The Extrafoveal Preview Effect is More Pronounced Where Perception is Poor

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Abstract

The pre-saccadic preview of a peripheral target enhances the speed and accuracy of its post-saccadic processing, termed the extrafoveal preview effect. Peripheral visual performance –and thus the quality of the preview– varies around the visual field, even at iso-eccentric locations. To investigate whether these polar angle asymmetries influence the preview effect, we asked human participants to preview four tilted Gabors at the cardinals, until a central cue indicated to which to saccade. During the saccade, the target orientation either remained or was flipped (valid/invalid preview). After saccade landing, participants discriminated the orientation of the (briefly presented) second Gabor. Gabor contrast was titrated with adaptive staircases. Valid previews increased participants' post-saccadic contrast sensitivity. This preview effect was inversely related to polar angle perceptual asymmetries; largest at the upper, and smallest at the horizontal meridian. Our finding reveals that the visual system actively compensates for peripheral asymmetries when integrating information across saccades.

Keywords: peripheral vision, trans-saccadic perception, visual stability, contrast sensitivity, eye movement programming, visual field asymmetries

Statement of Relevance

Even though visual sensitivity degrades with farther distance from fovea, we make use of peripheral information to monitor or preview the surroundings, for instance, when driving (pedestrians at eye level, instrument panel at the lower visual field, farther things in the upper visual field). When we make saccadic eye movements to foveate relevant items, the peripheral information "previewed" before the saccade supports post-saccadic vision. Because our vision differs around the visual field –at the same eccentricity it is best along the horizontal, worst at the upper vertical meridian– investigating whether peripheral information at different polar angles equally facilitates post-saccadic perception has implications for everyday life. Our study reveals that peripheral preview exerts a larger influence on subsequent foveal processing at locations where vision is worse. This finding suggests that the visual system actively compensates for differences in peripheral vision when integrating information across eye movements.

The Extrafoveal Preview Effect is More Pronounced Where Perception is Poor

When exploring their surroundings, humans often make fast saccadic eye movements to bring different parts of the scene onto the fovea, the central region of the retina with the highest visual acuity. Despite its low resolution, peripheral visual information plays a critical role in preparing and guiding saccades, a process termed *preview* (Rayner et al., 1980; Melcher & Colby, 2008). After a saccade, inputs previewed before the saccade are integrated with the post-saccadic percepts, to facilitate subsequent foveal processing (review: Huber-Huber et al., 2021). This *extrafoveal preview effect* occurs with a variety of stimuli, including low-level features (Ganmor et al., 2015; Wolf & Schütz, 2015; Fabius et al., 2020), words (Rayner et al., 1980), and objects (Buonocore et al., 2020; Huber-Huber et al., 2019; Liu et al., 2022). It is reflected both at the behavioral level –e.g., higher accuracy and faster reaction times (e.g., Huber-Huber et al., 2019)– and at the neural level –e.g., faster decoding time (Edwards et al., 2018).

Preview effect studies have focused on the horizontal meridian (HM), but peripheral vision varies greatly with polar angle: better along the horizontal than vertical meridian (HM>VM: horizontal-vertical anisotropy; HVA) and along the lower than upper vertical meridian (LVM>UVM: vertical meridian asymmetry; VMA) (Abrams et al., 2012; Carrasco et al., 2001; Greenwood et al., 2017). Visual sensitivity can be four times better for stimuli on the HM than VM (Himmelberg et al., 2020). These polar angle asymmetries are present in many visual tasks, such as contrast sensitivity (Rijskijk et al., 1980; Baldwin et al., 2012; Himmelberg et al., 2020), visual acuity (Barbot et al., 2021; Kwak et al., 2023), spatial resolution (Talgar & Carrasco, 2002; Montaser-Kouhsari & Carrasco, 2009), and crowding (Greenwood et al., 2017). However, it is unknown whether and how our heterogeneous peripheral vision affects the integration of pre- and post-saccadic information at different directions.

