. As the global effect (saccade averaging) was shown to be most pronounced for short latency saccades (e.g. Findlay, 1982; Ottes et al., 1985; Coëffé & O'Regan, 1987), we compared the mean latency of target saccades (landing closest to ST) and averaging saccades (landing closest to BTW in between ST and DIST). To do so, we again collapsed data across the different spatial predictability conditions and ran a 2-way repeated measures ANOVA

on the mean saccade latency for the factors saccadic go-signal delay and saccade landing bin (ST versus BTW). We found a significant main effect of go-signal delay ($F(3,24) = 1149.43$, $p < 0.001$), but, importantly, there was neither a significant main effect of saccade landing bin ($F(1,8) = 2.64$, $p > 0.05$), nor a significant interaction between go-signal delay and saccade landing bin ($F(3,24) = 0.18$, $p > 0.05$). In contrast to previous reports (e.g. Findlay, 1982; Ottes et al., 1985; Coëffé & O'Regan, 1987), our data therefore do not allow to conclude on a latency dependence of saccade averaging.

Visual discrimination performance

In order to assess the attentional correlates associated with the oculomotor effects obtained by the analysis of saccade endpoints, we proceeded with the analysis of visual discrimination performance after the onset of ST and DIST (i.e. only trials with a DTOA of either +50 or +100 ms).

Based on the accuracy improvements in the ST[fixed] and DIST[fixed] relative to the ST/DIST[variable] condition at delay[0], we evaluated whether spatial predictability modulated the deployment of visual attention during the preparation of undelayed saccades. In particular, we focused on assessing the influence of spatial predictability on the extent of attentional competition between the saccade target and the distractor. We therefore computed the difference in visual discrimination performance between ST and DIST (i.e. percent correct at ST - percent correct at DIST) at delay[0] and compared respective measures between the different spatial predictability conditions using paired *t*-tests (at a Bonferroni-corrected alpha of 0.0167).

Despite the significant improvements in saccade accuracy associated with spatial predictability, the difference in visual discrimination performance between ST and DIST did not significantly differ between the ST/DIST[variable] ($0.12 \pm 0.03\%$), ST[fixed] ($0.17 \pm 0.05\%$), and DIST[fixed] condition ($0.17 \pm 0.03\%$), with all three comparisons yielding a $p > 0.05$. Yet, it should be noted that the difference in visual discrimination performance was quantitatively smallest in the ST/DIST[variable] condition (for which we observed the lowest proportion of target saccades), suggesting that attentional competition was most pronounced when both saccade target and distractor were unpredictable (see leftmost plot in Figure 4B).

Next, we focused on potential modulations of visual discrimination performance associated with the differential saccade accuracy improvements across the spatial predictability conditions, which we observed for a saccadic go-signal delay of 100 ms. To this end, we compared the difference in visual discrimination performance at ST and DIST between delay[0] and

delay[100] for each spatial predictability condition using paired *t*-tests (at a Bonferroni-corrected alpha of 0.0167).

When ST and DIST were unpredictable (ST/DIST[variable]), the visual discrimination benefit at ST increased significantly from delay[0] to delay[100] ($0.12 \pm 0.03\%$ vs. $0.22 \pm 0.03\%$; $t(8) = 3.87$, $p < 0.01$, $d_z = 1.29$). Thus, the pronounced facilitatory effect of a 100 ms go-signal delay on saccade accuracy in the absence of spatial predictability was indeed reflected in a reduction of attentional competition between saccade target and distractor. Contrasting with this effect, the saccade target benefit did not significantly increase when the saccade target location was fully predictable ($0.17 \pm 0.05\%$ vs. $0.15 \pm 0.03\%$; $t(8) = 0.53$, $p > 0.05$, $d_z = 0.18$). This absence of a statistically significant reduction of attentional competition matches with the observation that saccade accuracy improved only slightly, but not significantly, with a 100 ms go-signal delay in the ST[fixed] condition. When the distractor location was fully predictable – leading to a modest and statistically significant improvement in saccade accuracy – the difference in visual discrimination performance between ST and DIST only approached statistical significance at the corrected alpha ($0.17 \pm 0.03\%$ vs. $0.27 \pm 0.04\%$; $t(8) = 2.91$, $p = 0.02$, $d_z = 0.97$).

