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The peripheral sensitivity profile at the saccade target reshapes during saccade preparation **M 🗘**



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ABSTRACT

Goal-directed eye movements (saccades) bring peripheral objects of interest into highacuity foveal vision. In preparation for the incoming foveal image, the perception of the saccade target may sharpen gradually before the eye movement is executed. Indeed, previous studies suggest that pre-saccadic attention shifts enhance sensitivity to high spatial frequencies (SFs) more than sensitivity to lower SFs. This pattern, however, was observed within a narrow frequency range and may reflect local changes in the shape of a broader underlying sensitivity profile. Depending on the development of the profile's shape, SFs above the previously examined range may profit less from saccade preparation. To assess the impact of saccade preparation on the shape of a broader sensitivity profile, we prompted observers to discriminate the orientation of a sinusoidal grating (the probe) presented briefly at the target of an impending saccade, at 10 dva (degree of visual angle) eccentricity. The probe's SF ranged from 1 to 5.5 cycles per dva (cpd) and was unpredictable on a given trial. We fitted observers' response accuracies across SFs with a log-parabolic, that is, inverted U-shaped function. Long before saccade onset, the profile peaked at .6 cpd and dropped off towards lower and higher SFs with broad bandwidth. During saccade preparation, the peak of the profile increased and shifted towards higher SFs while the bandwidth of the profile decreased. As a consequence of this reshaping process, presaccadic enhancement increased with SF up to 2.5 cpd, corroborating previous findings. Sensitivities to higher SFs, however, profited less from saccade preparation. We conclude that the extent of pre-saccadic enhancement to a particular SF is governed by its position on a broader sensitivity profile which reshapes substantially during saccade preparation. The shift of the profile's peak towards higher SFs increases resolution at the saccade target even when the features of relevant visual information are unpredictable.

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1. Introduction

When we inspect the night sky with the naked eye, the planet Jupiter appears as a dimly glowing spot, at times barely distinguishable from surrounding stars. A single glance through the lens of a telescope, however, reveals an intricate pattern of stripes and twirls covering the planet's surface. The difference in appearance can be so striking that unexperienced spectators may need to consult external landmarks such as towers, chimneys or, at a pinch, their own finger, to match the sharp telescopic image to the corresponding spot in the sky.

While this situation might be exceptional, the striking discord that two views of the same object can yield is easily experienced in our visual field. Since visual acuity is highest in the central two degrees (the fovea) and declines in the periphery (Frisén & Glansholm, 1975; Anton-Erxleben & Carrasco, 2013; Beard, Levi, & Klein, 1997; Loschky, McConkie, Yang, & Miller, 2005; Strasburger, Rentschler, & Jüttner, 2011), the resolution at which a stimulus can be perceived is limited by its distance from the current center of gaze. Instead of aiming telescopes, humans therefore execute rapid eye movements (i.e., saccades) towards objects of interest to bring them into the area of sharpest vision. With each saccade, the visual system is confronted with a similar correspondence problem as the spectator at night: to ensure the continuous perception of information at the saccade target, the low-resolution peripheral preview needs to be matched to its high-resolution foveal equivalent after eye movement landing.

During saccade preparation, the perception of the eye movement goal may sharpen gradually to bridge this phenomenological gap. Each saccade is preceded by an obligatory shift of attention to its target (e.g., Deubel & Schneider, 1996; Moore & Fallah, 2001). Pre-saccadic attention shifts manifest in enhanced detection and discrimination performance for stimuli presented at the eye movement goal (Kowler, Anderson, Dosher, & Blaser, 1995; Buonocore, Fracasso, & Melcher, 2017; Deubel, 2008; Deubel & Schneider, 1996; Hanning, Aagten-Murphy, & Deubel, 2018; Jonikaitis, Klapetek, & Deubel, 2017; Montagnini & Castet, 2007; Rolfs & Carrasco, 2012; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011; Szinte, Puntiroli, & Deubel, 2019) and an associated increase of their perceived contrast (Rolfs & Carrasco, 2012), reflecting the priority of the saccade target over other locations in the visual field. Two findings suggest that, beyond yielding general performance improvements, pre-saccadic attention shifts may harmonize pre- and post-saccadic target views. First, the spatial frequency (SF) observers are most sensitive to (henceforth peak SF) increases during saccade preparation (Li, Barbot, & Carrasco, 2016). Second, sensitivities to higher SFs increase more than sensitivities to lower SFs - even when an enhancement of high-SF content impairs performance (Li, Pan, & Carrasco, 2019). Since the presence of high-SF information in the foveal image constitutes the main phenomenological difference to the peripheral view, an asymmetric modulation of sensitivities may indeed render the presaccadic perception of the saccade target more similar to the post-saccadic one. In the current investigation, we aim to

establish how these sensitivity modulations transfer to a wider range of SFs, and to situations in which the features of relevant visual information at the saccade target are unpredictable. This question extends previous findings in two aspects:

First, more pronounced pre-saccadic enhancement of higher as compared to lower SFs was demonstrated within a narrow frequency range (Li et al., 2019). Peripheral sensitivities to individual SFs, however, constitute single points on a broader underlying sensitivity profile. This profile is known to reach its peak at a certain SF and drop off monotonically to either side (e.g., Lesmes, Baek, & Albright, 2010). As the simulated, hypothetical scenarios in Fig. 1 illustrate, a variety of changes in the shape of the profile would result in an enhancement of sensitivity to high SFs. For instance, the profile may shift towards higher SFs while its peak value increases and its width remain constant (Fig. 1, scenario A). A shift of the profile towards higher SFs, however, is no necessary pre-condition for the previously demonstrated pattern a combined increase in the profile's peak and width would suffice to produce more pronounced enhancement of higher SFs (scenario B). Alternatively, a shift of the profile towards higher SFs and an increase in its peak could be accompanied with a decrease in its width (scenario C). All of these scenarios are reconcilable with the finding that higher SFs—within the previously examined range-profit more from saccade preparation than lower ones (see Discussion for a consideration of their theoretical and empirical plausibility). Crucially, however, they have different implications for SFs above this range, for which enhancement may either continue to increase (scenario A and B, top panels) or decrease again (scenario C, top panel). Previous findings are agnostic to the development of the profile's overall shape and may not transfer to a wider range of SFs.

Second, an increase of peak SF as described above was demonstrated in a design in which observers discriminated the orientation of the same probe stimulus throughout the experiment (Li et al., 2016). The SF of relevant visual information at the saccade target was thus predictable on every trial. Right before saccade onset, the SF observers were most sensitive to had increased to a value close to the SF of the probe (Li et al., 2016). Since pre-saccadic attention shifts have been shown to sharpen sensitivities around the target's features (i.e., its orientation), both in the same investigation (Li et al., 2016) and a different study (Ohl et al., 2017), it is unclear if an increase of peak SF reflects perceptual tuning towards the probe's SF or an enhancement of its resolution. While such perceptual tuning on its own cannot account for the automatic high-SF enhancements demonstrated by Li et al. (2019), the SF content of visual information at the saccade target in this investigation was again predictable on each trial. In consequence, the demonstrated pattern of results may reflect an interaction between tuning and high-SF enhancement (see Discussion for a more extensive explanation of this issue). In any case, an assessment of tuningindependent sensitivity modulations requires a task in which the SF of the probe is unpredictable on an individual trial level, up until its appearance. To the best of our knowledge, this condition has not been met in any previous studies.



