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# Pre-saccadic attention spreads to stimuli forming a perceptual group with the saccade target



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#### ABSTRACT

The pre-saccadic attention shift—a rapid increase in visual sensitivity at the target—is an inevitable precursor of saccadic eye movements. Saccade targets are often parts of the objects that are of interest to the active observer. Although the link between saccades and covert attention shifts is well established, it remains unclear if pre-saccadic attention selects the location of the eye movement target or rather the entire object that occupies this location. Indeed, several neurophysiological studies suggest that attentional modulations of neural activity in visual cortex spreads across parts of objects (e.g., elements grouped by Gestalt principles) that contain the target location of a saccade. To understand the nature of pre-saccadic attentional selection, we examined how visual sensitivity, measured in a challenging orientation discrimination task, changes during saccade preparation at locations that are perceptually grouped with the saccade target. In Experiment 1, using grouping by color in a delayed-saccade task, we found no consistent spread of attention to locations that formed a perceptual group with the saccade target. However, performance depended on the side of the stimulus arrangement relative to the saccade target location, an effect we discuss with respect to attentional momentum. In Experiment 2, employing stronger perceptual grouping cues (color and motion) and an immediate-saccade task, we obtained a reliable grouping effect: Attention spread to locations that were perceptually grouped with the saccade target while saccade preparation was underway. We also replicated the side effect observed in Experiment 1. These results provide evidence that the pre-saccadic attention spreads beyond the target location along the saccade direction, and selects scene elements that-based on Gestalt criteria-are likely to belong to the same object as the saccade target.

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#### 1. Introduction

Human vision is a powerful tool that reliably extracts information from the world around us. To do so, the visual system structures the pattern of light that hits the retinae according to well-known principles of perceptual organization (grouping or Gestalt laws; Metzger, 1936/2006; Wagemans, 2018; Wagemans et al., 2012), and acts upon that structure using eye movements. Here we ask how the eye movements themselves interact with the process of perceptual organization, and thus shape perception in active vision.

The highest spatial resolution the human visual system has to offer is reserved to a small portion of the visual field-the central 2 degrees of visual angle (dva) around the current gaze location called the fovea-and it drops sharply towards the periphery (Beard, Levi, & Klein, 1997; Loschky, Mcconkie, Yang, & Miller, 2005). As a consequence, rapid eye movements (saccades) constantly change the current point of gaze, allowing us to see any location in great detail. But gaze direction is not the only factor that determines what we perceive best at any given moment. The mechanism that prioritizes parts of the visual field over others-and that "turns looking into seeing" (Carrasco, 2011)—is visual attention. Selective prioritization of visual information that is most relevant to our behavioral goals at a particular point in time allows us to process essential information while ignoring a vast amount of irrelevant detail (Buschman & Kastner, 2015; Desimone & Duncan, 1995). The allocation of selective attention to relevant items in a scene is often accompanied by overt eye-movements to those items but shifts of attention can also occur covertly (Carrasco, 2011). Using challenging visual discrimination tasks, such covert shifts of visual attention can be captured in psychophysical studies as short-lived and spatially selective increases in visual sensitivity in the visual periphery (Balz & Hock, 1997; Carrasco, 2011; Posner, 1980; Yeshurun & Carrasco, 1998, 1999, reviewed in; Carrasco, 2011).

Objects within a scene are important sources of information to guide the allocation of attention and accordingly our eyes visit the locations that are chosen based on them (Foulsham & Kingstone, 2013; Nuthmann & Henderson, 2010; Pajak & Nuthmann, 2013). These objects are likely to cover more than 2 dva of the visual field and will thus extend beyond the fovea upon saccade landing. There is ample evidence that attention spreads across objects that are currently fixated or attended covertly (Duncan, 1984; Egly, Driver, & Rafal, 1994; Jeurissen, Self, & Roelfsema, 2016; Malcolm & Shomstein, 2015), suggesting that perceptual organization of the scene drives attentional selection. Perceptual organization, in turn, is based on Gestalt principles, such as similarity and common fate (see Wagemans, 2018, for a review). In this study, we addressed the question if the preparation of a saccade to a location results in an inadvertent spread of covert attention to locations that, based on these Gestalt principles, are likely to belong to the same object.

#### 1.1. Pre-saccadic attention shifts

The execution of saccadic eye movements is neither necessary nor sufficient for the control of covert attention (Casteau & Smith, 2019; Hunt, Reuther, Hilchey, & Klein, 2019; Zhao, Gersch, Schnitzer, Dosher, & Kowler, 2012). At the same time, saccades cannot be executed without a preceding (presaccadic) shift of attention (reviewed in Zhao, Gersch, Schnitzer, Dosher, & Kowler, 2012). In studies of this presaccadic attention shift, observers typically have to execute fast and accurate eye movements to a cued stimulus (usually, one out of several stimuli presented on a display). Concurrently they have to perform a perceptual discrimination task on a probe presented either at the saccade target or at some other location. Performance in this discrimination task is a proxy for attentional allocation to the probed location. A large body of research using this dual-task procedure has demonstrated that these attention shifts drive performance selectively at the saccade goal and form an obligatory part of saccade preparation (Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995; Montagnini & Castet, 2007) unfolding just 100 msec before the execution of the movement (Deubel, 2008; Ohl, Kuper, & Rolfs, 2017; Rolfs & Carrasco, 2012; White, Rolfs, & Carrasco, 2013). Pre-saccadic attention shifts occur automatically even if participants are forced to allocate their attention away from the saccade target, that is, when attention is cued and probed at a different location than the saccade target (Castet, Jeanjean, Montagnini, ; Deubel, 2008; Hoffman & Subramaniam, 1995; Montagnini & Castet, 2007). Moreover, attention selects the saccade target even when it is located beyond the oculomotor range and thus cannot be reached by eye movements alone (Hanning, Szinte, & Deubel, 2019).

This behavioral evidence ties in nicely with the results of neurophysiological studies investigating the role of oculomotor brain areas—including the lateral intraparietal cortex, the frontal eye fields and the superior colliculus-in the control of covert attention (see Awh, Armstrong, & Moore, 2006, for a review). These studies first identified neurons in Superior Colliculus (SC) and frontal eye fields (area FEF) that-given sufficient electrical microstimulation-would elicit saccades to specific, stereotyped locations in the visual field. They then went on to provide two lines of evidence for a causal role of these neural populations in pre-saccadic attention shifts. First, sub-threshold stimulation of these neurons (which would not elicit a saccade) increased visual sensitivity specifically at the corresponding location in the visual field (Cavanaugh & Wurtz, 2004; Moore & Armstrong, 2003; Moore & Fallah, 2001, 2004). Second, reversible inactivation of these neurons resulted in corresponding, spatially specific deficits of the deployment of covert attention (Balan & Gottlieb, 2009; Lovejoy & Krauzlis, 2010; Wardak, Ibos, Duhamel, & Olivier, 2006; Wardak, Olivier, & Duhamel, 2004; Zénon & Krauzlis, 2012).

# 1.2. Relation between attention and perceptual organization

Thus far, pre-saccadic attention shifts have been considered a selective prioritization of a particular location, the saccade target. In natural vision, however, the pattern of light that hits the retinae is carefully organized and segmented according to principles of perceptual organization (grouping or Gestalt laws; Metzger, 1936/2006; Wagemans, 2018; Wagemans et al.,

2012). Parts of the same object, unlike parts of different objects, usually move in the same direction, they have the same color, and their contours align in a collinear fashion. Objectbased attention automatically enhances all aspects of an object (Duncan, 1984; Ernst, Boynton, & Jazayeri, 2013; Hollingworth, Maxcey-Richard, & Vecera, 2012; O'Craven, Downing, & Kanwisher, 1999; Richard, Lee, & Vecera, 2008) as it rapidly spreads along the object (Jeurissen et al., 2016). Whether covert attention per sé is a spatially selective mechanism or, instead, object-based by nature has been debated for decades and there is substantial evidence that both components are equally present in visual processing (Abrams & Law, 2000; Egly et al., 1994; Müller & Kleinschmidt, 2003; Yeshurun & Rashal, 2017).

Several studies (McCarley, Kramer, & Peterson, 2002; Theeuwes, Mathôt, & Kingstone, 2010) investigated if saccades are driven by laws of perceptual organization, using a modified version of the paradigm developed by Egly et al. (1994). These studies measured gaze direction and the duration of fixations on items in a display and showed that observers more often made eye movements within rather than between objects. Mean gaze duration on a particular item was longer preceding saccades to a different object than preceding saccades to the same object. These authors concluded that eye movements, much like covert attention, are guided by a perceptual representation of the objects. To explain observers' tendency to keep gaze within objects, Theeuwes et al. (2010) presented an adapted version of the biased competition theory of spatial attention (Desimone & Duncan, 1995). According to this account, attending to one object is accompanied by the inhibition of others, and eye movements are more likely to be executed within an already attended object. Malcolm and Shomstein (2015) corroborated this idea in an experiment in which participants inspected real-world scenes: People executed faster eye movements towards a target positioned at the same object as compared to an equidistant target placed at a different object.