In sum, these results point toward a systematic relationship between the spatiotemporal dynamics of selective visual attention and eye movement control, which might explain the relatively low accuracy of short-latency saccades under spatial uncertainty and the improving accuracy with increasing visual processing time.

Given the emergence of perceptual effects within the rather short time window induced by a saccadic delay of 100 ms, we next evaluated the time course of selective attentional processing by analyzing visual discrimination performance across longer go-signal delays. We first collapsed data across the different spatial predictability conditions within each go-signal delay for all trials with a positive DTOA (of either +50 or +100 ms) and computed visual discrimination performance for the ST, DIST, and CTRL locations. Subsequently, we compared the measures for ST and DIST to CTRL for each go-signal delay by means of paired *t*-tests (at a Bonferroni-corrected alpha of 0.0125 for both ST and DIST comparisons). This allowed us to assess the general time course underlying the selective deployment of attentional resources to the saccade target and the distractor relative to baseline (CTRL). Visual discrimination performance at ST was significantly enhanced relative to CTRL across all go-signal delays (all *p* values < 0.001), that is for delay[0] ($85.53 \pm 3.71\%$ vs. $53.37 \pm 1.10\%$; $d_z = 3.04$), delay[100] ($86.77 \pm 2.96\%$ vs. $52.12 \pm 1.28\%$; $d_z = 4.29$) delay[200] ($82.69 \pm 2.89\%$ vs. $50.24 \pm 0.96\%$; $d_z = 4.10$),
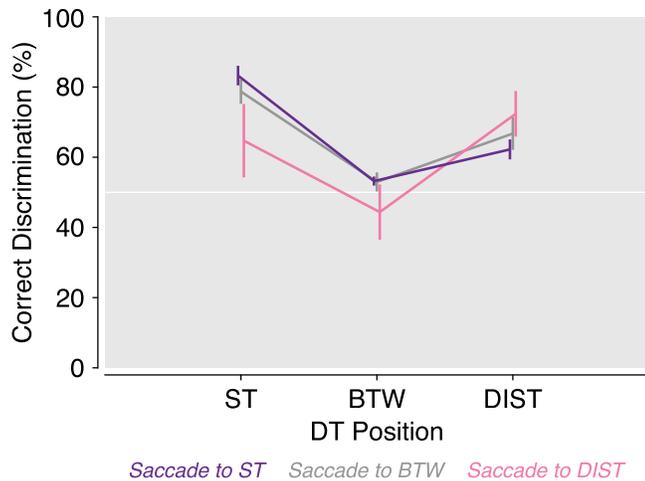
Figure 5. Visual discrimination performance depending on the saccade endpoint. Mean percentage of correct orientation discrimination at the ST, BTW, and DIST location before the execution of target saccades landing at ST (purple), averaging saccades landing at BTW (in between ST and DIST; grey), and distractor saccades landing at DIST (pink). Data were collapsed across all spatial predictability conditions (ST/DIST^{variable}, ST^{fixed}, and DIST^{fixed}), saccadic go-signal delays (0, 100, 200, and 300 ms), and positive DTOAs (+50 and +100 ms). Error bars represent SEM ($n = 9$).

and delay^{300} (74.24 ± 3.12% vs. 51.74 ± 0.89%; $d_z = 2.37$). At DIST, visual discrimination performance only remained significantly enhanced relative to CTRL for delay^0 (70.50 ± 3.75%; t(8) = 5.34, $p < 0.001$, $d_z = 1.78$) and delay^{100} (65.66 ± 3.44%; t(8) = 4.16, $p < 0.01$, $d_z = 1.39$), but not for delay^{200} (57.94 ± 3.17%; t(8) = 3.18, $p > 0.0125$, $d_z = 1.06$) and delay^{300} (55.54 ± 2.71%; t(8) = 1.83, $p > 0.05$, $d_z = 0.61$).