Fig. 1 – Illustration of different hypothetical scenarios (A–C) on how the visual sensitivity profile could reshape during saccade preparation (SP), along with their respective implications for pre-saccadic enhancement and perception across a wider SF range. Middle panels. At an early stage of saccade preparation (SP1), a parabolic profile describes the relation between SF and visual sensitivity (dark blue curve). As saccade preparation progresses (SP2 through SP5), this profile may reshape in various ways. Subpanels in the bottom left corner illustrate each depicted reshaping scenario. The profile's peak could increase (upward arrows in A, B and C), the profile could shift towards higher SFs (rightward arrows in A and C), and its bandwidth could increase (outward arrows in B) or decrease (inward arrows in C). In each scenario, vertical yellow lines indicate the extent of pre-saccadic enhancement for a given SF, i.e., the difference in sensitivity between the first and last pre-saccadic time bin. For all depicted scenarios, the difference between SP1 and SP5 increases with SF within the previously tested range from .67 to 2.25 cpd. In scenario A and B, the difference between curves continues to increase for SFs above this range (dashed yellow lines). As illustrated in scenario C, however, the curves may approach each other again at higher SFs (dashed red line). Top panels. Estimated enhancement (Enh; defined as the difference in sensitivity between the first and last pre-saccadic time bin) across the entire depicted SF range for each simulated reshaping scenario. All enhancement curves are reconcilable with previous findings since they increase within the previously tested range. However, predictions differ markedly for higher SFs for which enhancement may continue to increase (shaded yellow areas in A and B) or decrease again (shaded red area in C). Bottom panels. Illustrated perceptual consequences of reshaping. Simulated sensitivities in the last pre-saccadic time bin (SP5) were translated to contrast values and overlaid on a sinusoidal grating of increasing SF. The scenarios differ most notably with respect to the SF at which highest sensitivity is obtained (lowest in B; medium in A and C) and the range of SFs that can be perceived at comparable sensitivity (medium range in A; wider range in B; narrower range in C).

To address our question, we characterized pre-saccadic sensitivity modulations as the development of a broader sensitivity profile at the saccade target. Specifically, we probed sensitivities to SFs ranging from 1.0 to 5.5 cycles per degree of visual angle (cpd) while the SF of the probe on a given trial was unpredictable. We found that pre-saccadic sensitivity modulations are best described as a joint increase in the profile's peak, a decrease in its width, and a shift of its peak towards higher SFs (see scenario C). The combination of these modulations entailed that sensitivity to all tested SFs was enhanced during saccade preparation. The magnitude of this enhancement increased with SF up to 2.5 cpd, in accordance with previous findings obtained at the same visual eccentricity (10 dva; Li et al., 2016). Even higher SFs still profited from saccade preparation. However, the magnitude of enhancement decreased again. A monotonic increase of enhancement with SF does therefore not capture the impact of saccade

preparation on visual sensitivities to a wider SF range. Instead, sensitivity modulations are characterized best as a reshaping of the peripheral sensitivity profile at the saccade target. The shift of the profile's peak towards higher SFs seems to constitute a highly automatic mechanism that increases visual resolution at the saccade target even when its features are unpredictable.

2. Methods

2.1. Participants

Twelve human observers (10 females, 11 right-handed, 10 right-eye dominant) aged 18–38 years (md = 24.5) participated in the experiment. We chose a sample size in the typical range of studies investigating pre-saccadic attention shifts (e.g.,

Hanning, Deubel, & Szinte, 2019; Li et al., 2019). Normal or corrected-to normal visual acuity was ensured at the beginning of the first session using a Snellen chart (Hetherington, 1954) embedded in a Polatest vision testing instrument (Zeiss, Oberkochen, Germany). Observers yielding scores of 20/25 or 20/20 were invited to proceed with the experiment. Ocular dominance was assessed using the Miles test (Miles, 1930). Participants were recruited through word of mouth and via the local subject pool at Humboldt-Universität zu Berlin (PESA). They were naïve as to the purpose of the experiment, gave written informed consent before the study and were compensated with either course credit or a payment of 8.50€/hour. A bonus of 4€ was added upon completion of all five sessions. The study complied with the Declaration of Helsinki in its latest version and was approved by the Ethics Committee of the Institute of Psychology at Humboldt-Universität zu Berlin. The experimental question, paradigm and analyses were preregistered on the Open Science Framework (https://osf.io/whrxd). Raw and pre-processed data as well as experimental and analysis code is publicly available under https://osf.io/j73fx/.

2.2. Apparatus

The experiment was conducted in a dimly lit, sounddampened room. Stimuli were displayed on a gammacorrected 22.5-inch VIEWPixx monitor (VPixx Technologies, Saint-Bruno, QC, Canada) with a vertical refresh rate of 120 Hz, a resolution of 1920 \times 1200 pixels and a color depth of 10 bits per channel. Observers placed their head on a chin and forehead rest and faced the screen at a viewing distance of 57 cm. The position of the dominant eye was recorded at a sampling rate of 1 kHz using a desk-mounted infrared eyetracker (Eye-Link 1000 Plus; SR Research, Osgoode, Canada). Stimulus presentation was controlled by a DELL Precision T3600 Workstation (Debian GNU Linux 8) and implemented in Matlab 2015a (Mathworks, Natick, MA, USA) using the PsychToolbox (Brainard, 1997; Kleiner et al., 2007) and Eyelink toolbox (Cornelisen, Peters, & Palmer, 2002) extensions. Observers generated their responses on a standard QWERTY keyboard positioned centrally in front of them. Throughout the experiment, stimuli appeared on a uniformly gray background.

2.3. Procedure

Every participant completed five sessions within a 14-day period. Individual sessions were performed on separate days and lasted approximately 90 min. Every session involved a staircase procedure, followed by a contrast verification block and, lastly, the main experiment. In order to familiarize observers with the task, the staircase procedure was preceded by a slow-motion training block in the first session. In all parts of the experiment, observers reported the perceived orientation of a sinusoidal grating presented briefly at the goal of an impending saccade in a 2-AFC task (clockwise versus counter-clockwise).