This wide range of studies provides strong evidence that perceptual groups, formed pre-attentively on basis of gestalt criteria, guide visual attention. At the same time there is strong evidence that attentional selection itself gives rise to the formation of perceptual objects: Pooresmaeili and Roelfsema (2014) investigated the neurophysiological mechanisms that may underlie the spread of attention along selected objects. They measured activity in primary visual cortex (V1) of macaque monkeys performing a contourtracing task, in which subjects had to mentally trace a target curve and ignore a distractor curve (see also Roelfsema, Lamme, & Spekreijse, 1998). Attentional selection of contour elements-here, measured by an increased firing rate of neurons whose receptive field overlaps with these elements-spread gradually over the neural representation of the target curve, slowing down at the locations representing segments of the target curve that were close to the distractor. The results support the idea that, in V1, attention spreads according to Gestalt rules adding elements to each other until attention encompasses the entire object.

At this point, we might speculate that the pre-saccadic attention shift also spreads along the object at the target of an eye movement, gathering segments into a whole in accordance with Gestalt rules. Indeed, it seems plausible that selection of some part of an object-for instance with the intention to look at it or to grasp it-might reinforce the perceptual grouping of its elements. We provide two lines of evidence to support this prediction. Firstly, object-based attention as in the task tested by Pooresmaeili and Roelfsema (2014) relies on a tight interaction between V1 and areas that are involved in the planning of eye movements and shifts of attention (i.e., FEF, see Pooresmaeili, Poort, & Roelfsema, 2014), suggesting that planning of a saccade may influence the perceptual grouping of object elements. Secondly, Wannig, Stanisor, and Roelfsema (2011) showed an automatic spread of neural attentional selection to objects outside of the attentional focus, provided they were grouped with an attended stimulus by Gestalt criteria. In particular, they reported an increase in the activity of V1 neurons whose receptive fields contained stimuli that were grouped with saccade target by one of several Gestalt criteria, such as collinearity, similarity, common fate, or their combination. Since perceptual sensitivity was not probed behaviorally along the grouped items, it remains unclear if this neural signature entails behavioral consequences of visual selection.

Three studies, known to the authors, suggest that presaccadic selection might well be shaped by processes of scene segmentation. First, Puntiroli, Kerzel, and Born (2018) showed that the absence of placeholders around a saccade target led to the reduction of pre-saccadic attention as probed in a perceptual discrimination task. Similarly, Szinte, Puntiroli, and Deubel (2019) showed that the presence of a target object itself contributes to the spatial specificity of presaccadic selection: A target that was visible throughout saccade preparation yielded sharper spatial selectivity of the pre-saccadic attention shift than one that disappeared before saccade onset. Finally, Ghahghaei and Verghese (2017) showed that the spatial spread of pre-saccadic selection of a saccade target extends to the boundaries of a texture in which the target is located.

In the present study, we examined whether pre-saccadic attention automatically selects visual stimuli that are perceptually grouped by Gestalt principles (i.e., similarity and common fate) with a saccade target. This would corroborate the neurophysiological data by Wannig et al. (2011) in humans and show object-based attentional selection at the behavioral level. In two experiments, investigating delayed (Experiment 1) and immediate saccades (Experiment 2), we directly measure attention as sensitivity in a visual discrimination task and inspect the time course of attention allocation towards a saccade target and visual elements grouped (or not grouped) with it. In the delayed saccade task (Experiment 1), we found a complex pattern of results, with no consistent spread of attention to locations that formed a perceptual group (grouping by color) with the saccade target (Grouping effect). However, performance depended on the side of the probed location relative to the saccade target location (Side effect). In the immediate saccade task (Experiment 2), we simplified the experimental design and increased the strength of perceptual grouping by combining color with motion cues (common fate). We replicated the Side effect and found a robust effect of perceptual grouping: Attention spread to locations that were grouped with the saccade target by Gestalt criteria with a time

course that was largely independent of the course of saccade preparation and was different at the two sides of the stimulus configuration. We discuss possible explanations for this prominent Side effect in spread of pre-saccadic attention. First, we consider an attentional momentum mechanism as a driving force for this effect. Second, we assume that the interaction of visual short-term memory and attention during the saccade preparation might contribute to this effect especially during the early stages of saccade preparation.

#### 2. Experiment 1

#### 2.1. Materials and methods

#### 2.1.1. Participants

We recruited participants with normal or corrected-to-normal vision among students through campus mailing lists at Humboldt-Universität zu Berlin, Charité – Universitätsmedizin Berlin, and the Bernstein Center for Computational Neuroscience Berlin. Before starting the experimental sessions, each participant completed one initial training session and a staircase procedure (see below). Participants whose performance in one of the first two sessions was lower than 60% (5 participants) or who could not finish the training due to difficulties in the saccade task (4 participants) were not included in the study. We ultimately included the data from ten participants in our analyses (mean age  $\pm$  SD: 26  $\pm$  3.56, 8 females, 3 left-handed, 5 left-eye dominant)—five collected at campus Mitte and five at campus Adlershof after a relocation of the lab (equipment and setup remained the same).

All participants were naive as to the purpose of the study and gave written informed consent before their participation in the experiment. Participants received 7€ per session as compensation and an additional 10€ bonus after the completion of the last session. The study was conducted in accordance with the World Medical, Association (2013). The design of the study, research hypothesis, as well as the sampling and analysis plans, were preregistered on the Open Science Framework before data collection commenced (OSF; https://osf.io/c9zb3/ - main page; https://osf.io/c9zb3/wiki/ home/ - a wiki page with an introduction and a list of the preregistration sections; click on the tabs on the "Project Wiki Pages" panel to see the full preregistration content). All changes to the analysis plan are transparently identified, and the outcomes of pre-registered and post hoc analyses are distinguished. We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

#### 2.1.2. Equipment

The stimuli were presented on a 23.6-in. ViewPixx/3D screen (1920 \* 1080 pixels; VPixx Technologies Inc., Saint Bruno, QG, Canada) with a color depth of 10 bits on each of the RGB channels and a vertical refresh rate of 120 Hz. Sounds were synchronized with visual stimuli at sub-millisecond precision using the VPixx's DATAPixx3 VideoBahn architecture, allowing minimal delay between the scheduled initiation of a tone, and when the first audio waveform sample was played. The distance from the participant to the monitor was 57 cm; we used a chin and forehead rest to stabilize the participant's head. We recorded the eye position of the participant's dominant eye [confirmed beforehand using the Miles test (Miles, 1930)] with a sampling rate of 1000 Hz using an Eyelink 1000 Desktop Mount (SR Research, Ottawa, ON, Canada). The experiment was controlled on a workstation running the Debian 8 operating system, using Matlab (Mathworks, Natick, MA), the Psychophysics Toolbox 3 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) and the EyeLink Toolbox (Cornelissen, Peters, & Palmer, 2002).

#### 2.1.3. Experimental design

Each trial started with a fixation point (bull's eye with radius .3 dva), presented in the center of a gray screen (luminance of 77 cd/m<sup>2</sup>) for 300 msec before the stimulus set appeared. The stimuli were four vertically oriented gratings (50% contrast) located at the vertices of an imaginary diamond shape with a side length of 3 degrees of visual angle (dva) and a spatial frequency of 4 cycles per dva. The diamond's center was positioned at one of four diagonal locations, 5.2 dva away from the fixation point (Fig. 1a). Circular outlines with .78 dva radius enveloping these gratings had one of two colors, blue and brown (CIE Yxy 39.0 cd/m<sup>2</sup>, .11, .26 and 37.2 cd/m<sup>2</sup>, .40, .39, respectively), such that each color was shared by two stimuli (see Supplementary Material for a video of the stimulus display). On each trial, this grouping by color followed one of three arrangements (Fig. 1b). In the Tangential arrangement, the two locations at the same eccentricity from the center had outlines of the same color. In the Radial arrangement, the two locations on the same side relative to the diagonal from the central point to the diamond center had outlines of the same color. In the Diagonal arrangement, the two locations on the opposite vertices of the imaginary diamond had outlines of the same color.

Supplementary video related to this article can be found at https://doi.org/10.1016/j.cortex.2021.03.020.

