american physiological society®

JNP JOURNAL OF
NEUROPHYSIOLOGY®

RAPID REPORT

The effect of spatial structure on presaccadic attention costs and benefits assessed with dynamic 1/f noise

Nina M. Hanning[1,2,3] and Heiner Deubel[1]

[1]*Allgemeine und Experimentelle Psychologie, Ludwig-Maximilians-Universität München, München, Germany;* [2]*Department of Psychology and Center for Neural Science, New York University, New York, New York; and* [3]*Institut für Psychologie, Humboldt Universität zu Berlin, Berlin, Germany*

Abstract

Already before the onset of a saccadic eye movement, we preferentially process visual information at the upcoming eye fixation. This "presaccadic shift of attention" is typically assessed via localized test items, which potentially bias the attention measurement. Here, we show how presaccadic attention shapes perception from saccade origin to target when no scene-structuring items are presented. Participants made saccades into a 1/f ("pink") noise field, in which we embedded a brief orientation signal at various locations shortly before saccade onset. Local orientation discrimination performance served as a proxy for the allocation of attention. Results demonstrate that *1*) the presaccadic attention shift is accompanied by considerable attentional costs at the presaccadic eye fixation and *2*) saccades are preceded by shifts of attention to their goal location even if they are directed into an unstructured visual field, but the spread of attention, compared with target-directed saccades, is broad. We conclude that the absence or presence of saccade target objects markedly shapes the distribution of presaccadic attention and likely the underlying (space-based or object-based) cortical control mechanism. Our findings demonstrate the relevance of an item-free approach for measuring attentional dynamics across the visual field.

NEW & NOTEWORTHY Using a new psychophysical paradigm, we show that, if the visual field is unstructured, the well-established attention shift preceding saccadic eye movements is far less focused on the movement goal than previously suggested based on conventional protocols, implying that attention is strongly shaped by scene-structuring elements. Moreover, it comes at a significant cost: Although visual sensitivity at the saccade target increases during eye-movement preparation, foveal perception (at the current center of gaze) is markedly deteriorated.

object-based attention; presaccadic attention; psychophysics; saccadic eye movements; spatial attention

INTRODUCTION

We experience the world by making saccadic eye movements. Every few 100 ms, a saccade shifts our gaze and focuses our attention to a new location in space. Interestingly, spatial attention reaches the future eye fixation before the eyes start to move. This "presaccadic shift of attention" to the saccade target is indicated by perceptual benefits (1–3) and selective modulations of sensory (orientation and spatial frequency) tuning (4–7). These behavioral correlates of presaccadic attention have been extensively characterized at the saccade target and are described to be spatially highly specific, i.e., not spreading to neighboring items (1, 8, 9; see Ref. 10 for a recent review). This has led to the proposal that presaccadic attention selects objects rather than locations (e.g., 1). However, under the assumption that presaccadic attention

is object-based rather than space-based, what happens if saccades are programmed into an empty field, without visible target objects? To answer this question and study the effect of spatial structure, we investigated the spatial distribution of presaccadic attention from saccade origin to the target in a full-field noise paradigm. If presaccadic attention were purely object-based, the absence of a target structure should lead to the absence of a presaccadic benefit at the saccade goal. Conversely, if presaccadic attention was space-based, removing the saccade target structure should not affect the spread of presaccadic attention.

We used a novel full-field 1/f noise protocol (11) that allows assessing the spatial dynamics of visual attention across the field via local orientation signals embedded at various locations in the noise background. Similar to classic psychophysical protocols in which participants discriminate a stimulus-

www.jn.org

specific visual feature of a test item (e.g., the tilt of a Gabor patch, see Ref. 8 for other examples), our participants were asked to judge the orientation of an oriented subpart within the noise field (see Fig. 1A, "Test"). Local discrimination accuracy served as a proxy for attention deployment and is, unique to this 1/f noise stimulus, largely independent of retinal eccentricity in the visual range investigated in the current study (11). This property enables the continuous assessment and direct comparison of attentional effects from central to peripheral locations. Moreover, the noise protocol, unlike conventional paradigms (8), does not rely on discrete test items, which pose the risk of shaping the spread of presaccadic attention by structuring the visual scene (12, 13). Due to the paradigm's dynamic nature (the 1/f noise field is continuously changing), test signal presentation does not interrupt saccade programming—a problem observed with conventional discrimination protocols that rely on sudden-onset stimuli. Sudden-onset test items presented during eye movement preparation delay saccade execution (8), which is compatible with the phenomenon of saccadic inhibition, whereby a transient change in the scene causes depression in saccadic frequency ~100 ms thereafter (14). Given the tight coupling of eye movement preparation and visual attention, interrupting saccade preparation may likely also affect the temporal dynamics of visual attention. By embedding the discrimination signal in a continuously changing 1/f noise field (11), we could obtain an unbiased measure of the presaccadic shift and spread of attention, and how it is shaped by the presence of a saccade target structure.