2.3.1. Trial procedure in the main experiment

At the beginning of each trial in the main experiment, a white fixation dot with a diameter of .3 degrees of visual angle (dva)

was presented in the screen center (Fig. 2A). After stable fixation had been determined within a circle of 1.8 dva around the dot, two placeholders (dotted lines forming a circle of 3 dva diameter) appeared 10 dva to the left and right of fixation. After 708 msec (i.e., 85 monitor refresh frames), a flickering stream of noise images, each visible for 25 msec, appeared within the placeholders. This measure was implemented to prevent the otherwise sudden on- and offset of the probe stimulus from interfering with saccade preparation (Rolfs, et al., 2011; Hanning et al., 2019).

After a varying delay of 750–1250 msec, a horizontal white line of length .05 dva (the movement cue) protruded from the left or right side of the fixation dot, pointing towards the goal of the eye movement. Observers were instructed to saccade to the center of the respective stimulus stream as quickly as possible.

At varying times after cue onset, the probe stimulus was presented for 25 msec at the indicated location, effectively replacing one of the noise images in the stream. We defined three possible cue-probe delays per participant and session: While the shortest delay between cue and probe onset was fixed to 50 msec, the intermediate and longest delays were adjusted to each observer's median saccade latency measured in the staircase block (see 2.3.2.4 for details). The probe was a sinusoidal grating (Gabor patch) framed by a circular aperture of 3 dva diameter. The Gabor patch could exhibit a SF of 1.0, 1.5, 2.5, 3.5, 4.5, or 5.5 cpd and was oriented 10° to either the left or the right (Fig. 2B and C). Crucially, the features of the probe on a given trial were unpredictable due to the following manipulations: First, trials involving probes with different SFs were randomly interleaved. Second, the visual properties of the noise images preceding the probe were unpredictive of its features. Irrespective of the SF and orientation of the Gabor patch in a given trial, each noise image was bandpass-filtered to encompass orientations from 0 to 180° as well as SFs of .5*the lowest to 2*the highest possible probe frequency, corresponding to a SF range of .5-11 cpd (Fig. 2B).

In total, the stimulus stream (noise images and probe) was visible for 1025 msec. Once the stream had disappeared, observers reported the orientation of the probe by pressing the corresponding arrow key. Since we prioritized accuracy over the speed of response generation, the keyboard was locked until 500 msec after saccade onset had been detected. The next trial was initiated following a blank interval of 500 msec.

2.3.2. Session structure

2.3.2.1. TASK FAMILIARIZATION (SESSION 1). In the first session, we familiarized observers with the task and stimulus by presenting it in a slowed down, simplified version. For this purpose, stimulus presentation times were increased by a factor of six. The probe appeared in a predictive location and at maximum contrast. Participants generated verbal replies. Once an observer was able to perform the task at the current speed, presentation times were gradually reduced until reliable performance was reached when the trial was presented in normal speed.

2.3.2.2. STAIRCASE PROCEDURE (SESSIONS 1-5). To be able to demonstrate pre-saccadic variations in discrimination performance for all SFs in our experiment, we intended to



Fig. 2 – Trial procedure and stimulus properties. A. Stimulus sequence within a single placeholder (top) and for the entire display (bottom). Each trial started with the appearance of the fixation dot in the screen center and two landmarks 10 dva to the left and right of fixation. Afterwards, a stream of quickly alternating noise images (each visible for 25 msec) appeared within the landmarks. The presentation of the cue after a varying time interval marked the start of the saccade preparation period (color gradient). In the early (blue; dotted circle), intermediate (turquoise; dotted circle) or late (green; continuous circle) stage of saccade preparation, an oriented Gabor patch (the probe) was presented at the cued location. In the exemplary trial sequence depicted here, the probe appeared at the latest presentation time. Following the offset of the stimulus stream, observers reported the orientation of the probe (cw versus ccw). Stimuli are drawn to scale and plotted against a cropped section of the experimental screen. B. Noise properties. Top: Whereas the probe could have one out of six SFs ranging from 1 to 5.5 cpd (vertical lines), noise images encompassed SFs from .5 to 11 cpd (horizontal rectangle). Bottom: Whereas the probe could have an orientation (Ori) of 10° (cw) or -10° (ccw; vertical lines) relative to vertical, noise images could encompass all possible orientations (horizontal rectangle). C. Probe properties. Left: Probe stimuli of all potential SFs (columns) and orientations (rows). The probe appeared within a circular aperture of 3 dva diameter, at a contrast titrated for each observer and session. Right: Probe presentation times recorded in all sessions of a randomly chosen example observer (Obs 10; median saccade latency: 208 msec) and scaled to the time interval between cue onset (dark gray line) and saccade onset (Sac; yellow line; detected offline). Each line indicates the offset of the probe with respect to the onset of the eye movement in the respective trial. Colors indicate the affiliation of a trial to one of the three experimentally defined presentation conditions (off1, off2, off3; see panel A).

determine a probe contrast at which response accuracies in a baseline time bin were neither at chance nor at ceiling for any SF. Based on pilot data, we approached this goal by estimating the contrast value at which observers would be able to correctly identify the orientation of a 1.5 cpd Gabor patch in 75% of cases. For this purpose, we randomly interleaved trials corresponding to a 1-up 2-down and a 1-up 3-down staircase estimating the stimulus contrast to obtain 70.7% and 79.4% correct responses, respectively. In each staircase, minimum and maximum contrast values corresponded to 19% and 90%. The step size was set to 5%. To avoid a predictable development of probe contrasts across trials, we randomly chose one of the staircases to start at maximum contrast while the other staircase started at the minimum contrast value. While the time interval between saccade cue and probe onset varied systematically in the main experiment, the probe was presented 50 msec after the saccade cue in every staircase trial. In total, the staircase block comprised 120 trials (60 per staircase) and took observers approximately 10 min to complete. The two resulting threshold estimates, i.e., the mean of the last six reversals per staircase, were averaged to obtain the contrast level at which probes of all SFs were presented during the main experiment. If a staircase converged on the minimum

contrast value within fewer than six reversals, the minimum contrast (i.e., 19%) was registered as its threshold estimate.

2.3.2.3. CONTRAST VERIFICATION (SESSIONS 1–5). To obtain a benchmark performance estimate at the determined contrast level, we administered short verification blocks before the main experiment. These blocks additionally served to familiarize inexperienced observers with the general appearance of all possible probe stimuli.

For each of the six SFs, participants completed ten trials during which probes of only the respective SF were presented. Blocks were administered in order of increasing SF. Before each block, the probe with the current SF was presented in the screen center (4 sec at leftward, vertical and rightward orientation, respectively). Following the completion of a block, observers received feedback on their performance. After training trials had been performed for each SF in separation, the last block consisted of 24 trials during which probes of all SFs were randomly interleaved. If an observer yielded a mean response accuracy of 100% for two or more SFs, the probe contrast was reduced by 5%. If an observer yielded a mean accuracy of 50% or lower for two or more SFs, or if their response accuracy in the interleaved block was below 63%, the contrast value was increased by 5%. Across all observers and sessions, the probe was presented at a median contrast of 27.4% (std = 17.5%; median per session: 51.5%, 27.5%, 25.2%, 20.0%, 23.8%). In total, the verification blocks took observers 5–10 min to complete. They subsequently moved on to the main experiment.