To avoid any interference of the attentional probe with oculomotor variables (cf. Hanning, Deubel, & Szinte, 2019; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011), the stimuli flickered in alternation with patches of white noise, displayed at the same location, with the same size and circular outline (each frame was presented for 25 msec). 500 msec after stimulus onset, a movement cue (a black bar of .09 dva width and .23 dva length, sticking out from the fixation point towards the center of the saccade target) appeared to indicate which of the two locations proximal to the fixation was the saccade target (Fig. 1c represents the time course of events in a trial), while participants had to continue fixating in the center. Another 500 msec later, a tone (675 Hz for 33 msec) and the simultaneous disappearance of the movement cue served as the go signal for the saccade, informing participants that the movement has to be executed within 400 msec. At one of three stimulus onset asynchronies (SOA; probe onset at -50, 300, or 600 msec relative to movement cue onset), one of the four gratings changed its orientation for 25 msec (probe stimulus) whereas all other gratings remained at their original orientation (Fig. 1d). After this frame, all four gratings were replaced by white noise patches until the end of the trial. After eye





#### c Fixation



Fig. 1 – (a, b): Stimulus layout and trial procedure. (a): In any given trial, only one of the four possible locations was occupied by the stimulus set (here - bottom left relative to the central fixation point; three other possible locations are represented by the dashed circles that were not visible during the experiment). (b): Three arrangements of grouping, from left to right: Tangential, Radial, Diagonal. For simplicity, the saccade target is displayed in blue and at location A throughout. The other location with a blue outline is the stimulus grouped with the saccade target. (c): Time course of events in a trial. Each grey segment in a line represents a 25 msec frame. The offset of the movement cue coupled with a tone was the go signal for the saccade. Probes were presented with SOAs of either -50, 300, or 600 msec. (d): Schematic depiction of the dynamic stimulus stream.

movement execution, the participant had to report the perceived direction of orientation change (left arrow key for; right arrow key for) irrespective of the location of the probe. The response was self-paced, and accuracy was emphasized over speed. A 75 msec feedback tone, indicating whether the response was correct (low pitch - 180 Hz - for incorrect response; high pitch - 600 Hz - for correct response), was presented 200 msec after the key was pressed during the initial training session, but not during the main experiment. We controlled online (i.e., in real time) for fixation and eye movement onset as well as for the direction of the saccade. Trials with a fixation break, late saccade onset, and/or saccades outside a target region (radius of 1.5 dva from the target's center) were interrupted and repeated at the end of the current block of trials.

2.1.3.1. INITIAL TRAINING SESSION. The first session did not contain experimental trials. Participants were familiarized with the task, ran training blocks, and a staircase procedure. The training was divided into four stages, starting with the simplest task:

- 1. Training of the orientation-discrimination task without eye tracking. Participants were instructed to look at the location of the four stimuli and to report the direction of a tilt at the probed one. At this stage (and at stages 2 and 3), the angle of a tilt at a probed location was 30° relative vertical.
- 2. Training of the orientation-discrimination task with verbalization but without eye tracking. The task was similar to the one in Stage 1, but participants had to verbally report the probed location (top, bottom, right, or left) and direction of tilt before pressing the response key. The experimenter gave them verbal feedback regarding the reported location and the tilt direction.
- Training of the orientation-discrimination task with eye tracking. Participants trained both the oculomotor task and the discrimination task at the same time.
- 4. Training of the orientation-discrimination task at threshold with eye tracking. After the completion of a staircase procedure (see below), participants were trained using the obtained orientation threshold, combined with a saccade task.

2.1.3.2. STAIRCASE PROCEDURE. The goal of the staircase procedure was to titrate the difficulty of the orientationdiscrimination task by varying the angle of orientation change such that it would be possible for each participant to perform with  $75 \pm 15\%$  accuracy. As we assumed that distance from fixation would be a crucial factor that determines the difficulty of the discrimination task, we ran separate staircases for each eccentricity (close and distant locations) and established two independent thresholds for each. The angle of orientation change was defined for the upcoming trial depending on answers in the previous trials. For each eccentricity, one of the two staircases started with a 5° orientation change and followed a 1-up/3-down rule (step size: 4° before the first, 2° after the first, and 1° after the second reversal); the other one started with 20° and followed a 1-up/2-down rule (Levitt, 1971). We averaged the two thresholds, each obtained by averaging the angles in the last 6 reversals, for each eccentricity and used these values to define the probe's orientation change in the experimental procedure. The resulting stimulus orientations, which we used in the experimental sessions, were  $19.9 \pm 1.4^{\circ}$  (Mean  $\pm$  SEM) for the close and  $22.8 \pm 1.4^{\circ}$  for the distant locations.

During the staircase procedure, eye movements were recorded, but participants had to fixate the fixation point. The trial procedure and the stimulus timing were identical to the experimental trials (see above), including the presentation of a cue (which was task-irrelevant during this procedure). On each trial, participants reported the direction of the probe's orientation change. In total, the staircase procedure consisted of 256 trials. Participants had a self-paced break after every 32 trials. The staircase procedure was run during the initial training session after the training with eye tracking.

2.1.3.3. EXPERIMENTAL SESSIONS. Each session contained 6 blocks, with 96 trials in each. Each block consisted of trials with one particular SOA. Thus, in each session participants executed 2 blocks of each SOA (i.e., -50, 300, 600 msec). Block order within the sessions was randomized. In total, nine participants completed 2880 experimental trials across five experimental sessions, and one participant completed 2304 experimental trials across four experimental sessions (one session was cancelled because the lab moved to a new location during the data collection phase). Each session lasted approximately one hour, with at least one night between consecutive sessions.

#### 2.1.4. Data collection

During the data collection stage, we examined average performance after each session for both close and distant locations to make sure that participants performed reliably above chance (i.e., that the task was neither too easy nor too difficult). If the participant did not achieve a performance level in the range of  $75 \pm 15\%$  (across all conditions) we executed one more staircase procedure to adjust the level of difficulty.

#### 2.1.5. Data preprocessing

In total, we collected 28,224 trials across all observers. To detect saccades offline, we transformed raw eye positions into two-dimensional velocity space. We classified successive eye positions as saccades if they exceeded the median velocity by 5 SDs for a minimum duration of 8 msec (Engbert & Mergenthaler, 2006). Two saccadic events separated by less than 10 msec were merged into a single saccade. We discarded trials with missing samples in the recordings, and trials that included saccades with an amplitude larger than 1 dva before the execution of the instructed response saccade (Mean  $\pm$  SEM: 4.3  $\pm$  1.0% of trials per participant). In our assessment of eye movement parameters, we excluded trials in which, due to display delays, either probe onset or probe offset were delayed (9.6  $\pm$  .2% of trials per participant). Finally, for the analysis of discrimination performance, we also discarded trials in which saccade onset preceded probe offset. This was done to avoid including any trials in which the probe was (partially) presented while the saccade was in flight. Due to the implementation of this criterion,  $7.9 \pm .8\%$  of trials per

participant were excluded. A total of 22,471 trials (79.6%) remained for the final analysis (Mean  $\pm$  SEM: 2247  $\pm$  56 trials per participant).

#### 2.2. Results

#### 2.2.1. Eye movement parameters

In a first step, we inspected eye-movement parameters to assess if the presentation of the probe affected saccade programming (Hanning, Deubel, & Szinte, 2019; Rolfs et al., 2011), which in turn could have affected our measurements of attention. Specifically, if saccades were not affected by the presentation of the probe, then probe location should not affect saccade metrics. We ran two linear mixed-effects (LME) models to test the influence of SOA, Probe location, and their interaction as fixed effects and participant as a random factor, on saccade latency and landing error (relative to the center of the saccade target). Estimated effects, their standard errors, as well as t- and *p*-values are provided in Supplementary Tables 1.1 and 1.2.

2.2.1.1. SACCADE LATENCY. We observed a strong effect of SOA on saccade latency for all of the four Probe locations (Fig. 2, left). For probes at the Saccade target location presented at an SOA of -50 msec (baseline condition), the average latency was 117  $\pm$  3 msec; it was 16  $\pm$  2 msec and 38  $\pm$  2 msec longer for the 300 and 600 msec SOA, respectively. The slopes of the latency functions for other Probe locations did not differ significantly. The only exception was found for location C for the SOA of 600 msec, where latency increased slightly less with SOA than at the Saccade target (Estimate  $\pm$  SE:  $\beta = -6.08 \pm 2.45$ , t = -2.45, p = .013). We explain this difference in slopes as a difference in the shortest SOA: With an SOA of -50 msec, saccade latencies were 4  $\pm$  2 msec (location B;  $\beta$  = 3.71  $\pm$  1.69, t = 2.19, p = .029) and 6  $\pm$  2 msec (location C;  $\beta$  = 5.51  $\pm$  1.69, t = 3.26, p = .001) longer than when the Saccade target was probed. The delayed saccade task may have caused this effect: With an SOA of -50 msec, the go-signal occurred 525 after probe offset, providing sufficient time for the probe to interfere with



Fig. 2 – Saccade latency and landing error as a function of probe location and SOA, averaged across the three arrangements. Error bars are 95% confidence intervals (CIs).

saccade planning. For SOAs of 300 and 600 msec, saccade latency was independent of probe location.

2.2.1.2. LANDING ERROR. Participants made accurate saccades across all conditions (average errors of <.8 dva; Fig. 2, right) and probe location did not affect landing error. We found a subtle effect of SOA: when the probe was presented in the Saccade Target location, landing error was 2 arcmin smaller for the 600 msec versus the -50 msec SOA ( $\beta = -.03 \pm .01$ , t = -2.32, p = .02).