Thus, whereas attentional resources were deployed to both the saccade target and the distractor shortly after their onset (i.e. delay^{100} and delay^{200}), they were selectively sustained across time only at the saccade target but not at the distractor.

Finally, we directly investigated the spatial relationship between the presaccadic deployment of visual attention and the saccade endpoint. To this end, we computed separate measures of visual discrimination performance at ST, BTW, and DIST for each saccade endpoint bin (see Figure 5), which allowed us to contrast the attentional correlates of target saccades, averaging saccades, and distractor saccades. To exclusively evaluate the deployment of visual attention shortly before saccade onset, we again only included trials with a positive DTOA (i.e. +50 and +100 ms relative to FT offset). Moreover, due to the low amount of averaging and distractor saccades in several conditions (especially for longer go-signal delays), we

collapsed data across the different spatial predictability conditions and saccadic go-signal delays. For each subpopulation of saccades, we then conducted a paired *t*-test comparing visual discrimination performance between ST and DIST (at a Bonferroni-corrected alpha of 0.0167).

Before the execution of target saccades, visual discrimination performance was significantly enhanced at ST relative to DIST (83.27 ± 2.79% vs. 62.23 ± 2.84%; t(8) = 7.89, $p < 0.001$, $d_z = 2.63$). Thus, target saccades were clearly associated with a selective allocation of attentional resources to the instructed saccade target.

We also observed that visual discrimination performance was enhanced at ST (78.70 ± 3.46%) relative to DIST (66.76 ± 4.65%) prior to the execution of averaging saccades. This effect did, however, not reach statistical significance at the corrected alpha (t(8) = 2.84, $p > 0.0167$, $d_z = 0.95$), indicating that attentional competition between the saccade target and the distractor was not successfully resolved before the execution of averaging saccades. Following up on this comparison, to investigate whether visual attention was allocated to the endpoint of averaging saccades, we ran a one-sample *t*-test comparing visual discrimination performance at BTW (i.e. in between ST and DIST) to chance level (50%) for the subpopulation of averaging saccades. In line with previous studies (Van der Stigchel & de Vries, 2015; Wollenberg, Deubel, & Szinte, 2018), we did not find a significant enhancement of visual discrimination performance at the endpoint of averaging saccades (52.96 ± 2.71%; t(8) = 1.09, $p > 0.05$, $d_z = 0.36$). Thus, contrary to the selective enhancement at the endpoint of target saccades, the locus of visual attention was clearly dissociated from the endpoint of averaging saccades.

Last, for the subpopulation of distractor saccades, visual discrimination performance did not significantly differ between ST and DIST (64.72 ± 10.46% vs. 72.37 ± 6.50%; t(8) = 0.65, $p > 0.05$, $d_z = 0.22$). Interestingly, other than for target and averaging saccades, these data show that visual discrimination performance was quantitatively most enhanced at DIST rather than ST prior to distractor saccades (note, however, the comparably large variability in these data due to the small number of distractor saccades).

In sum, the differential pattern of results observed here provides evidence for a systematic relationship between the deployment of visual attention prior to saccade onset and the endpoint of saccades. Importantly, however, the absence of a selective enhancement of visual discrimination performance at the endpoint of averaging saccades demonstrates that the locus of visual attention does not necessarily coincide with the saccade endpoint.