2.3.2.4. MAIN EXPERIMENT (SESSIONS 1–5). Each observer performed six blocks of 72 trials each. Within each block, probes with different SFs were randomly interleaved. The median saccade latency in staircase trials served as the basis for probe timing in the main experiment. In order to obtain estimates of visual sensitivity throughout the saccade preparation period, we defined three possible delays between saccade cue offset and probe onset. The shortest delay did not vary across observers: the probe appeared 50 msec after the participant had been cued to make an eye movement. The longest delay was set to each observer's median saccade latency minus the duration of the probe (i.e., 25 msec). This measure ensured that the probe disappeared shortly before or at saccade onset on a sufficient number of trials. The intermediate delay was chosen to fall right between the shortest and longest one.

2.3.3. Online eye movement criteria

A trial was aborted if a blink was recorded at any time after stable fixation had been determined or if gaze position was recorded outside a radius of 1.8 dva around the fixation dot before cue onset. Likewise, the failure to initiate an eye movement by 400 msec after cue onset led to an abortion of the respective trial. Note that during the experiment, saccade onset was defined as the time point at which gaze position crossed a circular boundary with a radius of 2.5 dva around the fixation dot. Moreover, a trial was aborted if an initiated saccade landed farther than 2.5 dva away from the center of the cued stimulus stream. Aborted trials were appended at the end of each block.

2.4. Data analysis

2.4.1. Eye movement pre-processing

The pre-processing of eye movement data and all subsequent analysis steps were implemented in Matlab R2018b (Mathworks, Natick, MA, USA). We detected saccades offline using a velocity-based saccade detection algorithm (Engbert & Mergenthaler, 2006). Saccade onset was defined as the time point at which the current eye velocity had exceeded the median eye velocity by 5 SDs. The criterion for minimum saccade duration was 8 msec. In addition to the online exclusion criteria listed above, trials were excluded in offline analyses if more than one or no saccade was detected in the critical time window between 150 msec before and 400 msec after cue onset. Moreover, a trial was excluded if gaze position samples were missing before the response saccade was detected. Across all participants and sessions, these criteria resulted in an exclusion of 2.82% of trials. In the remaining trials (n = 24,768), a single response saccade was detected in the critical time window and landed within the accepted area around the center of the cued stimulus stream. All exclusion criteria were established prior to data analysis. In all

subsequent analyses, saccade onset will refer to the onset of the response saccade as determined in offline analyses.

2.4.2. Fitting of the pre-saccadic sensitivity profile

To describe the shape of the sensitivity profile, we fitted logparabolic functions to response accuracies. Each logparabolic function relates response accuracies (ordinate) to probe SFs (abscissa):

$$\begin{split} \log_{10}(acc) = & \log_{10}(PeakSens) - \log_{10}(2) \\ & * \left(\frac{\log_{10}(SF) - \log_{10}(PeakSF)}{\log_{10}(2^*BW)/2}\right)^2 \end{split}$$

By using this description, we were able to quantify presaccadic changes in the sensitivity profile as the development of three parameters over time: the peak sensitivity (PeakSens; i.e., the maximum response accuracy across all SFs), the peak SF (PeakSF; i.e., the SF at which peak sensitivity was obtained) and the bandwidth (BW) of the profile which describes its tuning width to a band of SFs.

Note that log-parabolas are typically used to describe the relation between SF and contrast sensitivity, i.e., the inverse of the contrast threshold per SF (see e.g., Lesmes, Baek, & Albright, 2010). In every session of our investigation, probes of all SFs were presented at the same contrast. Despite this conceptual difference, log-parabolas fitted our data on an individual observer level (for exemplary function fits see Fig. 3A; Supplementary Figure S1) and provided us with parameter estimates that allow comparisons to previous findings. It is nonetheless important to emphasize that log-parabolic fits to observers' orientation discrimination accuracies are purely descriptive. Unlike the contrast sensitivity function, the sensitivity profile characterized here relates response accuracies to a range of SFs presented at a constant contrast level.

In order to account for the reliability of each data point in the fitting process, we minimized the deviation between measured values and a weighted cost function. To obtain the weighted cost function, deviations between true values and values predicted by log-parabolic function fits were multiplied by a parameter directly proportional to the number of trials contributing to a given data point. Fitting was performed on an individual observer level using the Matlab function lsqnonlin (trust-region-reflective algorithm). The following lower and upper bounds were defined for each parameter: .5 and 1 for peak sensitivity (proportion correct), .1 and 8.5 for peak SF (cpd) and 10^{0.1} and 10⁵ for bandwidth. Bandwidth estimates were translated to more easily interpretable values (Full width at half maximum, FWHM; in cpd) after the fitting process. For this purpose, we determined the two x-coordinates at which the profile reached .5*PeakSens by solving the log-parabolic equation for SF. This returned two estimates in cpd: the lower and higher SF at which the profile reached half of its maximum. The resulting FWHM-estimate corresponds to the difference between those values.

For each trial, we determined the time difference between the offset of the probe and the onset of the saccade. Based on this difference, every trial was assigned to one of five presaccadic time bins (Fig. 3B; trial numbers per bin and SF in Supplementary Table S1). We were interested in the continuous development of the sensitivity profile's shape after the



Fig. 3 – Example observer fits (A) and number of trials per bin across observers (B). A. Log-parabolic function fits for an example observer (Obs 7) per pre-saccadic time bin (columns). The number in the slider above each column indicates the lower bound of the respective time bin in ms (see B). As bin colors change from blue to green, the probe had appeared closer and closer to saccade onset. Dots indicate the mean measured orientation discrimination accuracy per time bin and probe SF. Error bars correspond to the bootstrapped 95% confidence interval (1000 repetitions). Observer 7 yielded a median probe presentation contrast that is representative for the whole sample (Obs 7: 26.8%; whole sample: 27.4%). For example fits of observers with different probe contrasts, see Supplementary Figure S1. B. Histogram of probe offset times (ProbeOff) relative to saccade onset (SacOn). Bar heights and error bars indicate the mean and standard error of the mean (SEM) across observers, respectively. The gray rectangle in the background illustrates the median saccade duration. Each trial was assigned to one of five pre-saccadic bins (blue to green shades). Trials in which the probe disappeared during or after the eye movement are depicted in yellow and orange, respectively.

preparation of a goal-directed eye movement had been initiated. In consequence, our earliest sensitivity estimate stems from the earliest pre-saccadic time bin extending from 150 to 100 msec before saccade onset (dark blue in all plots). This bin is referred to as 'baseline' whenever sensitivities in later time bins are compared to sensitivities in the first bin, i.e., whenever pre-saccadic enhancement defined as the difference in performance between the first and any subsequent time bin is computed. Note that the first bin encompasses a larger time window than subsequent bins (50 vs 25 msec) so we could obtain a reliable estimate of baseline performance based on a large number of trials while still capturing an early stage of saccade preparation. In every bin, we obtained parameter estimates by fitting the weighted cost function to mean sensitivities on an individual observer level. We also inspected the development of parameters on a more continuous scale by selecting all trials within a time window of 25 msec duration, fitting the cost function to mean sensitivities in that interval, and iteratively moving the box-car window closer to saccade onset in 1 msec steps.