Based on these sanity checks, we conclude that our experimental design allowed us to present attentional probes without disrupting saccade preparation.

#### 2.2.2. Discrimination performance

2.2.2.1. PERFORMANCE AT THE SACCADE TARGET LOCATION. The main focus of our study was performance in the visual discrimination task, as it provides a sensitive measurement for the spatiotemporal allocation of visual attention. First of all, we predicted performance to be highest at the saccade target location for SOAs of 300 and 600 msec. We expected that it would increase continuously towards an SOA of 600 msec, as this time point should be closer to saccade onset, when presaccadic attention should be shifted to the saccade target. We found evidence for the former hypothesis but not for the latter (Fig. 3).

As a different location was grouped with the saccade target in each arrangement, we split the data into three subsets (one per arrangement) and ran separate analyses for each. As a first step, we ran generalized linear mixed-effects models (GLMER) to test the influence of SOA and probe location on the performance for all four locations using the Saccade target location and the -50 msec SOA as a baseline. The models included SOA, Probe location, the interaction SOA × Probe location as fixed factors, and participant as a random factor (detailed results in Supplementary Tables 2.1–2.3). First, we considered the effect of SOA on performance when the probe was presented at the Saccade target location. We observed a main effect of SOA for the Saccade target location for all three arrangements. The proportion of correct responses increased consistently with the SOA from -50 msec to 300 msec (from  $72.8 \pm 2.8\%$  to  $88.5 \pm 2.5\%$  in Tangential:  $\beta = 1.15 \pm .15$ , z = 7.75, p < .001; from  $67.9 \pm 2.5\%$  to  $86.4 \pm 1.9\%$  in Radial:  $\beta = 1.13 \pm .14$ , z = 8.14, p < .001; from  $67.9 \pm 3.3\%$  to  $88.3 \pm 1.3\%$  in Diagonal:  $\beta = 1.28 \pm .14$ , z = 8.85, p < .001). Contrary to our expectations, performance decreased again for the 600 msec SOA (Tangential:  $83.9 \pm 1.5\%$ ; Radial:  $75.8 \pm 2.9$ ; Diagonal:  $81.0 \pm 1.8\%$ ). Nevertheless, it was significantly higher than for the -50 msec SOA (Tangential:  $\beta = .75 \pm .15$ , z = 4.86, p < .001; Radial:  $\beta = .41 \pm .14$ , z = 2.94, p = .003; Diagonal:  $\beta = .72 \pm .14$ , z = 5.01, p < .001).

The observed decline in performance closer to saccade onset (in SOA 600 msec) is inconsistent with the wellestablished dynamics of pre-saccadic attention, which show that closer to saccade onset, performance in visual discrimination tasks increases monotonically (e.g., Deubel & Schneider, 1996; Kowler et al., 1995; Rolfs & Carrasco, 2012; Rolfs et al., 2011). A possible explanation resides in the timing of delayed saccade task (see Fig. 1c): At an SOA of 300 msec, participants already knew the location of the saccade target and, due to the allocation of covert attention, visual sensitivity at this location might have reached its peak at the moment of probe onset, whereas at an SOA 600 msec the probe appeared 100 msec after the go-signal, launching saccade preparation and the pre-saccadic attention shift. The go signal was coupled with the disappearance of the movement cue and a simultaneous tone. These exogenous events might have caused distraction for the general attentional processing of the stimulus display, yielding reduced performance for the 600 msec SOA. The similarity of this decrease in performance (i.e., from the



Fig. 3 – Orientation-discrimination performance as a function of stimulus arrangement, probe location, and SOA. In each panel, filled symbols indicate the location grouped with the saccade target. Error bars are 95% CIs.

300 msec to the 600 msec SOA; see Fig. 3) across all four locations is consistent with this reasoning.

Next, we compared performance at non-target locations with performance at the Saccade target location. We found that at an SOA of -50 msec, in the Radial and Diagonal arrangements, performance at the saccade target was comparable to performance at other locations, as the saccade target location was not yet cued at this point in time. In Tangential arrangement, however, performance at the Saccade target was slightly but significantly higher than at other locations (location B:  $\beta = -.25 \pm .12$ , z = -2.12, p = .034; location C:  $\beta = -.23 \pm .12$ , z = -1.99, p = .046; location D:  $\beta = -.36 \pm .12$ , z = -3.11, p = .002).

When the probe was presented after cue onset (300 and 600 msec SOAs), performance was significantly higher at the saccade target location than at other locations. To corroborate this finding, we ran a follow-up analysis using the same GLMER model as in the previous sections (Supplementary Tables 2.1–2.3) to compare the estimated marginal means with one another (using the emmeans package in R; pairs method with Holm's adjustment for multiple comparison (Holm, 1978). In each of the arrangements with an SOA of 300 msec, performance at the Saccade target location (location A) was significantly higher than at other locations. The performance benefit for the Saccade Target location compared to any other location was 7.6  $\pm$  2.1% or more. With an SOA of 600 msec, results were not as consistent for the Radial arrangement, but Tangential and Diagonal arrangement had the same pattern of results including a significant benefit at the Saccade target location (see Supplementary Tables 3.1-3.3 for detailed results).

To sum up, after movement cue onset, visual sensitivity increased at the saccade target location more markedly than at any of the non-target locations. Performance then dropped after the onset of the saccade go signal but still remained higher than before cue onset.

2.2.2.2. PERFORMANCE AT NON-TARGET LOCATIONS GROUPED WITH THE SACCADE TARGET. As a next step, we analyzed performance at the location grouped with the saccade target. In particular, we tested whether performance at these locations was higher than at non-grouped locations for the SOAs 300 and 600 msec (detailed results of these comparisons are in the Supplementary Tables 3.1–3.3). In the Tangential arrangement, performance at location B (grouped with the saccade target) was comparable to that at other location C (grouped with the saccade target), was comparable to that at location B and higher than at location D, but only for the 300 msec SOA ( $\beta = .48 \pm .13$ , z = 3.79, p = .002). In the Diagonal arrangement, performance at location D (grouped with the saccade target) was comparable to that at other locations.

In summary, we did not find a consistent effect of grouping with the saccade target on performance in the pre-saccadic orientation discrimination task.

#### 2.2.3. Focused follow-up analysis

To better understand the results, we decided to run a reduced, exploratory follow-up analysis that investigated the differences in the allocation of attention between critical conditions. While this analysis was post-hoc, it allowed us to address two concerns. First, we wanted to eliminate a possible influence of the distance of the probe location from the fixation point. Second, averaging the results across different arrangements allowed us to increase statistical power. We ran this analysis in three steps, each addressing a separate question.

2.2.3.1. SACCADE-TARGET EFFECT. First, we analyzed the difference between performance at the saccade target versus the non-target location close to the fixation point (A vs B; Fig. 4a). Using only the data from these probe locations, we ran a GLMER with SOA (-50 msec as a baseline), Probe location (Saccade target as a baseline), the interaction SOA  $\times$  Probe location as fixed factors, participant as a random factor, and performance as the predicted outcome (see Supplementary Table 4.1). The intercept represents performance in the baseline condition (Saccade target location at SOA -50 msec). This analysis revealed that performance at the non-target location was lower than at the saccade target ( $\beta = -.18 \pm .07$ , z = -2.60, p = .009) as soon as -50 msec before cue onset (-50 msec SOA). We observed a main effect of SOA: Performance at the Saccade target location was higher after a 300 msec than after a -50 msec SOA. Performance then declined at the 600 msec SOA. Finally, there was an interaction between probe location and SOA: The increase of performance at the non-target location in SOA 300 msec was less prominent (by about 10%) than at the target location  $(\beta = -.79 \pm .11, z = -7.32, p < .001)$ . This observation strengthens the conclusions of our previous analyses that attention was allocated towards the saccade target, and that performance was reduced in SOA 600 msec for both target and non-target stimuli.

 $2.2.3.2.\ Grouping$  effect. In order to test the average effect of grouping, we focused only the radial and diagonal arrangements, in which one of the distant elements was grouped with the saccade target. In particular, we compared the average performance at the two distant locations (Fig. 4b) when they were either grouped (C in radial arrangement and D in diagonal arrangement) versus not grouped with the saccade target (D in radial arrangement and C in diagonal arrangement). We ran a GLMER with SOA (-50 msec as the baseline), Grouping (grouped or not grouped with the saccade target) and interaction SOA  $\times$  Grouping as fixed factors, and participant as random factor (detailed results are presented in Supplementary Table 4.2). We found an effect of SOA, showing that performance in the 300 msec SOA condition was elevated with respect to the baseline ( $\beta$  = .42 ± .09, z = 4.95, p < .001). No other effects, including the effect of Grouping, were significant.