MATERIAL AND METHODS

Participants

We used sample sizes comparable with previous work on presaccadic attention (8, 9, 15). Nine participants (aged 18–29, 7 female) completed *experiment 1* and nine participants (aged 20–29, 5 female) completed *experiment 2*. All participants were healthy, had normal vision, and were naive as to the purpose of the experiment (except for one author, N.M.H.). The protocols for the study were certified by the ethical review board of the Faculty of Psychology and Education of the Ludwig-Maximilians-Universität München (Approval No. 13_b_2015), in accordance with the Declaration of Helsinki. All participants gave written informed consent.

Apparatus

Eye position of the dominant eye was recorded using a SR Research EyeLink 1000 Desktop Mount eye tracker (Osgoode, Ontario, Canada) at a sampling rate of 1 kHz. Manual responses were recorded via a standard keyboard. The experimental software was implemented in MATLAB (MathWorks, Natick, MA), using the Psychophysics (16, 17) and EyeLink toolboxes (18). Participants sat in a dimly illuminated room with their heads positioned on a chin rest. Stimuli were presented at a viewing distance of 60 cm on a 21-in. γ-linearized SONY GDM-F500R CRT screen (Tokyo, Japan) with a spatial resolution of 1,024 by 768 pixels and a vertical refresh rate of 120 Hz.

Experimental Design

Experiment 1.

Participants fixated a central black (~0 cd/m^2) fixation dot (radius 0.15°) on gray background (~60 cd/m^2) (see Fig. 1A and Supplemental Video S1). Once stable fixation was detected within a 1.75° from fixation for at least 200 ms, a rectangular dynamic 1/f noise background (24.0° × 4.0°, mean luminance ~60 cd/m^2) was presented and remained on the screen throughout the trial. The background noise was updated at 60 Hz, changing gradually from one noise image to another within four frames (see Ref. 11 for details). After a random fixation period (400–800 ms), a black (~0 cd/m^2) arrow cue (length ~0.5°, height ~0.4°) was presented
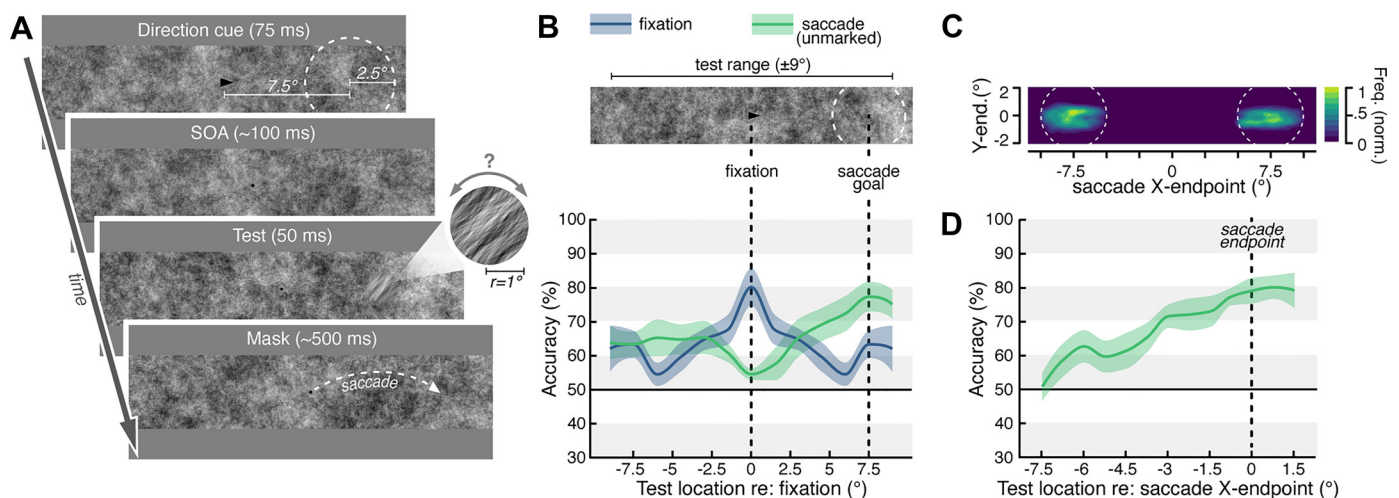