2.4.3. Statistical inference

After obtaining time-resolved estimates of all three function parameters (i.e., peakSens, peakSF, BW), we intended to quantify how each of them developed during saccade preparation. For this purpose, we compared the fits of two linear mixed-effects models per function parameter. Model fitting was performed with the Matlab function fitlme. In the 'nochange' model, the variance in estimated parameter values was explained by a random intercept of observer alone. In the 'change' model, the variance in parameter estimates was explained by a fixed effect of time bin and correlated random effects for intercept and slope: change: parameter Values ~ bin + (bin | sub)

where 'parameterValues' refers to the estimated parameter values from all pre-saccadic time bins and 'sub' denotes different observers. Note that within each observer, the effect of intercept and slope could be correlated. We implemented this measure to account for systematic relationships between an observer's intercept and slope: for instance, if an observer's peak sensitivity was high to begin with (high intercept), it was likely to increase less over time due to ceiling effects, resulting in a shallower slope. Model comparisons were administered via BF₁₀ scores. To take the higher complexity of the 'change' model into account, the calculation of Bayes Factors was based on BICs ($BF_{10} = e^{(BIC(change) - BIC(no-change))/2}$; Wagenmakers, 2007). A $BF_{10} < 1$ indicates a better fit of the 'change' model. Conversely, a $BF_{10} > 1$ indicates a better fit of the 'no-change' model. The strength of evidence was evaluated based on the convention proposed by Lee and Wagenmakers (2013), with BF₁₀ -values of 1–3, 3–10, 10–30, 30–100 and > 100 indicating anecdotal, moderate, strong, very strong, and extreme evidence, respectively.

In a second step, and as a proof of concept, we investigated if pre-saccadic changes in a certain parameter were necessary to explain observed response accuracies, or if they could be accounted for equally well by assuming that the parameter remained constant over time. For this purpose, we compared the fits of seven linear mixed-effects models. In each model, we described the relation between observed response accuracies and response accuracies predicted by a certain combination of time-variant and time-constant parameter estimates. For instance, to inspect a model in which only presaccadic changes in peak sensitivity contributed meaningfully to the development of response accuracies (PeakSens-only), we determined the values of a log-parabolic function with the following parameters in every bin: the previously obtained bin-specific estimate for peak sensitivity, the mean estimate for peak SF across all bins, and the mean estimate for bandwidth across all bins. We then described the relation between these predicted (x-axis) and observed (y-axis) response accuracies with a linear mixed-effects model. If a model involving a certain parameter combination explained the observed variance in response accuracies perfectly, we would observe an intercept of zero and a slope of one since all data points would fall on the line of unity. We allowed both intercept and slope to vary across observers to account for inter-individual differences in model fits, and accounted for possible correlations between observer-specific slopes and intercepts. For each model, we used the following syntax:

observedAcc ~ predictedAcc + (predictedAcc | sub)

where 'observedAcc' refers to observed response accuracies, 'predictedAcc' refers to response accuracies predicted by the respective parameter combination, and 'sub' denotes different observers. By iterating through every possible parameter combination, we obtained models in which only one function parameter was assumed to vary across time (PeakSens-only, PeakSF-only, BW-only), models in which two parameters were assumed to vary (PeakSens & PeakSF, Peak-Sens & BW, PeakSF & BW) and a model in which bin-specific estimates were entered for all parameters (All). Arguably, a simple upward shift of the profile constitutes the most parsimonious explanation of general performance improvements at the saccade target. To obtain a baseline for model selection, we therefore compared each fit to the PeakSensonly account. Again, model comparisons were administered via BF10 scores derived from BIC values. A BF10 > 1 indicates a better fit of the respective model as compared to the PeakSens-only account.

3. Results

3.1. Pre-saccadic development of the sensitivity profile

The fitted sensitivity profile for each pre-saccadic time bin is plotted in Fig. 4A. Saccade preparation was accompanied by an upward shift of the profile, resulting in a gradual increase in peak sensitivity (Fig. 4B). This increase was supported by a clear advantage of the 'change' over the 'no-change' model, $BF_{10} = 87.27$, and a positive fixed effects coefficient for 'bin' (slope $\beta = .944$). Moreover, the SF at which peak sensitivity was obtained increased monotonically from .63 cpd in the first presaccadic time bin (-150 to -100 msec before saccade onset) to 1.62 cpd in the last bin (final 25 msec before saccade onset), $BF_{10} = 4.25 \times 10^7$ ($\beta = .237$). Finally, we observed a decrease in the bandwidth of the profile, $BF_{10} = 8.49 \times 10^3$ ($\beta = -3169.1$). The combination of these modulations entailed a continuous increase in mean sensitivity defined as the average response accuracy across all SFs at the saccade target, $BF_{10}\,{=}\,2.35\,{\times}\,10^{12}$ $(\beta = .031).$

Two models clearly outperformed the account assuming a simple upward shift of the profile (PeakSens-only; Fig. 4C): The model assuming variations of SF and bandwidth with bin, $BF_{10} = 6.22 \times 10^{58}$, and the model assuming a variation of all

three parameters, $BF_{10} = 1.99 \times 10^{90}$. Moreover, the latter clearly outperformed the former, $BF_{10} = 2.63 \times 10^{18}$. The intercept of the 'All' model was not significantly different from zero [-.018, 95% CI (-.051 .014)] and its slope was not significantly different from one [1.02, 95% CI (.985 1.064)], validating our fitting approach. Intercepts and slopes of all remaining models along with their random effect estimates can be found in the Supplementary Materials (Supplementary Table S2). Combined, these results suggest that pre-saccadic changes in response accuracies are best described by a joint variation of the peak sensitivity, peak SF and bandwidth of the underlying sensitivity profile.