Discussion

This study aimed to investigate the perceptual correlates of top-down eye movement control during episodes of oculomotor competition between a saccade target and a proximal distractor. We manipulated the predictability of target and distractor locations and variably delayed movement execution in a dual-task paradigm consisting of a saccade task and a visual discrimination task. This design allowed us to concurrently assess the influence of increasing top-down control on saccade accuracy (i.e. saccade endpoint distributions) and the deployment of visual attention during movement preparation (i.e. visual discrimination performance). To our knowledge, this is the first study to systematically examine the spatiotemporal dynamics of visual attention associated with the capacity to exert top-down control over saccadic eye movements, which was solely inferred from the assessment of saccade endpoints in similar, previous studies.

The influence of spatial predictability on saccade accuracy and attentional selection

We assumed that efficient oculomotor control would be challenged by bottom-up visual competition between the saccade target and the distractor, presumably dominating the dynamics of saccade target selection early on during movement preparation (van Zoest et al., 2004; van Zoest & Donk, 2005). Accordingly, our first main hypothesis implicated that spatial predictability of target and distractor locations would provide an efficient top-down signal counteracting initial bottom-up competition, thereby enhancing movement accuracy even for short-latency saccades. Furthermore, we expected that this improvement in saccade accuracy would be reflected at the perceptual level prior to saccade onset, with attentional resources being more selectively deployed to the saccade target relative to the distractor.

Interestingly, 100 ms prior to saccade target and distractor onset, visual discrimination performance at both locations was comparable (and close to chance level) across all spatial predictability conditions. Thus, being able to predict the saccade target or the distractor location did not affect the endogenous deployment of visual attention. This indicates that the beneficial effect of spatial predictability on oculomotor selection emerged only during movement preparation. We believe that the variability of the saccadic go-signal can account for the absence of an early endogenous attentional effect. Because the fixation target offset indicated the saccadic go-signal, participants had to maintain attentional resources at fixation, which likely interfered with their ability to predictively attend to a location in the periphery.

In line with our prediction, we observed a distinct effect of spatial predictability on the accuracy of short-latency saccades. Without a saccadic delay (i.e. delay^0), the proportion of target saccades significantly increased (whereas, conversely, the proportion of averaging and distractor saccades decreased) when either the saccade target or the distractor location was predictable (ST^{fixed} and DIST^{fixed}) compared to when both were unpredictable (ST/DIST^{variable}). Thus, spatial predictability improved oculomotor control even though only little time had elapsed between the presentation of the oculomotor cues and movement onset. Consistent with earlier observations (Heeman et al., 2014; Aagten-Murphy & Bays, 2017), this demonstrates that top-down mechanisms can effectively attenuate adverse effects of bottom-up competition on eye movement control in a rather fast fashion. Interestingly, our data furthermore suggest that this facilitatory effect does not depend on whether the saccade target or the distractor location could be predicted, as the proportion of target saccades did not differ between the ST^{fixed} and DIST^{fixed} condition. Yet, even though these two conditions likewise reduced spatial uncertainty, they differed in an important way. Whereas the saccade target was fully predictable in the ST^{fixed} condition, it could appear at one out of two possible locations in the DIST^{fixed} condition (clockwise or counterclockwise from the distractor). Accordingly, one might have expected a higher proportion of target saccades in the former compared to the latter condition. The absence of such an effect therefore may indicate that the mechanism subserving an early top-down modulation of oculomotor control incorporates spatial predictability in a rather unspecific manner, insensitive to the exact contingencies underlying the prediction. Alternatively, the oculomotor system might simultaneously prioritize two potentially task-relevant locations (saccade targets) without costs, such that potential differences between the two conditions were obscured. Future research may resolve this issue via assessing the effects of increased target and distractor ambiguity on saccade accuracy in dual-task designs similar to ours.