Figure 1. Visuospatial attention during fixation and saccade preparation. *A*: task. Participants (*n* = 9) fixated a central fixation dot on dynamic 1/f noise background and either made a 7.5° saccade in cue direction into the unstructured field (saccade trials) or kept fixating (fixation trials; ~15%, randomly intermixed). Shortly before saccade onset, a brief orientation signal was embedded at a random location on the horizontal (±9° around fixation). Participants indicated its tilt (here clockwise) at the end of the trial. *B*: group average discrimination performance relative to central fixation. Data mirrored (fixation trials) or flipped to represent rightward saccades (saccade trials). *C*: normalized saccade landing frequency maps averaged across participants. *D*: group average discrimination performance relative to saccade endpoint. Colored areas (*B* and *D*) indicate ±1 SE.

centrally for 75 ms, randomly pointing either leftward or rightward (saccade trials). Participants were trained to perform a 7.5° saccade in arrow cue direction as fast and as precise as possible. Approximately 175 ms after cue onset (this delay was adjusted online to the average saccade latency of each individual participant, to aim for a discrimination signal presentation in the last 100 ms before saccade onset[1]), a local orientation signal tilted 40° clockwise or counterclockwise from vertical was embedded in the background noise at a randomly chosen location between −9° and +9° (relative to fixation on the horizontal meridian). This orientation signal was windowed by a radial cosine (radius 1.0°, sigma 0.9°). Participants were informed that this test signal would appear anywhere on the horizontal, independent of cue/saccade direction. After 50 ms, the orientation signal was masked by the reappearance of nonoriented noise for 500 ms; during this interval, the saccade occurred. In ∼15% of trials (fixation trials, randomly intermixed), no arrow cue was presented, and participants were instructed to keep fixating. At the end of each trial, the dynamic 1/f background noise disappeared and participants indicated via button press in a nonspeeded manner whether they had perceived a clockwise or a counterclockwise orientation. They did not receive feedback on the correctness of their response.

After initial training, participants performed four experimental blocks of 160 trials each. We controlled online for broken eye fixation (further than 1.75° from the fixation target before the cue onset), too short (<170 ms), or too long (>400 ms) eye movement latencies, and imprecise movements (not landing within 2.5° from saccade target center). Erroneous trials were repeated in random order at the end of each block (on average 95 trials per participant).

To ensure a consistent level of discrimination difficulty across participants, the signal's orientation filter strength σ (i.e., visibility level) used in the main experiment was titrated in a pretest for each participant. This task was identical to the main experiment fixation condition. For each trial, we randomly selected the orientation filter strength (σ = 15–65) and determined the filter width corresponding to 90% discrimination accuracy by fitting cumulative Gaussian functions to the discrimination performance via maximum likelihood estimation (19).

Experiment 2.
Task and timing were identical to *experiment 1* with the following differences (see Fig. 2A and Supplemental Video S2). In 50% of the experimental blocks (marked blocks), three black (∼60 cd/m²) circular frames (radius 1.2°) marked central fixation and the potential saccade targets ±8° on the horizontal relative to fixation. In the other 50% of experimental blocks, as in *experiment 1*, no frames were presented (unmarked blocks), and participants were trained to perform a ±8° saccade into the unstructured noise field. There were no intermixed fixation trials. The local orientation signal was embedded in the background noise at 1 out of 21 evenly spaced horizontal positions from −10° to +10° retinal eccentricity (randomly chosen independent of saccade direction, including locations within the placeholders). The signal's orientation filter width σ was titrated in a pretest as described for *experiment 1*.

After an initial training, participants performed 8 experimental blocks (4 marked and 4 unmarked blocks, randomly interleaved) of 190 trials each. We controlled online for broken eye fixation (further than 1.75° from the fixation target before the cue onset), too short (<170 ms) or too long (>400 ms) eye movement latencies, and imprecise movements (not landing within 2.5° from saccade target center). Erroneous trials were repeated in random order at the end of each block (on average 61 marked trials and 86 unmarked trials per participant).

Eye Data Preprocessing

For both experiments, we scanned the recorded eye-position data offline and detected saccades based on their velocity distribution (20) using a moving average over 20 subsequent eye position samples. Saccade onset and offset were detected when the velocity exceeded or fell below the median of the moving average by 3 SDs for at least 20 ms. We included trials in which no blink occurred during the trial and correct eye fixation was maintained within a 1.75° radius centered on central fixation throughout the trial (fixation trials) or until cue onset (eye movement trials). Moreover, we only included those eye movement trials in which the initial saccade landed within 2.5° from the required target location and in which the test signal was presented within 100 ms before saccade onset (i.e., the saccade started only after test signal presentation, but not later than 100 ms after signal offset); on average 10.15 (*experiment 1*) and 10.34 (*experiment 2*) trials per participant were discarded due to this temporal criterion. In total, we included 4,896 trials in the analysis of the behavioral results (on average 544 trials per participant) for *experiment 1* and 11,795 trials (on average 1,311 trials per participant) for *experiment 2*.