3.2. Pre-saccadic enhancement by SF

To investigate the extent of pre-saccadic enhancement for each probed SF, we determined the difference between response accuracies in the earliest time bin (baseline; 150 msec-100 msec before saccade onset) and every subsequent bin (Fig. 5A). If higher SFs profited more from saccade preparation than lower ones, this difference should increase monotonically with SF. In general, response accuracies decreased with SF in the baseline bin (see Fig. 4A, panel 1). More pronounced pre-saccadic enhancement for higher SFs could thus be explained by ceiling effects for lower SFs. To stretch out the upper end of the accuracy range, we performed an arcsine transformation on response accuracies before calculating difference scores. Within each time bin, we then computed Helmert contrasts, comparing the difference score for a given SF (e.g., 2.5 cpd) to the mean difference score across all lower SFs (e.g., 1.0 and 1.5 cpd) with a left-tailed onesample t-test (Bonferroni-Holm corrected). We obtained one significant comparison: In the last bin, the pre-saccadic increase in accuracy for a 2.5 cpd stimulus significantly exceeded the mean accuracy increase for probes of 1.0 and 1.5 cpd, t(11) = -2.86, p = .039. A BF₁₀ of 4.18 was obtained for this comparison, indicating moderate evidence for an increase of enhancement up to 2.5 cpd. For higher SFs, this comparison failed to reach significance, ps = 1.0 (all $BF_{10} s < 3.35$). We observed a similar pattern of results when using untransformed response accuracies and d'-scores as the main performance measure (Supplementary Figure S2).

Finally, to provide a fine-grained description of sensitivity changes during saccade preparation, we determined the profile's parameters within a sliding window of 25 msec length and used these parameter estimates to predict response accuracies for a range of SFs (Fig. 5B). This analysis suggests that, at an eccentricity of 10 dva, sensitivities to all SFs within the range of .4–7.0 cpd are expected to increase during saccade preparation. In agreement with our estimate of peak SF right before saccade onset, the highest response accuracy of 99.0% is to be expected for a 1.59 cpd stimulus. The most pronounced increase in response accuracy with respect to the baseline time bin employed in previous analyses (lower border of -150 msec) is to be expected for a SF of 2.77 cpd.

3.3. Saccade latencies and endpoints

We did not observe an influence of the on- and offset of the probe stimulus on saccade latencies. While this should have



Fig. 4 – Pre-saccadic development of the sensitivity profile. A. Log-parabolic function fits per pre-saccadic time bin (panels 1–5) and for all bins (panel 6). The number in the slider above each panel indicates the lower bound of the respective bin in ms. *Sac* denotes the onset of the eye movement. Thin lines are observer-specific function fits. Thick lines show the average predicted accuracies across observers. Shaded areas correspond to the SEM of predicted accuracies. Dots indicate the measured response accuracy per bin and SF, averaged across observers. B. Pre-saccadic development of individual function parameters (panels 1–3) and mean sensitivity at the saccade target (panel 4). In all panels, dots indicate mean parameter values in a given pre-saccadic bin (blue to green) and for probes visible exclusively during the saccade (orange). Thin black lines are mean parameter values estimated within a sliding box-car window of 25 msec length (step size of 1 msec). Thicker black lines and shaded areas surrounding them constitute smoothed versions of these estimates obtained with an 'rlowess' filter, and their SEMs, respectively. C. Comparison of models in which one (light brown), two (medium brown) or three (dark brown) function parameters were assumed to vary with time bin. Negative Δ BICs indicate an advantage of the alternative over the PeakSens-only (Sens) model.

manifested in two local minima separated by the probe's presentation duration in Fig. 6A (see Hanning et al., 2019), the probability of eye movement initiation varied rhythmically, with segments of lower and higher probability alternating in a cadenced fashion. Notably, all segments exhibited a duration of approximately 25 msec which equals the presentation duration of a single element in the stimulus stream (noise image and probe). We therefore suggest that the rhythmic stream of noise images preceding the appearance of the probe increased and decreased the probability of saccade initiation in a regular manner, representing repeated instances of saccadic inhibition (e.g., Reingold & Stampe, 2002; Rolfs, Engbert, & Kliegl, 2008) that occur whenever a stimulus change is detected (White & Rolfs, 2016). Since the appearance of the probe stimulus itself did not interfere with saccade preparation, this observation, while interesting, does not affect the interpretability of our findings.

We furthermore intended to ensure that variations in response accuracy across bins could not be traced back to variations in the spatial precision and accuracy of saccade planning. To investigate if the precision of stimulus targeting influenced response accuracies, we estimated bivariate Gaussian Kernel densities for the saccade endpoint coordinates recorded in each bin (Fig. 6B). We then compared the fit of a linear mixed-effects model in which response accuracies were explained by a main effect of time bin and correlated random effects for intercept and slope by observer, to a model in which response accuracies were explained by main effects of bin and horizontal and vertical Kernel densities, as well as correlated random effects for intercept and slope by observer for each factor. The model restricted to an effect of bin outperformed the model including effects of Kernel densities by far, $BF_{10} = 4.77 \times 10^7$. Similarly, to inspect if the accuracy of stimulus targeting, defined as the absolute distance between recorded saccade endpoints and the center of the cued stimulus stream, influenced response accuracies, we compared the fits of a time-bin-only model and a model allowing for an influence of distance on response accuracies. Again, the former clearly outperformed the latter, $BF_{10} = 500.50$. We therefore conclude that neither the precision nor the accuracy of stimulus targeting had a meaningful impact on response accuracies.

4. Discussion

Each goal-directed eye movement brings a peripheral object of interest into high-acuity foveal vision. In preparation for the



Fig. 5 – Pre-saccadic sensitivity enhancement for all probed SFs (A) and pre-saccadic sensitivity development for a range of SFs (B). A. The extent of pre-saccadic enhancement, that is, the difference between arcsine-transformed response accuracies in the baseline time bin (zero line) and every subsequent time bin (blue to green lines) across observers. Bins are color-coded in accordance with previous plots. The numbers in the legend refer to the lower bin border in ms. Shaded areas indicate ±1 SEM. Just before the saccade (-25 msec; light green), pre-saccadic enhancement increased with SF up to 2.5 cpd, manifesting in a significantly higher difference score as compared to the mean difference score across all lower SFs. B. Heat map depicting the development of response accuracies as a function of SF during saccade preparation. X-axis values reflect the centers of a sliding window of 25 msec length. The color for each combination of SF and probe offset indicates response accuracy as predicted by a log-parabolic function with parameter values estimated within the respective time window. Solid white lines highlight the SFs probed in our experiment. Dashed black lines indicate the SF at which the highest response accuracy (PeakSens) was reached right before saccade onset, and the SF exhibiting the largest enhancement defined as the difference between response accuracies in the first and last moving window (maxEnh).

incoming foveal image, the perception of the saccade target may sharpen gradually before the eye movement is executed. Previous findings supporting this idea may reflect local consequences of more complex pre-saccadic sensitivity modulations (Li et al., 2019) or perceptual tuning towards the probe's features (Li et al., 2016). To resolve these ambiguities, we determined the shape of a broad peripheral sensitivity profile at different stages of saccade preparation. On a given trial, observers were unable to predict the SF of the probe.

Within the previously examined SF range, and right before saccade onset, higher SFs were indeed enhanced more than lower SFs. In the same time bin, however, SFs above 2.5 cpd profited less from saccade preparation. The assumption of a monotonic increase of enhancement with SF does therefore not capture the impact of saccade preparation on visual sensitivities to a wider SF range. Instead, sensitivity modulations in our investigation are best described as a joint increase in the sensitivity profile's peak, a decrease in its width, and a shift of its peak towards higher SFs (see Fig. 1; scenario C). The extent of pre-saccadic enhancement to a specific SF is contingent on its position on the reshaping sensitivity profile.