There are two opposing hypotheses. According to the optimal integration framework (Ernst & Banks, 2002; Ernst & Bülthoff, 2004; Körding & Wolpert, 2004), trans-saccadic integration is similar to other types of sensory integration across modalities, during which the brain integrates information by weighing the sensory evidence based on relative precision. Estimated reliability is maximized when stronger sensory signals (e.g., higher signal-to-noise ratio, reduced uncertainty) receive higher weights (Ernst & Bülthoff, 2004). Correspondingly,

preview benefits in reading were reduced or extinguished when the preview word was located at a farther eccentricity, e.g., two versus one word from the current fixation (McDonald, 2005; Angele & Rayner, 2011). More evidence comes from gaze-contingent tasks that presented stimuli according to the observers' gaze positions and systematically varied the relative visibility of peripheral and foveated targets by changing either the stimulus contrast (Wolf & Schütz, 2015) or eccentricity (Liu et al., 2022), or by adding noise (Hutzler et al., 2019; Liu et al., 2022). These studies have revealed that with incongruent pre- and post-saccadic percepts, trans-saccadic perceptual judgements were increasingly biased towards the peripheral preview as its visibility increased. Because object visibility also varies with polar angle, one could expect the magnitude of the preview effect around the visual field to follow the same pattern: a larger preview effect on the HM, where peripheral vision is best, followed by the lower- and then the upper- vertical meridian.

In contrast, the visual system might actively compensate for polar angle asymmetries in peripheral vision when integrating information across saccades, enhancing post-saccadic vision more at locations where it is needed the most. Endogenous attention, the voluntary allocation of processing resources based on one's goals or expectations (Carrasco, 2011), is an example of this process. Depending on the current task demand, endogenous attention can exert different perceptual effects (e.g., Barbot & Carrasco, 2017; Sharp et al., 2018). For example, it either increased or decreased the temporal integration window when observers were instructed to segregate or integrate two closely presented stimuli. Moreover, this effect was more pronounced when baseline performance was worse (Sharp et al., 2018). A similar active compensation mechanism during trans-saccadic integration would enhance post-saccadic visual sensitivity more where peripheral vision is worse, eliminating polar angle asymmetries in peripheral vision.

However, polar angle asymmetries in peripheral vision are resilient; they are not alleviated by spatial covert attention: Both exogenous attention –which is involuntary, fast and transient (Carrasco et al., 2001; Roberts et al., 2018)– and endogenous attention –which is voluntary, slower and sustained (Purokayastha et al., 2021)– similarly improve performance around the visual field, thereby preserving the polar angle asymmetries. Pre-saccadic attention, which is automatically deployed to the target of an upcoming eye movement during saccade preparation (Kowler et al., 1995; Deubel & Schneider, 1996; Deubel, 2008; Rolfs & Carrasco, 2012; Hanning et al., 2019), enhances perception similarly around the visual field (Kwak et al., 2023) or even exacerbates polar angle asymmetries, by

benefitting performance less where it is already the worst (Hanning et al., 2022a,b). Thus, neither covert nor pre-saccadic attention overcomes polar angle asymmetries in peripheral vision.

Pre-saccadic attention contributes to trans-saccadic integration, but the latter entails more processes (Huber-Huber et al., 2019; Huber-Huber et al., 2021) and relies on a prolonged interaction among the oculomotor network and the visual system before and after saccades (Schall & Hanes, 1993; Caruso et al., 2018). Therefore, to investigate whether and how the extrafoveal preview effect, a measure for trans-saccadic integration, interacts with polar angle asymmetries in peripheral vision, we precisely quantified the two phenomena and evaluated their relation.

Our findings are consistent with the compensation hypothesis. Unlike previous reports that polar angle asymmetries are preserved or even exacerbated by covert and pre-saccadic attention (Carrasco et al., 2001; Purokayastha et al., 2021; Hanning et al., 2022a,b; Kwak et al., 2023), we found the largest preview effect at the UVM, followed by the LVM, and lastly the HM –inversely correlated with peripheral polar angle asymmetries during fixation.

Method

Participants

We recruited 15 participants at NYU-NY. All participants gave informed consent before the experiment, received allowance, and had normal or corrected-to-normal vision. All but two participants (authors XL and NH) were naïve to the purpose of the experiment. One participant was excluded for having a threshold estimate three SD away from group average in the valid preview condition (see Procedure). The remaining 14 participants (9 females; all right-handed) had an average age of 28.14 (± 4.74) (M ± SD) years old. The experiment was approved by the NYU Abu Dhabi ethical committee and all experimental procedures were in agreement with the Declaration of Helsinki.

Apparatus

The experiment was coded with MATLAB PsychToolbox-3 (Kleiner et al., 2007), Eyelink toolbox (Cornelissen et al., 2002), as well as the Palamedes toolbox (Prins &

Kingdom, 2018) for the PEST staircase procedure (Pentland, 1980), and was run on an Apple iMac Intel Core 2 Duo computer (Cupertino, CA, USA). Stimuli were displayed on a gamma-linearized 20-inch ViewSonic G220fb CRT screen (Brea, CA, USA) (1280×960 screen resolution; 100 Hz refresh rate) with a gray background (luminance: 128 cd/m^2). Participants sat at a viewing distance of 57 cm. Eye positions of the dominant eye were recorded by an EyeLink 1000 Plus eye tracker (SR Research, Ontario, Canada), with the desktop mount, at a sampling rate of 1000 Hz.