Behavioral Data Analysis and Visualization

To visualize discrimination performance across space in *experiment 1*, we interpolated between the group-averaged discrimination accuracy (% correct) for each test location, separately for the saccade and fixation conditions. Figure 1B shows 13 evenly spaced bins (width 0.75°) between −9° and +9° relative to central fixation; Fig. 1D shows 13 evenly spaced bins (width 0.75°) between −7.5° and +1.5° relative to the respective horizontal saccade landing position. Similarly, for *experiment 2*, we plot the interpolated group-averaged discrimination accuracy for marked and unmarked blocks. Figure 2B shows 21 evenly spaced test locations between −10° and +10° relative to central fixation; Fig. 2D shows 13 evenly spaced bins (width 0.75°) between −7.5° and +1.5° relative to the respective horizontal saccade landing position.

Throughout the text, we present group-averaged measurements with their respective 95% confidence interval. For all statistical comparisons, we used permutation tests to determine significant performance differences between two

---

[1]We evaluated participants' saccade latencies online (saccade onset was approximated by the recorded eye position leaving the 1.75° fixation boundary). We determined each participant's median saccade latency across all previous trials of the current block (with correctly executed saccade) and presented the test signal 50 ms beforehand.
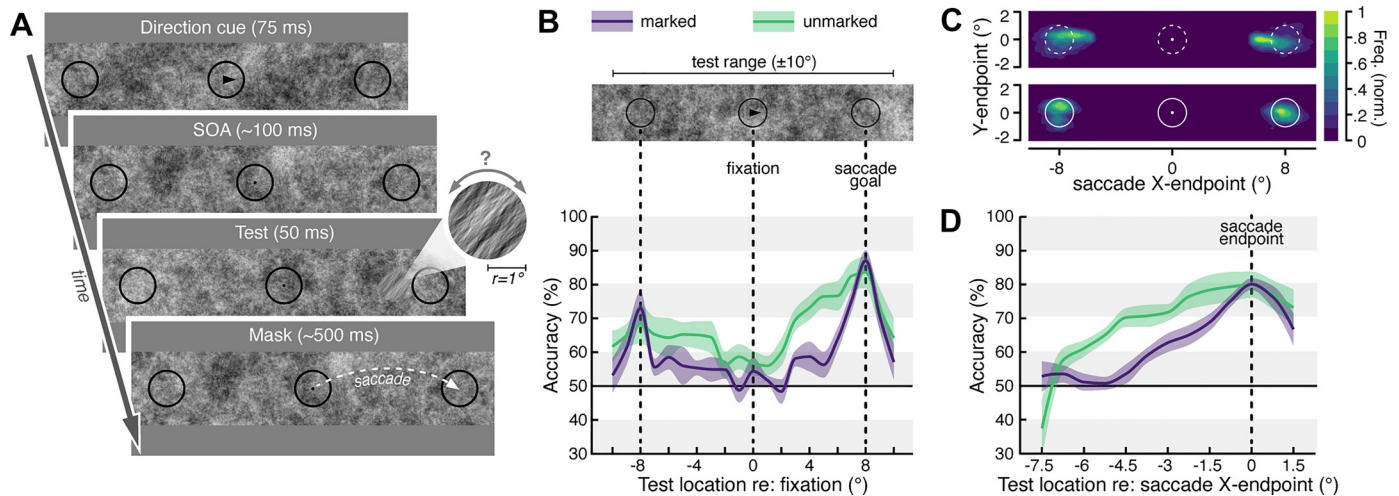
Figure 2. The influence of objects on presaccadic attention. *A*: task. Participants (*n* = 9) prepared an 8° saccade in arrow cue direction. In 50% of the experimental blocks, central fixation and the two potential target locations were framed (marked), in the other half no frames were presented (unmarked). Shortly before saccade onset, a brief orientation signal was embedded at a random location (±10° around fixation, within or between the frames). Participants discriminated its orientation after the saccade. *B*: group average discrimination performance relative to central fixation. Data flipped to represent rightward saccades. *C*: normalized saccade landing frequency maps averaged across participants for unmarked (*top*) and marked blocks (*bottom*). *D*: discrimination performance relative to saccade endpoint. Colored areas (*B* and *D*) indicate ±1 SE.

conditions or locations. We resampled our data to create a permutation distribution by randomly rearranging the labels of the respective conditions for each participant and computed the difference in sample means for 1,000 permutation resamples (iterations). We then derived *P* values by locating the actually observed difference between the two compared conditions ($\overline{x}_{diff}$) on this permutation distribution, i.e., the *P* value corresponds to the proportion of the differences in sample means that fell below or above the actually observed difference (*P* values were Bonferroni-corrected for multiple comparisons).