Though unable to predict the SF of the probe, observers reached maximum accuracy for a SF of 1.6 cpd in the last 25 msec before saccade onset. This value is strikingly similar to previous findings obtained with a predictable, 1.5 cpd probe at the same eccentricity (Li et al., 2016). Due to this parallel, we suggest that – while perceptual tuning to the saccade target's orientation (Li et al., 2016; Ohl et al., 2017) may provide a head start for post-saccadic foveal processing of *saccade target features* – the simultaneously observed increase in peak SF seems to constitute an approximation of *foveal spatial resolution*.

We replicate both an increase of enhancement with SF within the previously examined range, and an increase in peak SF to approximately 1.6 cpd. These parallels are striking considering the marked differences in stimulus appearance, predictability and operationalization between our study and previous investigations. In particular, while the probe in our experiment consisted in a single sinusoidal grating of a certain SF, Li et al. (2019) probed sensitivity to a compound stimulus created by overlaying target and mask elements with potentially dissimilar SF content. Observers reported the orientation of the target component. More pronounced enhancement of higher SFs in their investigation manifested in performance improvements if the target element exhibited a higher SF than the mask, and performance decrements if the mask exhibited a higher SF than the target. Li et al. (2019) evaluated changes in performance with respect to a neutral baseline condition in which observers did not execute an eye movement. In our study, by contrast, we compared observers' sensitivities between early and later stages of saccade preparation. Furthermore, the previously demonstrated increase in peak SF to approximately 1.6 cpd was obtained by fitting the gain of orientation tuning towards the target's orientation at different SFs (Li et al., 2016). We, on the other hand, estimated peak SF by fitting measured orientation discrimination accuracies.

Despite marked operational differences, we obtained similar findings. In consequence, the mechanism governing a reshaping of the sensitivity profile can be considered remarkably robust and likely reflects altered neuronal activation in visual and saccade-related areas. Neurophysiological studies have demonstrated a pre-saccadic shift of classical receptive fields (cRFs; determined under steady fixation). More specifically, the RFs of neurons preferring the pre-



Fig. 6 – Saccadic frequency aligned to probe onset (A) and densities of saccade landing coordinates (B). A. Distribution of the number of trials in which the saccade was initiated (SacOn) at a certain time after probe onset (ProbeOn). Bar heights and error bars indicate the mean and SEM across observers, respectively. The red rectangle indicates the time interval during which the probe was visible on screen. Instead of observing signature signs of saccadic inhibition (i.e., two local distribution minima separated by the probe's presentation duration), the probability of eye movement initiation varied in a rhythmic manner, with segments of lower and higher probability alternating periodically. B. Bivariate Gaussian Kernel densities of saccade landing coordinates per pre-saccadic time bin. Bins are color-coded in accordance with previous plots. The number labelling each density plot indicates the lower bound of the respective time bin in ms. Across bins, saccades landed well within the accepted area (medium gray circle; dashed outlines) around the cued stimulus stream (white circle). Note that the distance between stimulus streams and the central fixation dot was reduced for illustration purposes.

saccadic foveal location under fixation converge towards the peripheral eye movement target (Neupane, Guitton, & Pack, 2016; Tolias et al., 2001; Zirnsak, Steinmetz, Noudoost, Xu, & Moore, 2014). As a result, neurons with cRFs closer to the fovea contribute increasingly to the processing of information at the saccade target location. Since neurons exhibit different SF tuning characteristics depending on the eccentricity of their cRFs (see, e.g., Fig. 6b in Chen, Sonnenberg, Weller, Witschel, & Hafed, 2018, for example tuning curves of three superior colliculus neurons), a gradually increasing involvement of neurons with more foveal cRFs may underly the reshaping of the sensitivity profile towards its foveal form. As a direct perceptual consequence, the phenomenological quality of the saccade target may indeed approximate the post-saccadic foveal image.

This approximation, however, may often be imperfect. The eccentricity of the saccade target in particular can be expected to influence the shape of the sensitivity profile and impose limitations on the degree of pre-saccadic foveal approximation. Even if RF shifts in early visual areas govern sensitivity modulations, the resolution of the incoming visual signal remains – at the very least – limited by a decline in ganglion cell density towards the retina's periphery (for an overview see Watson, 2014). In our investigation, natural bounds on spatial resolution may underlie the observed decrease in the profile's bandwidth – higher SFs may simply have approached their resolution limit at the given

eccentricity. Crucially, while our study differed from previous investigations (Li et al., 2016, 2019) in the parameters outlined above, the main commonality is the eccentricity of the saccade target. In all studies, it was presented at a distance of 10 dva from fixation. We therefore expect both overlapping findings, namely an increase of enhancement with SF up to 2.5 cpd, and an increase of peak SF to 1.6 cpd, to be contingent on target eccentricity.

Even at an eccentricity of 10 dva, sensitivities to all SFs tested in our investigation profited from saccade preparation. Estimating the profile's parameters and predicting sensitivities for a broader-than-tested SF range suggests that presaccadic enhancement would have extended to SFs as high as 7 cpd. When free-viewing static or dynamic images without eye movement prompts, observers routinely generate saccades of much smaller amplitudes (around 2-6 dva; see e.g., Henderson & Hollingworth, 1999; Tatler & Vincent, 2008; Dorr, Martinetzk, Gegenfurtner, & Barth, 2010; Tatler, Hayhoe, Land, & Ballard, 2011). Furthermore, low SFs typically exhibit highest spectral power in natural images (for a review see Billock, 2000). In more naturalistic viewing behavior, sensitivities to relevant SF content at the eye movement target may therefore be enhanced to (near-)foveal resolution. Human and nonhuman observers have been shown to adjust their saccade amplitudes in an optimal fashion: saccade amplitudes depend on both image (e.g., Koch & Ullman, 1985; Mannan, Ruddock, & Wooding, 1997; Parkhurst, Law, & Niebur, 2002) and task

characteristics (e.g., Rothkegel, Schütt, Trukenbrod, Wichmann, & Engbert, 2019), and are tailored to a decorrelation of neural signals (IN MICE; Samonds, Geisler, & Priebe, 2018). Due to their adaptive nature, it would be interesting to investigate if saccade amplitudes are additionally optimized to enable a pre-saccadic approximation of foveal resolution, given the SF content of an image.