However, other than expected, we did not observe a systematic effect of spatial predictability on the deployment of attentional resources (measured as visual discrimination performance) to the saccade target and the distractor during the preparation of undelayed saccades (i.e. delay^0). This indicates that top-down signals facilitating fast eye movement control do not necessarily transfer to perception. Yet, whereas the mean difference in visual discrimination performance between saccade target and distractor was comparably large in the ST^{fixed} and DIST^{fixed} conditions, it was quantitatively less pronounced in the

ST/DIST^{variable} condition, for which we observed the lowest proportion of undelayed saccades landing at the saccade target. This may indicate that the facilitatory effect of spatial predictability on rapid eye movement control was associated with more efficient attentional target selection.

The influence of visual processing time on saccade accuracy and attentional selection

Our second main hypothesis was deduced from observations indicating that top-down mechanisms increasingly influence saccade target selection as a function of time (van Zoest et al., 2004; van Zoest & Donk, 2005; van Zoest & Donk, 2006; Carrasco, 2011; Heeman et al., 2014). Thus, we predicted that delayed saccadic go-signals – by increasing saccade latencies and thereby visual processing time prior to saccade onset – would facilitate voluntary eye movement control and attentional selection of the saccade target.

In line with this prediction, we observed a significant effect of the saccadic go-signal delay on the proportion of target saccades, replicating previously reported effects of increased movement preparation time on top-down eye movement control during oculomotor competition (Heeman et al., 2014; Aagten-Murphy & Bays, 2017). On top of this general effect, our data indicate that spatial predictability differentially affected the early time course of top-down eye movement control. A saccadic go-signal delay of 100 ms yielded a large and significant increase in the proportion of target saccades in the ST/DIST^{variable} condition. The same delay, however, yielded only a moderate (but significant) improvement in saccade accuracy in the DIST^{fixed} condition and no significant improvement in the ST^{fixed} condition. Thus, while being able to predict the saccade target or the distractor location accelerated top-down eye movement control (at delay^0), additional visual processing time was required to achieve a similar level of oculomotor control when saccade target and distractor locations were unpredictable. Indeed, the saccade endpoint distributions obtained in the different spatial predictability conditions for a go-signal delay of 100 ms approached each other, which suggests that already a short prolongation of visual processing time can compensate for the adverse effect of spatial uncertainty on saccade accuracy. Such a dependency of top-down oculomotor control on exposure to task-relevant visual input is in line with recent evidence from a study on memory guided saccades (Arkesteijn, Donk, Smeets, & Belopolsky, 2020), which showed that sufficient target and distractor presentation time reduces saccade averaging.

As evident in the distribution of saccade endpoints, longer delays of 200 ms and 300 ms did not notably alter saccade accuracy. This suggests that top-down control over saccadic eye movements was effectively deployed within the first 300 ms upon the visual presentation of the oculomotor cues, such that the large majority of saccades landed at the saccade target. A similar temporal pattern was reported by Aagten-Murphy and Bays (2017). Our data further add up to the proposal that saccade endpoint deviations away from a saccade target linearly decrease across a saccade latency range of up to 320 to 340 ms (Heeman et al., 2014). The current data indicate that saccade accuracy does not further improve at latencies above this range. More generally, our data support a framework in which bottom-up and top-down mechanisms operate at a different time scale, controlling saccade target selection at short and longer latencies, respectively (van Zoest et al., 2004; van Zoest & Donk, 2005; van Zoest & Donk, 2006).

In line with our prediction, the distinct improvement in saccade accuracy associated with a saccadic go-signal delay of 100 ms in the ST/DIST^{variable} condition was reflected in a reduction of attentional competition between saccade target and distractor. For this condition, the visual discrimination benefit of the saccade target over the distractor significantly increased from delay^0 to delay^{100}. Further, in line with the far less pronounced improvements in saccade accuracy, a saccadic go-signal delay of 100 ms did not significantly improve visual discrimination at the saccade target relative to the distractor in the ST^{fixed} and DIST^{fixed} conditions. These differential effects suggest that bottom-up visual competition between saccade target and distractor was initially (at delay^0) highest when their locations were unpredictable, such that voluntary eye movement control improved only later (at delay^{100}), once attentional resources could be more efficiently biased toward the saccade target.