Data Deposition

Eyetracking and behavioral data are available at https://doi.org/10.17605/OSF.IO/UZBWD.

RESULTS

In *experiment 1*, we trained the participants to perform horizontal saccades of ~7.5° into a 1/f noise field, without target objects being presented, and compared their presaccadic orientation discrimination performance—a proxy for the allocation of attention—to their performance during continued eye fixation (Fig. 1*A* and Supplemental Video S1). During fixation (Fig. 1*B*, blue), discrimination performance was highest for orientation signals occurring at the center of gaze (0°: 80.24% [70.17, 90.31]%; mean [95% CI]) and decreased with retinal eccentricity. In contrast, during saccade preparation (<100 ms before saccade onset; Fig. 1*B*, green), performance was highest at the (unmarked) saccade goal (7.5°: 77.43% [69.43, 85.43]%). Thus, presaccadic attention shifted to the saccade goal even in the absence of an actual motor target. Interestingly, the attention shift was not limited to the 7.5° saccade goal; also, at neighboring locations (4.5° to 9°), performance was enhanced compared with fixation (4.5°: 69.21% [60.25, 78.17]%, $\overline{x}_{diff}$ = 14.64%, *P* = 0.0260; 6°: 72.43% [62.91, 81.95]%, $\overline{x}_{diff}$ = 17.86%, *P* = 0.0160; 7.5°: 77.43%

[69.43, 85.43]%, $\overline{x}_{diff}$ = 22.86%, *P* = 0.0050; 9°: 75.18% [67.38, 82.98]%, $\overline{x}_{diff}$ = 20.61%, *P* = 0.0470). This spread is surprising, as presaccadic attention is often described to be narrowly focused on the saccade target (e.g., Refs. 1, 8).

Notably, the absence of a saccade target caused considerable saccade landing variance (Fig. 1*C*). This, however, does not explain the atypically broad presaccadic attention benefit. When the data are evaluated relative to saccade end point (accounting for motor variance; Fig. 1*D*), the performance benefit remained widespread, i.e., was likewise not spatially focused on the saccade end point. Saccades thus draw attention to their goal even when directed into an unstructured visual field, albeit with lower spatial selectivity.

Our data moreover reveal that saccade preparation comes at a cost. Although discrimination performance peaked at the center of gaze during fixation, we observed the weakest performance there right before saccade onset. Foveal performance was significantly reduced from 0 to 1.5° compared with fixation (0°: 54.57% [51.47, 57.67]%, $\overline{x}_{diff}$ = 25.67%, *P* = 0.0010; 1.5°: 57.46% [48.83, 66.09]%, $\overline{x}_{diff}$ = 10.21%, *P* = 0.0460). The presaccadic shift of attention, thus, is accompanied by a removal of processing resources from the presaccadic center of gaze.

To quantify the impact of objects on the spread of presaccadic attention, in *experiment 2*, we marked potential saccade target locations and central fixation in half of the experimental blocks (Fig. 2*A* and Supplemental Video S2). When the saccade target was unmarked (Fig. 2*B*, green), as in *experiment 1*, presaccadic discrimination performance was highest at the saccade goal (8°: 83.69% [75.12, 92.26]%), but the benefit spread, and performance was similarly enhanced at the neighboring location (6°: 77.17% [68.97, 85.37]%, $\overline{x}_{diff}$ = 6.52%, *P* = 0.174). In contrast, when the saccade target was marked, we observed a spatially far more specific presaccadic attention shift. The performance benefit was centered at the saccade target and decreased steeply for the neighboring locations (Fig. 2*B*, purple). Peak performance at the marked

target location was significantly higher (8°: 87.67% [82.26, 93.08]%) than at the adjacent locations not overlapping with the marker (6°: 64.55% [57.79, 71.31]%, $\overline{x}_{diff}$ = 23.12%, P = 0.002; 10°: 55.84% [47.82, 63.86]%, $\overline{x}_{diff}$ = 31.83%, P = 0.002). When directly contrasting discrimination accuracy for marked and unmarked trials from fixation to saccade goal, performance was significantly higher between 3° and 5° when no markers were presented (0.005 < P < 0.035), further highlighting a broad, unfocused presaccadic attention shift in the absence of target items.