The demonstrated reshaping of the sensitivity profile increased visual sensitivities for a wide SF range. In a parsimonious fashion, this mechanism may serve to ensure a presaccadic enhancement of relevant information across images that vary in SF content and composition. While all scenarios in Fig. 1 would have achieved this goal, some reshaping possibilities are less plausible based on previous literature or theoretical considerations. In Li et al. (2016), and in stark contrast to scenario B, enhancement started to manifest at a SF of approximately 1.3 cpd and was absent for lower SFs. Moreover, an increase in bandwidth, especially when coupled with an increase in peak SF, would entail pronounced peripheral sensitivity up to a high SF range. As stated above, sensitivity enhancements above a certain SF range - the boundary of which depends on eccentricity - are physiologically implausible due to natural constraints on peripheral visual resolution. We would like to point out that simulating the scenarios in Fig. 1 required making assumptions about both the initial shape of the profile and the development of each parameter over time. Different initial parameter values and different assumptions on the dynamics of their development would alter the exact shape of functions in each scenario and, as a result, generate different predictions for the magnitude of enhancement to single SFs on the curve. In consequence, Fig. 1 should not be consulted to judge the relative plausibility of one scenario over another. Instead, it serves as a simple illustration that a variety of reshaping possibilities are reconcilable with an increase of enhancement with SF up to the previously examined boundary.

In addition to pre-saccadic sensitivity enhancements at the saccade target, sensitivity for low-SF information has been shown to decrease globally right before and during eye movements - a phenomenon known as saccadic suppression (Volkmann, Riggs, White, & Moore, 1978; Burr, Holt, Johnstone, & Ross, 1982; Volkmann, 1986; Burr, Morrone, & Ross, 1994; Ross, Burr, & Morrone, 1996; Chen & Hafed, 2017; Idrees, Baumann, Franke, Münch, & Hafed, 2020). Our design differs from classical studies demonstrating saccadic suppression (starting with Volkmann et al., 1978) in the following aspects: First, saccadic suppression is typically measured for orientations parallel to the eye movement trajectory. These orientations generate no temporal luminance modulation, that is, no effective image motion, as they sweep across the retina during the eye movement. In our design, observers executed horizontal saccades while the probe was oriented either slightly counter-clockwise or slightly clockwise from vertical. Moreover, the probe was embedded in a stream of flickering noise images that generated local motion energy even during fixation. If and how effectively saccadic suppression operates in the presence of orientation- and flicker-induced temporal luminance modulations is uncertain. Second, saccadic suppression is typically observed for SFs below 1 cpd while higher SFs are largely unaffected (Burr et al., 1982, 1994; Chen & Hafed, 2017; Volkmann et al., 1978). We did not probe sensitivities to SFs below 1 cpd. Nevertheless, a reshaping of the sensitivity profile as demonstrated in our study suggests that sensitivity to those SFs would have decreased from the penultimate (-50 to -26 msec) to the last (-25 to 0 msec) presaccadic time bin. This decrease may indeed reflect a suppression of low SFs. Alternatively, it may result from a shift of the narrowing profile towards higher SFs or rely on a combination of both processes.

Besides a reduction in visual sensitivity right before saccade onset, a second mechanism may have influenced response accuracies in addition to the pre-saccadic shift of attention to the target: Previous investigations suggest that predictive remapping of attention (Hunt & Cavanagh, 2011; Rolfs et al., 2011) or peri-saccadic mislocalization (De Pisapia, Kaunitz, & Melcher, 2010) can unmask elements of rapid stimulus sequences presented at the target of an impending saccade. In our investigation, a remapping of the noise stream that followed the presentation of the probe may have been equivalent to the removal of a spatiotopic backward mask. This could have contributed to an increase in response accuracies on a subset of trials. The steady increase in peak sensitivity, peak SF and mean sensitivity, however, is unlikely to result from a presaccadic unmasking of the probe stimulus. In any case, if different pre-saccadic mechanisms interact, they appear to do so in a continuous rather than discrete fashion.

A number of additional factors may influence the shape of the sensitivity profile. For instance, we did not vary the predictability of the probe's features. It is possible that the sensitivity profile adapts to predictable SF information at the saccade target. While tuning towards predictable stimulus features on its own cannot account for the findings of Li et al. (2019), they may rely on an interaction between tuning and high-SF enhancement. As outlined previously, the stimulus in their investigation was created by overlaying a target and a mask component. Across experiments, the SF of the target and the SF of the mask component remained constant throughout a given block of trials, rendering the SF content at the saccade target perfectly predictable on an individual trial level. Tuning to the SF of the target component may have reduced the effect of the lower and higher SF mask. Tuning to the SF of the mask or tuning to the compound SF content of the stimulus (i.e., target and mask combined) may have interacted with high-SF enhancement, potentially increasing the impact of the 1.5 cpd mask. It is conceivable, therefore, that the parameters of the sensitivity profile, in particular its peak SF and bandwidth, adapt flexibly to the predictable SF content of visual information at the saccade target.

Moreover, we embedded the probe in a dynamic stream of noise images to prevent salient stimulus on- and offsets (cf. Rolfs et al., 2011). To ensure that the noise stream would affect sensitivity to all SFs equally and leave tuning unaffected, we filtered each noise image to contain a widerthan-probed SF range. While we cannot provide experimental proof that SF tuning was — or is in general — uninfluenced by the presentation of a dynamic stimulus stream, we observe striking parallels to previous findings obtained without embedding the test stimulus in a noise stream (Li et al., 2019). Since the shape of the sensitivity profile seems to be highly robust, our results can inform stimulus selection in future studies that aim to investigate a presaccadic increase in visual sensitivity. At an eccentricity of 10 dva, a probe of 2.6 cpd is expected to yield the largest effect. Future investigations are needed to establish if the demonstrated sensitivity modulations serve a functional purpose or constitute a simple byproduct of saccade preparation. If a pre-saccadic approximation of foveal resolution facilitated trans-saccadic object continuity (see Li et al., 2019, for a similar proposal), this may manifest in more optimal post-saccadic oculomotor behavior or improved perceptual judgments. Moreover, direct evidence for an approximation of foveal resolution could be established by measuring post-saccadic foveal in addition to pre-saccadic peripheral sensitivities.

5. Conclusions

The peripheral sensitivity profile at the target of a saccade reshapes substantially during eye movement preparation. Previously demonstrated enhancement benefits for high SFs constitute local consequences of this reshaping process and do not transfer to a wider SF range. Instead, the extent of presaccadic enhancement to a particular SF is contingent on its position on the reshaping sensitivity profile. We suggest that the observed sensitivity modulations reflect a pre-saccadic approximation of foveal resolution that may serve to bridge the phenomenological gap between pre- and post-saccadic target views across a broad range of SFs.

Data inclusion statement: 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.

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Author contributions

Both authors developed the experimental question and study design. L.M.K. collected and analyzed the data. Both authors interpreted the findings. L.M.K. drafted the manuscript and M.R. provided revisions.

Open practices

The study in this article earned Open Materials and Preregistered badges for transparent practices. Materials for the study are available at: https://osf.io/whrxd.

Declaration of competing interest

The authors declare no competing interests.

Supplementary data

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