2.2.3.3. SIDE EFFECT. Focusing again on the radial and diagonal arrangements only, we inspected the difference in performance between the distant location on the same side (C) versus the different side (D) as the saccade target (Fig. 4c). We ran a GLMER with SOA (-50 msec as a baseline), Probe location (on the same or on the different side relative to the saccade target) and the interaction SOA  $\times$  Probe location as fixed factors, as well as participant as random factor (Supplementary)



Fig. 4 – Orientation-discrimination performance as a function of SOA and probe location. (a): Saccade target versus Nontarget location close to the initial fixation location. (b): Distant locations either grouped or not grouped with the saccade target. (c): Distant location either on the same side or on the different side of the stimulus configuration relative to the saccade target. The bottom panels show performance differences between the two locations, both for individual participants (gray) and averaged across participants (black). Error bars are 95% CIs.

Table 4.3). The intercept represents performance in the baseline condition (same side at SOA -50 msec). We found a significant effect of SOA: Performance was higher after a 300 msec SOA than a -50 msec SOA at the location that was at the same side of the stimulus configuration as the saccade target ( $\beta = .51 \pm .09$ , z = 5.88, p = <.001). In addition, we obtained an interaction effect: Performance at the different side did not increase as markedly as on the same side as the saccade target (SOA 300 msec:  $\beta = -.34 \pm .12$ , z = -2.79, p = .005; SOA 600 msec:  $\beta = -.25 \pm .13$ , z = -1.92, p = .055). Thus, attention was allocated towards the stimulus that was on the same side of the configuration relative the saccade target after a 300 msec SOA. This effect was not predicted before the beginning of the study, and it will be addressed in more detail in Experiment 2.

2.2.3.4. PERFORMANCE AS A FUNCTION OF TIME RELATIVE TO SACCADE ONSET. As a final step, we examined the dynamics of presaccadic attention relative to saccade onset. For this purpose, we used the data from the SOA 600 msec condition, that is, when the probe was presented 100 msec after the go signal. Due to the variability in each individual's saccade latency, we could determine post-hoc the time points when the probe was presented relative to saccade onset. As a function of time between probe offset and saccade onset (across all observers), we split the data into 4 bins that each contained an equal number of trials. The first bin featured earlier stages of saccade preparation contained trials in which the probe offset happened 262 to 69 msec before saccade onset. The last (fourth) bin contained trials in which the probe offset happened only 25 to 1 msec before saccade onset (Fig. 5).

Our first goal here was to evaluate the shift of attention to the saccade target and its dynamics. We hypothesized that, due to stronger attention allocation towards the saccade target, performance at the saccade target location would be higher in trials in which the probe was presented closer to saccade onset. Second, we inspected whether the effects of Grouping and Side were observed in this reduced data set. Similar to the reduced analysis section, we ran GLMER models to test the influence of *Target, Grouping*, and *Side*, with Time between probe offset and saccade onset, rather than SOA, as a factor (Fig. 5; Supplementary Tables 5.1–5.3).

*Target*: Performance at the saccade target location (A) was higher than at the close non-target location (B) throughout saccade preparation (i.e., across all time bins). Contrary to our expectation, discrimination performance declined at both the saccade target and the non-target locations, starting from the earliest stages of saccade preparation to the time point shortly before saccade onset (Fig. 5a). For the Saccade target, this decline became significant in the last 25 msec before saccade onset ( $\beta = -.62 \pm .20$ , z = -3.10, p = .002). While the difference between the saccade target and the non-target locations continued to increase towards saccade onset not reaching the level of significance, there was no significant difference in the



Fig. 5 – Orientation-discrimination performance as a function of probe offset time relative to saccade onset, across all trials with an SOA of 600 msec. (a): Saccade target versus non-target location close to the initial fixation location. (b): Distant locations either grouped or not grouped with the saccade target. (c): Distant location either at the same side of the stimulus configuration relative to the saccade target. Error bars are 95% CIs.

steepness of the decline for the Non-target compared to the Saccade target location.

Grouping & Side: As in the reduced analysis reported above, we focused on the distant locations (C and D) and the radial, and diagonal arrangements, in which one of the distant elements was grouped with the saccade target. We found neither effects of Grouping (Fig. 5b) or Side (Fig. 5c), nor an effect of the Time between probe offset and saccade onset on orientation discrimination performance (Supplementary Tables 5.2 and 5.3).

#### 2.3. Discussion

In Experiment 1, we employed a delayed saccade task to test whether attention is allocated towards stimuli that are perceptually grouped with a saccade target. We presented a cue identifying the saccade target 500 msec before the saccade go signal, and probed attention at four locations at three time points during the trial (50 msec before the cue, 300 msec after the cue and 100 msec after the go signal). While the largest effect was clearly the difference in performance at the saccade target versus any of the non-target locations, we also found a moderate effect of Grouping on attentional allocation at SOA 300 msec: When the stimulus grouped with the saccade target was displayed on the same side of the stimulus configuration, visual discrimination was better than at ungrouped locations. Here, however, we were unable to disentangle whether the increase in performance was mainly driven by perceptual grouping or by the effect of the probed side that we encountered in additional analyses.

One of the reasons for finding only subtle evidence for the impact of grouping on attentional selection might be the

choice of grouping features: Pairs of stimuli were grouped by the color of their circular outline. To facilitate the spread of attention, color might not be the most efficient feature. Indeed, Wannig et al. (2011) found that grouping by color had a smaller effect on the spread of neural attentional selection compared to grouping by other factors such as collinearity or common fate. Another limitation of Experiment 1 is the nature of the delayed saccade task. In this task, the saccade go signal – the disappearance of the cue coupled with a tone – might have distracted attentional processing. For SOAs of 600 msec, this distractor occurred shortly before the probe onset, and possibly led to the observed decline in perceptual sensitivity at the saccade target location, as the time approached saccade onset (Fig. 5a). This decline is in apparent contradiction with previous studies that showed a continuous increase in performance at saccade targets, even within the last 100 msec before saccade onset (e.g., Deubel, 2008; Ohl et al., 2017; Rolfs & Carrasco, 2012; Rolfs et al., 2011). It should be noted, though, that performance at the saccade target suffered less from the decline than other locations. We speculate that the particular delayed saccade task used here might have equally overshadowed a potential grouping effect.

To overcome the limitations of Experiment 1, we designed Experiment 2, in which we strengthened the grouping using additional shared features based on the study by Wannig et al. (2011). Moreover, we explicitly disentangled the effect of grouping from the effect of the probe side relative to saccade target, and excluded the distracting effect of the go signal on

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pre-saccadic attention by changing the paradigm from a delayed to an immediate saccade task.

#### 3. Experiment 2

#### 3.1. Materials and methods

#### 3.1.1. Participants

We recruited participants with normal or corrected-to-normal vision among students through campus mailing lists at Humboldt-Universität zu Berlin. As in Experiment 1, each participant completed one initial training session and a staircase procedure before starting the experimental sessions. Participants whose performance in one of the first 2 sessions was lower than 60% (in distant or close locations; 6 participants) or who could not finish the training due to difficulties in the saccade task (1 participant) were not included in the study. Data from two participants was excluded after data collection as they provided less than 50% of analyzable trials. Ultimately, we included the data from eleven participants in our analyses (mean age  $\pm$  SD: 26  $\pm$  3.56 years, 8 females, 3 left-handed, 5 left-eye dominant).

All participants were naïve as to the purpose of the study and gave written informed consent before their participation in the experiment. Participants received 7€ per session as compensation and an additional 12€ bonus after the completion of the last session. The study was conducted in accordance with the World Medical, Association (2013). The design of the study, research hypothesis, as well as the sampling and analysis plans, were preregistered on the Open Science Framework before data collection commenced (OSF; https://osf.io/yde5u/ – main page; https://osf.io/yde5u/wiki/home/ – a wiki page with an introduction and a list of the preregistration sections; click on the tabs on the "Project Wiki Pages" panel to see the full preregistration content). All changes to the analysis plan are transparently identified, and the outcomes of pre-registered and post hoc analyses are distinguished.

#### 3.1.2. Equipment

All equipment used was identical to that described in Experiment 1.

#### 3.1.3. Experimental design

Each trial started with a fixation point, presented for 300 msec, before the stimulus set appeared. The stimuli were the same as in Experiment 1: Four vertically oriented gratings located at the vertices of an imaginary diamond shape (see Fig. 1a). Grouping between pairs of stimuli was achieved by a circular outline of the same color, the same phase shift of the grating stimulus, and the exact same pattern of oscillatory movement. Specifically, each stimulus was moved around their initial location in bounded motion by adding a random amount of displacement (drawn anew in each segment of 25 msec, and separately for x and y coordinates from a Gaussian distribution with a mean of 0 pixels and a standard deviation of 2.2 pixels) to the centers of each of the grouped stimuli (see Supplementary Material for a video of the stimulus display). In the radial arrangement (Fig. 1b, middle), objects on the same side relative to the diagonal were grouped. In the diagonal arrangement (Fig. 1b, right), objects on the opposite vertices of the imaginary diamond were grouped. In this case, thus, the objects on the same side had a different color, phase shift, and movement pattern (ungrouped). Flicker rate and the nature of noise frames were the same as in Experiment 1.