Saccades made to a marked target landed closer to and scattered less around the indicated location than saccades directed to an unmarked goal (Euclidean distance marked: 0.82° [0.73, 0.91]° vs. unmarked: 1.17° [1.02, 1.32]°, $\overline{x}_{diff}$ = 0.35°, P = 0.001; end point variance marked: 0.19° [0.17, 0.21]° vs. unmarked: 0.30° [0.26, 0.34]°, $\overline{x}_{diff}$ = 0.11°, P = 0.004; Fig. 2C). Yet again, the lower accuracy and precision of saccades in trials without marked motor target did not explain the broader spread of visual attention. When comparing performance around the end point of saccades made to marked and unmarked targets, the presaccadic benefit was spatially more focused when a target was presented (Fig. 2D, purple vs. green). Accuracy for both types of trials peaked at the actual landing position (marked 0°: 80.58% [77.05, 84.11]%; unmarked 0°: 81.18% [74.01, 88.35]%), yet when contrasting performance across space, it was significantly higher from −6° to −3° relative to the end point when no markers were presented (0.004 < P < 0.044).

The shaping effect of markers on the spatial distribution of attention furthermore becomes evident at the −8° location, opposite the saccade target. The mere presence of a marker, even when not a saccade target, caused a weak but spatially specific performance peak (Fig. 2B, purple; −8°: 73.11% [63.83, 82.39]%) compared with the neighboring locations (−10°: 52.01% [44.08, 59.94]%, $\overline{x}_{diff}$ = 21.10%, P = 0.002; −6°: 58.94% [52.38, 65.50]%, $\overline{x}_{diff}$ = 14.17%, P = 0.042). No corresponding benefit was observed in unmarked trials (Fig. 2B, green; −8°: 68.07% [57.65, 78.49]%; vs. −10°: 61.14% [52.58, 69.70]%, $\overline{x}_{diff}$ = 6.93%, P = 0.282; vs. −6°: 64.87% [53.56, 76.18]%, $\overline{x}_{diff}$ = 3.20%, P = 0.999).

DISCUSSION

We investigated presaccadic visual processing using a 1/f noise paradigm (11) in which local test signals are seamlessly embedded in dynamically changing background noise. This way, participants cannot anticipate potential test locations or times, and the unbiased spread of presaccadic attention can be evaluated in the absence of scene-structuring items.

Consistent with previous work, we show that during saccade preparation, attention is selectively allocated toward the saccade target (1–9). Crucially, our results document that saccades are preceded by shifts of attention even when they are not directed to a localized target, but into an unstructured field. However, in contrast to the spatially highly specific deployment of attention to a physical saccade target, the presaccadic attention shift is far less focused when no target is presented, and this is not explained by the relatively higher saccade landing variance. In line with previous research (12, 13, 21), this demonstrates that it is not the

saccade end point that determines the spread of attention, but the presence (or absence) of scene-structuring objects.

Our present study and former evidence that objects mold the distribution of visual attention (11–13, 21) are in line with an fMRI study investigating how attention modulates perception depending on the size of the "attention field" (i.e., the attended area), which was manipulated using placeholder objects (30). Similar to our study, attention field size, approximated via the spread of cortical activity measured by fMRI, narrowed when placeholders marked the test location, as compared with when scene-structuring objects were absent and spatial uncertainty was high. The distribution of attentional resources across the visual field thus is shaped by scene-structuring objects, which in turn affects both behavioral and neural responses (22, 23).

Finally, our results reveal that the attention shift to the saccade target is accompanied by a significant removal of processing resources from the presaccadic center of gaze. Although visual sensitivity increased at the saccade goal during saccade preparation, perception at the eye fixation, where performance peaks during maintained fixation, decreased so dramatically that it even became worse than at any other tested location (±9° relative to fixation). Not even the presence of an object structure, which summoned attention in the periphery (Fig. 2B, purple), helped to maintain attention at the fovea during saccade preparation. The observed presaccadic foveal sensitivity reduction bears some similarity to the consequences of "inhibition of return" (24). Processing of a previously attended location, here the center of gaze, is suppressed, presumably to free processing resources for new locations of interest. Based on our results, we propose that when actively sampling visual information by making saccades, once the desired information has been extracted from the current eye fixation, attentional resources are withdrawn and selectively deployed to the next relevant location—the future eye fixation. This is in line with previous models of attentional orienting stating that to initiate a saccade or shift attention covertly (without moving the eyes) from one point to another, visual attention must be disengaged from its current focus, shifted to the new target, and reengaged there (25, 26).