Across longer saccadic delays (delay^{200} and delay^{300}), visual discrimination performance (obtained after collapsing data across the different spatial predictability conditions) decreased both at the saccade target and the distractor. This general decline in visual discrimination benefits most likely reflects a decay of automatic bottom-up attentional effects elicited by the salient visual onsets at saccade target and distractor. Importantly, however, whereas discrimination performance at the distractor approached chance level upon a saccadic delay of 200 ms, it remained selectively enhanced at the saccade target across the entire latency range. Thus, despite a general decay of the initial bottom-up attentional effects at both the saccade target and the distractor, our data indicate that the operation of selective top-down mechanisms allowed for more sustained attentional facilitation of the saccade target. Future studies could extend our insights by systematically varying visual processing time

(i.e. the presentation time of the saccade target and the distractor) independent from movement preparation time (i.e. the saccadic go-signal delay). Such a design will allow to determine whether the improvement of saccade accuracy over time depends on prolonged visual processing per se or more generally on extended movement preparation time.

The link between visual attention and saccade accuracy

Finally, the current study directly examined the relationship between visuospatial attention and the accuracy of saccadic eye movements. The analysis of visual discrimination performance as a function of the saccade endpoint allowed us to separately approximate the perceptual correlates of target saccades, averaging saccades, and distractor saccades.

Indeed, our data provide evidence linking the selective deployment of visual attention during movement preparation to the accuracy of subsequently executed saccades. For the subpopulation of target saccades, visual discrimination performance was markedly and significantly enhanced at the saccade target relative to the distractor. Thus, consistent with previous work (see also: Van der Stigchel & de Vries, 2018: page 2, lines 5–9; Wollenberg et al., 2018: page 10, lines 8–10), these data suggest that prior to saccades successfully landing at an intended target, attentional resources were selectively deployed to the movement endpoint.

This attentional benefit at the saccade target was reduced before the execution of averaging saccades, such that we observed no significant discrimination benefit for the saccade target over the distractor for these saccades. Interestingly, whereas our recent work (Wollenberg et al., 2018) demonstrated that saccade averaging is associated with an equal deployment of attentional resources to both competing oculomotor cues, the current data indicate that visual attention may be biased toward the saccade target even before the execution of averaging saccades. Note, however, that in the former study we used two physically identical saccade targets among which participants could freely choose, whereas in the current study we differentiated target and distractor by color. This increased visual discriminability of saccade target and distractor may well explain the perceptual bias toward the target observed here. Importantly, our data further showed that visual discrimination performance remained around chance level at the location between saccade target and distractor (BTW) before the execution of averaging saccades, which demonstrates that the endpoint of averaging saccades was not visually selected before movement onset. This decoupling between

the locus of visual attention and the endpoint of averaging saccades is consistent with previous reports (Van der Stigchel & de Vries, 2015; Wollenberg et al., 2018). Together with similar dissociations observed at the behavioral (Belopolsky & Theeuwes, 2012; Smith, Schenk, & Rorden, 2012; Born, Mottet, & Kerzel, 2014; Hanning et al., 2019) and neuronal level (Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Thompson, Biscoe, & Sato, 2005; Gregoriou, Gotts, & Desimone, 2012), our data argue against an obligatory coupling between selective attention and the operations of the oculomotor system: Presaccadic attention is not necessarily deployed to the movement endpoint, but rather to the intended motor goal.

Finally, before the execution of distractor saccades, we observed that visual discrimination performance was not significantly enhanced at the saccade target relative to the distractor, but visual processing resources rather were slightly biased toward the distractor. However, as the total number of distractor saccades was very low, these data were much noisier compared to the data obtained for target saccades and averaging saccades, which limits interpretation. Still, our results point toward an interesting perceptual correlate of distractor saccades: Compared to target and averaging saccades, the discrimination benefit at the distractor was notably highest prior to distractor saccades. Distractor saccades therefore may reflect selection errors rather than systematic saccadic inaccuracies explained by an incomplete saccade target selection process that precedes averaging saccades.