One second after stimulus onset, a movement cue appeared at the fixation point to indicate which of the two stimuli proximal to the center was the saccade target (Fig. 6). The movement cue served as the go signal, prompting participants to execute the saccade within 400 msec. At one of five SOAs (25, 75, 125, 175, or 225 msec after movement-cue onset), one of the four gratings briefly changed its orientation (probe stimulus) whereas all other gratings remained at their original orientation.

As in Experiment 1, we probed attention at all four locations, avoiding potential confounds that could arise when participants expected particular locations to be probed. After saccade execution, participants reported the perceived direction of the orientation change (left arrow key for ; right arrow key for) irrespective of its location. The response was selfpaced. Contrary to Experiment 1, the feedback tone, indicating whether the response was correct, was presented after the key press throughout the entire experiment.

As in Experiment 1, the initial training session contained training blocks and a staircase procedure. In Experiment 2, the staircase consisted of 160 trials. During training and the staircase procedure, different arrangements were interleaved. In experimental trials, to strengthen the grouping, we blocked the arrangements: Each block contained 32 trials and had one particular arrangement. The order of arrangements within the session was randomly interleaved. Each session contained 20 blocks, such that approximately 3840 trials were recorded from each participant across six experimental sessions, with at least one night between two consecutive sessions.

#### 3.1.4. Data collection

As in Experiment 1, we examined average performance after each session for both close and distant locations. If a participant did not achieve a performance level in a range of  $75 \pm 15\%$ (across all conditions), we executed another staircase procedure to adjust the level of difficulty.

#### 3.1.5. Data preprocessing

In total, we collected 40,974 trials across all observers. Data preprocessing was similar to that in Experiment 1. We discarded  $3.9 \pm .7\%$  of trials (Mean  $\pm$  SEM) per participant after saccade extraction. In our assessment of eye movement parameters, we excluded trials in which, due to missed frames, either probe onset or probe offset were delayed ( $4.0 \pm .1\%$  of trials per participant). For the analysis of discrimination performance, we excluded trials in which the probe appeared (partially) during saccade execution ( $33.5 \pm 1.7\%$  of trials per participant). A total of 25,011 trials (61.0%) remained for the final analysis (Mean  $\pm$  SEM: 2274  $\pm$  62 trials per participant).



Time for saccade 400 ms from the Go signal

#### 3.2. Results

#### 3.2.1. Eye movement parameters

As in the first experiment, we started by inspecting eve-movement parameters to assess whether the presentation of the probe affected saccade metrics. Fig. 7 presents the average saccade latency and landing error for each of the four probed locations across five time points of the probe onset relative to the cue onset. We did not find an effect of the probe location or the timing of the probe on the saccade metrics (detailed results of the LME model are reported in Supplementary Tables 6.1, 6.2). The only exception was a subtle effect of the probe location on the saccade latency at the earliest probe onset: Latency was 2 msec slower with the probe in the location D in comparison with the Saccade target ( $\beta = 1.85 \pm .92$ , t = 2.02, p = .05). Thus, saccade preparation was largely unaffected by probe presentation, as intended by this type of experimental display (Hanning, Deubel, & Szinte, 2019; Rolfs et al., 2011).

#### 3.2.2. Discrimination performance

As in Experiment 1, we divided the analysis of allocation of attention into three steps, each addressing a separate question.



Fig. 7 – Eye movement parameters across 2 arrangements as a function of probe location and time of the probe onset relative to saccade go signal. Error bars are 95% CIs.

3.2.2.1. SACCADE-TARGET EFFECT. First, we analyzed the difference between performance at the Saccade target versus performance at the Non-target location close to the fixation point (A vs B), both of which were potential target locations (Fig. 8a). Using only the data featuring A and B as probe locations, we ran a GLMER with Probe location (saccade target as a baseline), Time of the probe offset relative to saccade onset, and the interaction of these two variables as fixed factors, as well as participant as a random factor, and performance as the predicted outcome (see Supplementary Table 7.1). The intercept represents performance in the baseline condition (saccade target location at the earliest stage of saccade preparation). This analysis revealed that performance at non-target locations was lower right from the start (probe offset 340-126 msec before saccade onset). We also observed a main effect of the time of the probe presentation relative the saccade onset: Performance at the Saccade target location increased continuously throughout saccade preparation from 77.5  $\pm$  1.7% at the earliest stage to 90.8  $\pm$  1.0% at the latest stage  $(\beta = 1.05 \pm .11, z = 9.85, p < .001)$ . Finally, there was an interaction between probe location and SOA: Performance increased across time only at the saccade target location; at the non-target location, it remained stable at a medium level of about 70% correct (interaction effect parameters:  $\beta = -.99 \pm .13$ , z = -7.46, p < .001). These results confirm that pre-saccadic attention shifted towards the saccade target. The dynamics of this pre-saccadic shift are compatible with those observed in previous studies (Deubel, 2008; Ohl et al., 2017; Rolfs & Carrasco, 2012; Rolfs et al., 2011). As this effect is a precondition for our main research question, we can justifiably investigate the spread of pre-saccadic attention towards distant elements of the stimulus configuration.

3.2.2.2. GROUPING EFFECT. Next, we focused on the distant locations (C and D) as one of them was always grouped with the saccade target (C in radial and D in diagonal arrangement) while the other was not (D in radial and C in diagonal arrangement). We ran a GLMER with Grouping (grouped with the saccade target as a baseline), Time of probe offset relative to saccade onset, and the interaction of these two variables as fixed factors, participant as a random factor, and performance as the predicted outcome (see Supplementary Table 7.2). The time of probe presentation affected



Fig. 8 – Discrimination performance in Experiment 2. (a): Saccade target versus non-target location close to fixation point (b): Distant locations perceptually grouped versus not grouped with the saccade target. (c): Distant locations at the same side versus different side of the stimulus configuration relative to the saccade target. (d): The two distant locations plotted separately when each of them was either grouped versus not grouped with the saccade target. Error bars are 95% CIs. Graphs at the bottom of the panels (a), (b), and (c) show performance differences between the two locations, both for individuals (gray) and averaged across participants (black).

performance at the grouped locations, showing an increase 125 to 83 msec before saccade onset (by  $3.3 \pm 2.5\%$  in grouped locations and by  $2.0 \pm .9\%$  in non-grouped locations;  $\beta = .16 \pm .08$ , z = 1.97, p = .048). This analysis, however, does not support a significant effect of Grouping on performance per sé. Indeed, we found no evidence that performance in the Non-grouped location developed differently. Inspection of Fig. 8b suggests that this reflects the fact that the difference between Grouped and Non-grouped locations changes over time, increasing towards the middle stages of saccade preparation before collapsing just before the saccade. To obtain the temporal profile of a potential effect of grouping, therefore, we compared the estimated marginal means for Grouped versus Non-grouped locations, within the same GLMER model. When the probe was presented within 125 to 41 msec before saccade onset, performance at the location grouped with the saccade target was higher than in the Nongrouped location (by 4.1  $\pm$  1.6% for the time bin 125 to 83 msec:  $\beta = .20 \pm .08$ , z = 2.52, p = .035; by  $5.3 \pm 1.4\%$  for the 82 to 41 msec bin:  $\beta$  = .26 ± .08, z = 3.26, p = .005). Thus, attention was allocated towards the stimuli perceptually grouped with a saccade target as saccade preparation was underway (Supplementary Table 7.2.1).

3.2.2.3. SIDE EFFECT. Third, we compared performance at location C (same side as the saccade target) and location D (different side) independently of whether these were grouped or not grouped with the saccade target. We ran GLMER with Probe location (grouped with the saccade target as a baseline), Time of probe offset relative saccade onset, and their interaction as fixed factors, participant as a random factor, and performance as the predicted outcome (see Supplementary Table 7.3). This analysis showed a main effect of probe side on performance, which was higher on the same side as the saccade target throughout saccade preparation ( $\beta = -.25 \pm .08$ , z = -3.20, p = .001). The performance difference peaked in the time bin 125 to 83 msec before saccade onset at  $9.1 \pm 1.6\%$  and then declined closer to saccade onset to the level of performance at the earliest stages of saccade preparation (Fig. 8c).

3.2.2.4. GROUPING EFFECT BY SIDE. Finally, we compared performance at location C (same side as the saccade target) in two arrangements: When it was either grouped or not grouped with the saccade target (Fig. 8d). The same analysis was done for location D (different side than the saccade target). This analysis was preregistered as a main focus of our study as it allowed showing the pure effect of grouping for each side of the stimulus configuration separately. For each of these two locations, we ran a GLMER with Grouping (grouped with the saccade target as a baseline), Time of probe offset relative saccade onset, and the interaction of these two variables as fixed factors, participant as a random factor, and performance as the predicted outcome (see Supplementary Tables 7.4, 7.41 and 7.5, 7.51). In the Same-side condition, performance changed over time, increasing initially (125-41 msec before saccade onset), before dropping again. A significant interaction between Time and Grouping occurred 82 to 41 msec before saccade onset ( $\beta = -.34 \pm .16$ , z = -2.15, p = .032), when performance rose at location C when it was grouped with the saccade target (4.8 ± 1.6%) and almost remained the same when it was not grouped (-.1 ± 4.5%). In the Different-side condition, the effect of grouping was stable throughout saccade preparation: performance was consistently higher at location D when it was grouped with the saccade target (parameters for non-grouped vs grouped contrast:  $\beta = -.33 \pm .11$ , z = -3.04, p = .002). Overall, the time course of attention allocation was different for stimuli grouped with the saccade target depending on the side of the stimulus configuration on which the grouped element appeared.