Our observation of "presaccadic foveal blindness" as well as the spread of attention around the saccade goal could not have been investigated using conventional, item-based paradigms, since the mere presentation of local test items conflates the attention measurement (11). In fact, our results have implications for many of the previous studies on the spatial extent of visual attention. They demonstrate the dependence of the obtained attention measurement on the spatial structure provided by the employed stimulus design—a bias that is typically neglected in traditional psychophysical paradigms. An item-free approach, such as the 1/f noise paradigm, thus provides an ideal tool to investigate the spatiotemporal dynamics of (presaccadic) attention and its dependence on spatial structure, without biasing the intended measurement.

There is evidence that different cortical mechanisms within the ventral and dorsal stream control space-based and object-based attention (e.g., 23, 27, 28). Our results speak to the role of both mechanisms during the preparation of saccadic eye movements. We hypothesize that when a

saccade is prepared to a visual object, as is normally the case, object- and spaced-based mechanisms work in parallel, but object-based attention dominates, leading to a tight tuning of perceptual processing onto the saccade target object (e.g., Refs. 1, 8). However, if no insulated visual items are available, as studied here for saccades into an unstructured noise field, presaccadic attention shifts result solely from the space-based mechanism, which is characterized by a considerably broader spatial tuning. The low spatial selectivity of space-based attention is in line with the broad spread of attention found in classical reaction time studies of visual-spatial attention (e.g., Ref. 29). Future physiological studies may reveal that different attention-related brain regions become active before saccades to objects and before saccades into unstructured displays.

DATA AVAILABILITY

Eyetracking and behavioral data are available at https://doi.org/10.17605/OSF.IO/UZBWD.

SUPPLEMENTAL DATA

Supplemental Videos S1 and S2: https://doi.org/10.17605/OSF.IO/UZBWD.

ACKNOWLEDGMENTS

GRANTS

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

N.M.H. and H.D. conceived and designed research; N.M.H. performed experiments; N.M.H. analyzed data; N.M.H. and H.D. interpreted results of experiments; N.M.H. prepared figures; N.M.H. drafted manuscript; H.D. edited and revised manuscript; N.M.H. and H.D. approved final version of manuscript.

ENDNOTE

At the request of the authors, readers are herein alerted to the fact that additional materials related to this manuscript may be found at https://doi.org/10.17605/OSF.IO/UZBWD. These materials are not a part of this manuscript and have not undergone peer review by the American Physiological Society (APS). APS and the journal editors take no responsibility for these materials, for the website address, or for any links to or from it.

REFERENCES

1. **Deubel H**, **Schneider WX.** Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Res* 36: 1827–1837, 1996. doi:10.1016/0042-6989(95)00294-4.

2. **Kowler E**, **Anderson E**, **Dosher B**, **Blaser E.** The role of attention in the programming of saccades. *Vision Res* 35: 1897–1916, 1995. doi:10.1016/0042-6989(94)00279-u.

3. **Montagnini A**, **Castet E.** Spatiotemporal dynamics of visual attention during saccade preparation: independence and coupling between attention and movement planning. *J Vis* 7: 8–16, 2007. doi:10.1167/7.14.8.

4. **Li H-H**, **Barbot A**, **Carrasco M.** Saccade preparation reshapes sensory tuning. *Curr Biol* 26: 1564–1570, 2016. doi:10.1016/j.cub.2016.04.028.

5. **Ohl S**, **Kuper C**, **Rolfs M.** Selective enhancement of orientation tuning before saccades. *J Vis* 17: 2, 2017. doi:10.1167/17.13.2.

6. **Li H-H**, **Pan J**, **Carrasco M.** Presaccadic attention improves or impairs performance by enhancing sensitivity to higher spatial frequencies. *Sci Rep* 9: 2659, 2019. doi:10.1038/s41598-018-38262-3.

7. **Kroell LM**, **Rolfs M.** The peripheral sensitivity profile at the saccade target reshapes during saccade preparation. *Cortex* 139: 12–26, 2021. doi:10.1016/j.cortex.2021.02.021.

8. **Hanning NM**, **Deubel H**, **Szinte M.** Sensitivity measures of visuospatial attention. *J Vis* 19: 17, 2019. doi:10.1167/19.12.17.

9. **Hanning NM**, **Szinte M**, **Deubel H.** Visual attention is not limited to the oculomotor range. *Proc Natl Acad Sci USA* 116: 9665–9670, 2019. doi:10.1073/pnas.1813465116.