Top-down control of saccade target selection at the neuronal level

At the neuronal level, the increase in saccade accuracy over time observed in this study can be explained by reduced competition among neuronal populations encoding the saccade target and the distractor as potential motor goals within a retinotopic saccade map (e.g. Trappenberg et al., 2001; Godijn & Theeuwes, 2002). Upon initial feed-forward (bottom-up) excitation of neuronal populations encoding both potential motor goals, active suppression of distractor-related activity within the saccade map across time may have facilitated accurate downstream oculomotor programming at longer latencies. For instance, Bichot and Schall (2002) showed that distractor-related activity in the monkey FEF starts to decay after an initial buildup, which matches with the deterioration of visual discrimination performance at the distractor over time observed in this study. Similarly, it has been suggested that visual attention can be transiently allocated at two separate locations at short latencies, but subsequently narrows down on a single target location due to competitive

interactions within oculomotor key structures (Dubois, Hamker, & Van Rullen, 2009; Zirnsak, Beuth, & Hamker, 2011). Moreover, the described dynamics are in line with the model of Trappenberg et al. (2001), which proposes that visual bottom-up signals can modulate activity within the saccade map very quickly, whereas cortical top-down processes can modulate activity only after a delay. Therefore, once the exogenous effect of bottom-up excitation via the visual onsets vanishes, top-down inhibition may lead to a decay of activity at the site of the distractor in the saccade map. Similarly, top-down selection of the saccade target emerging over time presumably may lead to a more pronounced sustainment of activity at the site of the saccade target. Crucially, despite their well-established involvement in the programming of saccadic eye movements, both FEF and SC are known to carry signals underlying visual selection (Corbetta, 1998; Moore & Armstrong, 2003; McPeek & Keller, 2004; Moore & Fallah, 2004; Müller et al., 2005). We therefore propose that both FEF and SC serve as neuronal substrates underlying the perceptual and oculomotor dynamics observed in our study.

Conclusions

Our study concurrently assessed the influence of top-down control on the spatiotemporal dynamics of visual attention and the accuracy of saccadic eye movements during episodes of competition between a saccade target and a proximal distractor. In line with earlier observations, our results demonstrate that both spatial predictability and longer visual processing time can effectively facilitate voluntary eye movement control. While being able to predict either the location of the upcoming target or the distractor likewise improves the capability to rapidly move the eyes in a goal-directed fashion, prolonged visual processing time prior to saccade onset allows for improved saccade accuracy even under spatial uncertainty. Interestingly, our data indicate that the top-down signals underlying the rapid control of saccadic eye movements do not affect visual perception prior to movement preparation. Over time, however, top-down eye movement control appears to emerge concurrently with the operation of selective attentional mechanisms, which allow to better distinguish the intended saccade target from the proximal distractor at the perceptual level. Finally, we report strong evidence for a systematic interaction between the presaccadic deployment of visual attention and the endpoint of saccades: Our data demonstrate that perceptual target selection is most efficiently resolved prior to the execution of saccades accurately landing at the saccade target, whereas target selection is not readily resolved before saccades deviating away

from it. The systematic relationship between visual attention and saccade accuracy does, however, not entail a mandatory coupling between the locus of visual attention and the saccade endpoint, as attentional resources are not deployed to the endpoint of averaging saccades.

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Amended October 1, 2020: In the second paragraph of the Results, the word "subtracting" has been changed to "computing" in the sentence that originally read "Saccadic go-signal delays did, however, not increase saccade latencies exactly proportional to their duration, which becomes evident when subtracting the mean saccade latency increase relative to the corresponding saccadic go-signal delay duration."