#### 3.3. Discussion

In Experiment 2, we added two grouping features to the stimulus design: a synchronized pattern of oscillatory movement of individual stimuli, and a consistent phase shift, for grouped locations. We used an immediate rather than a delayed saccade task and reduced the number of stimulus arrangements while blocking trials for each. In contrast to Experiment 1, the pre-saccadic attention shift toward the saccade target continuously increased the sensitivity at the target location as time approached saccade onset. Under these conditions, we also found a reliable effect of grouping on the allocation of attention. In particular, attention spread to stimuli that formed a perceptual group with the saccade target. This result is particularly remarkable as these grouped locations were never relevant to the movement task. This experimental strategy may well have reduced the behavioral relevance of these locations, but at the same time, it allowed us to study the effect of grouping under a conservative condition in which grouping effects cannot be accounted by relevance of the grouped location for the eye movement task.

Finally, and consistent with Experiment 1, we observed an effect of probe side on attentional allocation, in which the stimulus located on the same side of the stimulus arrangement as the saccade target profited most during saccade preparation. In addition, the Grouping effect had a different time course on the two sides: On the same side, the effect was observed in the middle stages of saccade preparation, whereas on the different side it was stable over time. Overall, these results support the hypothesis that grouping facilitates the spread of attention from the saccade target to the stimuli located on both sides of the stimulus configuration.

#### 4. General discussion

Shortly before saccadic eye movements, visuospatial attention is deployed to the saccade goal. The aim of the present study was to examine whether this form of pre-saccadic selection extends to locations that are part of a perceptual group with the saccade target. In two experiments, we showed that pre-saccadic selection is not strictly limited to the movement target location. Specifically, pre-saccadic attention can spread towards locations that are perceptually grouped with the saccade target (Grouping effect) or displayed on the same side of the stimulus configuration relative to the saccade trajectory (Side effect).

Perceptual grouping is a process through which fragmentary bits of visual information are structured into coherent percepts, i.e., objects. One putative mechanism for the emergence of objecthood is object-based attention, and this process is guided by grouping factors (Wannig et al., 2011). Although unequivocal evidence points to the role of perceptual grouping in formation of objects (for reviews of psychophysical evidence see Wagemans et al., 2012, and Peterson & Kimchi, 2014; for neural evidence see Roelfsema, 2006), it remained unknown whether objecthood confers a robust behavioral advantage when an action is planned to a new object. The current study manipulated grouping independently from location, and could show how objects are prioritized over space-as measured by improved discrimination accuracy—when they form a perceptual group with a saccade target.

The magnitude of the observed effects depended on the nature of the saccade task. In Experiment 1, participants made delayed saccades towards the cued location. Before saccade onset, we probed visuospatial attention using a tilt discrimination task for a stimulus displayed in one of four locations of the stimulus configuration. We used color as a grouping feature such that one of the locations was grouped with the saccade target, and two other locations constituted a group of their own, with a different color. In this experiment, we did not find a prominent Grouping effect, but we did find a strong Side effect on the allocation of attention towards items irrelevant to the oculomotor task. In Experiment 2, participants executed saccades immediately, as the cue to the saccade goal served directly as a go signal for the movement. We strengthened the grouping by combining color and motion (both of the probed object and the internal phase of the grating stimulus) as grouping features. In this experiment, we demonstrated a significant effect of Grouping, in addition to a Side effect, on the pre-saccadic deployment of attention.

#### 4.1. What is the unit of pre-saccadic selection?

Before goal-directed eye or hand movements, the visual system prioritizes the movement target (Deubel, Schneider, & Paprotta, 1998; Hanning, Aagten-Murphy, & Deubel, 2018; Jonikaitis & Deubel, 2011; Khan, Song, & McPeek, 2011; Rolfs & Carrasco, 2012; Rolfs, Lawrence, & Carrasco, 2013; see Baldauf & Deubel, 2010 for a review). In natural vision, these targets are usually parts of extended objects in the scene, posing the question: What is in the focus of visual attention—the target location of the movement (location-based selection), or the object that the movement is aiming for (object-based selection)?

A number of studies showed that attention selects locations that are relevant to the oculomotor plan and restricted to the movement target locations (Deubel, 2008; Deubel & Schneider, 1996; Hanning, Szinte, & Deubel, 2019; Rolfs et al., 2011). Most of these previous studies placed individual placeholders, landmarks or other objects at potential probe locations in the scene, and can thus not be used to speak to the issue of location-versus object-based selection. The authors are aware of three studies, however, that form an exception to this rule, as they addressed the impact of such target objects on the deployment of pre-saccadic attention.

First, Puntiroli et al. (2018) conducted several experiments with participants performing eye movements either to a location with a placeholder or to an empty screen location. During saccade preparation, a discrimination probe flashed at the saccade target or at one of the other two equidistant locations. By varying different spatiotemporal combinations of the presence/absence of placeholders, the authors investigated how objects that surround the saccade target affect the saccade-target benefit. They reasoned that placeholders might interfere with the attentional probe and impair discrimination performance at probed locations, producing a crowding effect. Pre-saccadic attention overcame this performance decrement induced by the placeholders only at the saccade target location, whereas discrimination performance at other locations was diminished. To the extent that the placeholder constitutes an object, these results are consistent with an object-based selection of the saccade target.

Second, Szinte et al. (2019) investigated the spatial spread of pre-saccadic attention around a target location. Using a visual-sensitivity-mapping paradigm, they probed visuospatial attention with an orientation discrimination task, performed at different eccentricities from a target stimulus, before saccade onset. If the target stimulus remained visible during saccade preparation, an increase in visual sensitivity was spatially confined to the target location. In cases when the target stimulus disappeared before saccade onset, sensitivity increased at locations further away from the target. This decrease in spatial specificity of pre-saccadic attention was not reflected in eye movement accuracy; saccade endpoints were equally accurate for both the sustained and the transient target. These results suggest that the pre-saccadic attention shift and oculomotor programming are two partially separable processes, for which visual selection is affected more strongly by the configuration of the visual scene.

Finally, Ghahghaei and Verghese (2017) used a perceptual discrimination task to probe visual sensitivity around the saccade target location on a textured background. They observed uniform enhancement of visual sensitivity across the entire texture along with the target provided the texture was the figure in a figure-ground relation (i.e., it was a circle on top of an outer orthogonally oriented texture). In cases when the textured background was uniform, sensitivity dropped sharply with distance from the saccade target. When participants attended the target covertly, the enhancement of sensitivity within the figure decreased significantly. These results suggest that the active interaction with a target yields visual selection of the surface of its surrounding figure, not only of the goal of the movement.

These behavioral studies, however, do not reveal the exact mechanisms through which the perceptual organization of scenes guides the allocation of pre-saccadic attention. On the other hand, whereas a neurophysiological study by Wannig et al. (2011) provided evidence that the spread of attention is guided by the Gestalt principles, the behavioral consequences of these neuronal modulations had not been investigated.

The present study extends these findings, showing that perceptual grouping provides structure that scaffolds the presaccadic deployment of attention. Consistent with the previous findings reviewed above (Ghahghaei & Verghese, 2017; Puntiroli et al., 2018; Szinte et al., 2019; Wannig et al., 2011), our results suggest that pre-saccadic selection of a saccade target leads to an involuntary selection of an extended object consisting of the saccade target proper as well as locations grouped with it.

Much like attention to features (Kalogeropoulou & Rolfs, 2017), this selection may carry into the next fixation and give rise to selection of the entire object fixated. Indeed, Malcolm and Shomstein (2015) showed that, in real-world scenes, observers made faster saccades towards locations within the currently fixated object than towards locations at the same eccentricity but within a different object. Response times in a visual discrimination task mirrored this pattern.

#### 4.2. The time course of pre-saccadic selection

The time course of pre-saccadic attention shifts has been well established in different paradigms using immediate saccade tasks (e.g., Deubel, 2008; Hanning, Deubel, & Szinte, 2019; Li, Barbot, & Carrasco, 2016; Ohl et al., 2017; Rolfs & Carrasco, 2012; Rolfs et al., 2011). In these paradigms, visual sensitivity is comparable at all potential saccade target locations at movement cue onset. During the preparation of a saccade to one specific location, visual sensitivity then rapidly increases at the saccade target, peaking shortly before movement onset. At non-target locations, in contrast, performance remains at about the same level throughout the pre-saccadic period, or it even drops (Ohl et al., 2017).