10. **Li H-H**, **Hanning NM**, **Carrasco M.** To look or not to look: dissociating presaccadic and covert spatial attention. *Trends Neurosci* 44: 669–686, 2021. doi:10.1016/j.tins.2021.05.002.

11. **Hanning NM**, **Deubel H.** A dynamic pink noise protocol to assess spatial-temporal attention without biasing perceptual processing (Preprint). *BioRxiv*, 2021. doi:10.1101/2021.07.10.451930.

12. **Puntiroli M**, **Kerzel D**, **Born S.** Placeholder objects shape spatial attention effects before eye movements. *J Vis* 18: 1, 2018. doi:10.1167/18.6.1.

13. **Szinte M**, **Puntiroli M**, **Deubel H.** The spread of presaccadic attention depends on the spatial configuration of the visual scene. *Sci Rep* 9: 14034, 2019. doi:10.1038/s41598-019-50541-1.

14. **Reingold EM**, **Stampe DM.** Saccadic inhibition in voluntary and reflexive saccades. *J Cogn Neurosci* 14: 371–388, 2002. doi:10.1162/089892902317361903.

15. **Hanning NM**, **Aagten-Murphy D**, **Deubel H.** Independent selection of eye and hand targets suggests effector-specific attentional mechanisms. *Sci Rep* 8: 9434, 2018. doi:10.1038/s41598-018-27723-4.

16. **Brainard DH.** The psychophysics toolbox. *Spat Vis* 10: 433–436, 1997.

17. **Pelli DG.** The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spat Vis* 10: 437–442, 1997.

18. **Cornelissen FW**, **Peters EM**, **Palmer J.** The Eyelink Toolbox: eye tracking with MATLAB and the Psychophysics Toolbox. *Behav Res Methods Instrum Comput* 34: 613–617, 2002. doi:10.3758/bf03195489.

19. **Prins N**, **Kingdom FAA.** Applying the model-comparison approach to test specific research hypotheses in psychophysical research using the Palamedes toolbox. *Front Psychol* 9: 1250, 2018. doi:10.3389/fpsyg.2018.01250.

20. **Engbert R**, **Mergenthaler K.** Microsaccades are triggered by low retinal image slip. *Proc Natl Acad Sci USA* 103: 7192–7197, 2006. doi:10.1073/pnas.0509557103.

21. **Li H-H**, **Pan J**, **Carrasco M.** Different computations underlie overt presaccadic and covert spatial attention. *Nat Hum Behav* 5: 1418–1431, 2021. doi:10.1038/s41562-021-01099-4.

22. **Reynolds JH**, **Heeger DJ.** The normalization model of attention. *Neuron* 61: 168–185, 2009. doi:10.1016/j.neuron.2009.01.002.

23. **Yantis S**, **Serences JT.** Cortical mechanisms of space-based and object-based attentional control. *Curr Opin Neurobiol* 13: 187–193, 2003. doi:10.1016/s0959-4388(03)00033-3.

24. **Klein RM.** Inhibition of return. *Trends Cogn Sci* 4: 138–147, 2000. doi:10.1016/s1364-6613(00)01452-2.

25. **Posner MI**, **Cohen Y.** Components of visual orienting. In: *Attention and Performance X*, edited by Bouma H, Bowhuis DG. Hillsdale, NJ: Erlbaum, 1984, p. 531–556.

26. **Fischer B**, **Breitmeyer B.** Mechanisms of visual attention revealed by saccadic eye movements. *Neuropsychologia* 25: 73–83, 1987. doi:10.1016/0028-3932(87)90044-3.

27. **Fink GR**, **Dolan RJ**, **Halligan PW**, **Marshall JC**, **Frith CD.** Space-based and object-based visual attention: shared and specific neural domains. *Brain* 120: 2013–2028, 1997. doi:10.1093/brain/120.11.2013.

28. **Serences JT**, **Schwarzbach J**, **Courtney SM**, **Golay X**, **Yantis S.** Control of object-based attention in human cortex. *Cereb Cortex* 14: 1346–1357, 2004. doi:10.1093/cercor/bhh095.

29. **Pinker S**, **Downing CJ.** The spatial structure of visual attention. In: *Attention and Performance XI*, edited by Posner M, Marin O. Hillsdale, NJ: Erlbaum, 1985.

30. **Herrmann K**, **Montaser-Kouhsari L**, **Carrasco M**, **Heeger DJ.** When size matters: attention affects performance by contrast or response gain. *Nat Neurosci* 13: 1554–1559, 2010. doi:10.1038/nn.2669.