When using an immediate saccade task (Experiment 2), we largely replicated this classical time course (Fig. 8a) and considered these dynamics to be a signature of a pre-saccadic attention shift to the saccade target. Using a delayed saccade task (Experiment 1), however, performance followed a different time course (Figs. 4a and 5a): Following an initial increase of performance at the saccade target, performance dropped overall closer to saccade onset, but remained better at the saccade target than in any other locations (see also Deubel & Schneider, 2003).

In both experiments, we observed the performance benefit at the saccade target location (compared to locations of the same eccentricity) at the earliest stages of the saccade preparation (Figs. 5a and 8a). Indeed, in one condition of Experiment 1 (SOA of -50 msec), discrimination performance was better at the saccade target location before the target was defined by the movement cue. These results suggest that factors other than a pre-saccadic attention shift contribute to the saccade-target benefit. Visual short-term memory may provide an explanation of these early effects. Within a second after the disappearance of a memorized array of stimuli, saccades effectively stabilize memory representation that were previously seen at the saccade target (Ohl & Rolfs, 2017, 2018, 2020). Thus, a saccade to the item that contained a probe might increase performance by stabilizing the representation of that probe in visual short-term memory. In the present experimental paradigm, it is hard to disentangle the influence of visual short-term memory and pre-saccadic attention shift on performance across the whole time course of saccade preparation, but at the earliest stages of saccade preparation, when attention is not yet focused on the saccade target, memory is likely to play a larger role.

#### 4.3. The side effect

Across both experiments, we found a strong Side effect (pun not intended): In the locations distant from the initial fixation position and irrelevant to the oculomotor task, discrimination performance was higher if the probe was on the same side of the stimulus configuration relative to the saccade trajectory (Figs. 4c and 8c). This effect occurred independently of perceptual grouping. We did not predict this Side effect in Experiment 1, and we are not aware of other studies reporting a similar effect.

We hypothesize that the Side effect might be explained by a phenomenon called attentional momentum (Pratt, Spalek, & Bradshaw, 1999; Spalek & Hammad, 2004)-the finding that attention is biased to keep moving in the direction of its most recent movement (in the direction of the saccade, in our scenario). To test this post-hoc hypothesis, we decided to measure left-to-right and top-to-bottom visual-field biases that were described in the study of attentional momentum by Spalek and Hammad (2004). According to their results, the attentional momentum effect was stronger when covert attention was directed from left-to-right and from top-to-bottom in comparison with the opposite directions. Spalek and Hammad (2005) suggested that these biases could be explained by the natural environment, that is, humans' sensitivity to downward motion (objects in the natural world tend to move in top-to-bottom direction) and the reading direction (they found an opposite right-to-left bias in Egyptian participants who have a right-to-left reading pattern).

In the study by Spalek and Hammad (2004), attention was measured using response time in a signal-detection task: The attentional momentum effect was stronger when observers' attention moved in the bottom-right than in the top-left direction. We thus inspected if our Side effect reflected the same bias. If, indeed, attentional momentum drives the Side effect, this effect should be stronger towards the bottom-right than in other directions. As a control analysis, we also compared differences in saccade-target selection: If the Side effect was driven by a pre-saccadic attention shift without a role of attentional momentum, the effect size should be independent of the location of the stimulus configuration on the screen.

Figure S1.1 represents the results of this analysis, showing that the Side effect was indeed most pronounced for the bottom right quadrant of the screen. The saccade target enhancement, in contrast, was comparable across all four quadrants (Figure S1.2). We may consider this anecdotal evidence for the role of attentional momentum in the Side effect.

Although attentional momentum provides a plausible explanation for the Side effect during later stages of saccade preparation, it remains unclear what impacts performance immediately after cue onset, when attention is not yet shifted in the direction of the target. To account for this, we need to assume that attentional momentum enhances visual shortterm memory representations not only at the saccade target (Ohl & Rolfs, 2017, 2018, 2020) but also at the distant location on the same side of the stimulus configuration. This hypothesis is worth testing in future experiments on perceptual grouping in visual short-term memory in active vision.

The Side effect was an unexpected result of our study, but it is necessary to take it into consideration when analyzing the Grouping effect in our paradigm. Although we did not make any strong predictions regarding the Side effect in Experiment 2, it shaped the way we decided to investigate the Grouping effect, that is, to analyze the time course of the Grouping effect separately for each side of the stimulus configuration (Fig. 8d).

#### 4.4. The impact of perceptual grouping

In Experiment 2, we demonstrated a reliable Grouping effect: Discrimination performance was better at those locations that perceptually grouped with the saccade target compared to the same locations when they were not grouped by Gestalt criteria. This result complements and corroborates findings by Wannig et al. (2011), who showed enhanced visual responses in primary visual cortex (V1) when items presented in a neuron's receptive fields were perceptually grouped with the saccade target.

In addition, we found a difference in the time course of presaccadic selection of the grouped items, depending on what side of the stimulus configuration they were on: The Grouping effect for the location on the same side as the saccade target was most prominent in the middle stages of saccade preparation; on the different side, it was prominent throughout the pre-saccadic period (Fig. 8d). This result may indicate that the processing of grouped items on the same and different side of a saccade target involves neuronal populations with different sizes of receptive fields, presumably residing in different cortical areas. While attention spreads gradually from the saccade target to a grouped item on the same side, likely due to involvement of smaller and closer-by receptive fields, its extension to a grouped item on the different side may involve neurons with larger receptive fields that select the whole object at the same time. Such a multiscale selection by objectbased attention has been shown to underlie object-based attention in a contour-grouping task (Pooresmaeili & Roelfsema, 2014), and its involvement in pre-saccadic attentional selection is an exciting direction for future neurophysiological investigations.

In our experimental design, grouping was achieved by a combination of three visual features (color, external, and internal motion). This raises the question, whether the observed Grouping effect can be considered a consequence of feature-based selection (e.g., White & Carrasco, 2011). Indeed, our finding of improved performance at distant locations grouped with the saccade target appears compatible with the hypothesis that pre-saccadic attention automatically selects

elements that share the same features with the saccade target. Three previous studies addressed the effect of presaccadic selection on feature-based attention in the absence of grouping, none of which found strong support for an involuntary selection of object features that would drive feature-based attention.

First, Born, Ansorge, and Kerzel (2012) examined whether congruency between the color of the saccade target and the probe location (discrimination target: direction of offset of the vertical bar in a cross) affected the deployment of presaccadic attention. Indeed, the authors found an effect of color congruency: performance was higher when the probe was of the same color as the saccade target than when it was not. However, this effect was reliable only when the color was an indicator of the saccade target (and, thus, taskrelevant) and when it was constant across the entire block of trials. Second, Jonikaitis and Theeuwes (2013) also found the allocation of attention in a non-saccade-target location that shared the same color as the saccade target. This increase in visual sensitivity was again present only when the target color was relevant for the oculomotor task, as instructed at the beginning of the entire block of trials. Finally, in a similar task, in which a stimulus' motion direction was irrelevant to both the saccade and the discrimination task, White et al. (2013) found no evidence for feature-based selection of motion direction. However, they did find an intertrial effect on pre-saccadic feature-based attention. Their task used a brief luminance-change, imposed on a moving stimulus, to probe attentional deployment in an array of six independently moving random-dot kinematograms. Performance in the detection task was higher for the probes that were moving in the same direction as the saccade target, but only if the direction of the probe and target motion was also the same in the previous trial. In agreement with these results, Eymond, Cavanagh, and Collins (2016) did not find the effect of congruency of saccade target color and visual-search-target color on the response times in a search task executed immediately upon saccade landing. Their finding of a classical priming of pop-out effect (repetition of target feature in the subsequent trials speeded up the responses) is also compatible with the results of White et al. (2013). Again, one could argue that the experience on the previous trial gave rise to an implied task-relevance of the (factually irrelevant) feature.

Together these results suggest, therefore, that pre-saccadic feature-based selection requires that the feature is relevant to the observer's task. In our experiment, perceptual grouping—or the features giving rise to it—were never task relevant. We conclude, therefore, that the Grouping effect we observed is a consequence of involuntary object-based selection based on Gestalt principles, rather than of feature-based attention.

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#### Author contributions

O.S. and M.R. developed the experimental question and study design. O.S. collected and analyzed the data. All authors interpreted the findings. O.S. drafted the manuscript and M.R. and A.P. provided revisions.

#### **Open practices**

The study in this article earned Open Data, Open Materials and Open Practices badges for transparent practices. Preregistered materials from this study are available at https://osf. io/c9zb3/wiki/home/ and https://osf.io/yde5u/wiki/home/.

All raw and processed data (including all behavioral and eye-tracking data) and analysis code for all experiments as well as experiment presentation script is archived on the OSF, together with the complete documentation: https://osf.io/bzpyv/.

#### Declaration of competing interest

The authors declare no competing interests.

#### Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cortex.2021.03.020.

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