Procedure

The experiment included a *baseline fixation task* and two eye-movement tasks (*integration task* and *post-view only task*), performed in separate experimental sessions. Participants first completed the fixation task (**Fig. 1a**), followed by the eye-movement tasks. In all tasks, participants judged the orientation of a Gabor patch (clockwise/counterclockwise relative to vertical, 2-alternative forced choice task). To measure contrast sensitivity, stimulus contrast per experimental condition (4 locations × 4 tasks) was separately adjusted by an adaptive staircase procedure (PEST; see Supplemental Material).

In all tasks, a white central fixation dot (0.3 dva diameter; dva: degree of visual angle) and four black placeholders centered at four isoeccentric locations (8 dva) along the upper, lower, left, and right meridian of the fixation dot were presented throughout the trial. Each placeholder consisted of four corners (0.3 dva in length, 0.1 dva in width), indicating the possible locations of upcoming stimuli and potential saccade targets. Each trial started with participants fixating on the central fixation dot. Once we detected continuous fixation (within a radius of 1.5 dva) for 700 ms, the trial continued depending on the specific task.

<u>*Baseline fixation task*</u>. After the initial fixation, four Gabor patches (spatial frequency = 4 cpd; diameter = 2.5 dva; σ = 0.625 dva) were presented at the center of the placeholders for 100 ms while participants kept fixating on the central fixation dot. Three Gabors were vertically oriented distractors, one Gabor was a target tilted ±15° relative to vertical. The location of the target was randomly selected and unbeknownst to the participants until its presentation. 400 ms after the Gabor offset, the fixation dot color changed to grey and the placeholder at the target location turned white, prompting participants to indicate the tilt direction of the target by pressing a button on a standard keyboard, without time pressure. Audio feedback was provided for 200 ms immediately following the response.

Integration task. After the initial fixation, participants (while still fixating at the central fixation dot) peripherally viewed four Gabors, which were presented within the placeholders and independently tilted slightly clockwise or counterclockwise relative to vertical (**Fig. 1b**). The tilt angles of the Gabors were determined by a thresholding task beforehand (see Supplemental Material). After 400 ms of preview, a saccade cue (red line of 0.45 dva in length, 0.05 dva in width) superimposed on the fixation dot, indicated to which Gabor participants had to make an immediate saccade. We monitored gaze positions online. As soon as saccade onset was detected (i.e., when two consecutive gaze samples ~1 ms apart deviated more than 0.18 dva), a visual mask was displayed at each location for 10 ms. This mask (bandpass filtered random noise, same contrast and size as the Gabor patch) served to equalize the visual input changes in the valid and invalid conditions (**Fig. 1c**). Note that participants reported to be unaware of the mask due to saccadic suppression (Ross et al., 2001).

The offline saccade detection algorithm, used to more accurately detect saccadic eye movements (see Data Analysis section), shows an average interval between actual saccade onset and mask onset of 15.23 (± 5.52) ms (**Fig. 1d).** Immediately after the mask, the target stimulus –either identical to the preview stimulus (*valid* condition) or with a flipped tilt angle (e.g., from +1° to -1°) (*invalid* condition; **Fig. 1d**) was presented at the saccade target. The target stimulus disappeared 80 ms after we detected participants' gaze within 2 dva from saccade target center (i.e., the online approximation of a saccade offset). On 98.52% trials, the saccade landed after target stimulus onset, with an average target-saccade interval of 21.42 (± 11.22) ms **(Fig. 1e).** For the remaining trials, target stimulus onset occurred within 20 ms after saccade offset, i.e., within the time range of saccadic suppression (Vallines & Greenlee, 2006). After target stimulus disappearance, participants indicated the tilt orientation of the target stimulus. Participants were explicitly instructed to base their judgement on the post-saccadic target stimulus, which they foveated after the saccade. To prevent participants from impulsively responding to the preview, before the integration task, participants completed at least 36 practice trials with prolonged post-saccadic target duration (300 ms), followed by another 36 practice trials with 80 ms post-saccadic target duration. We would only start the main experiment after participants reached 80% correct orientation discrimination performance in the invalid condition of the first practice.

Postview task. To measure performance in a neutral, no-preview condition, in this task no Gabors were presented for preview. Participants merely fixated on the central fixation until

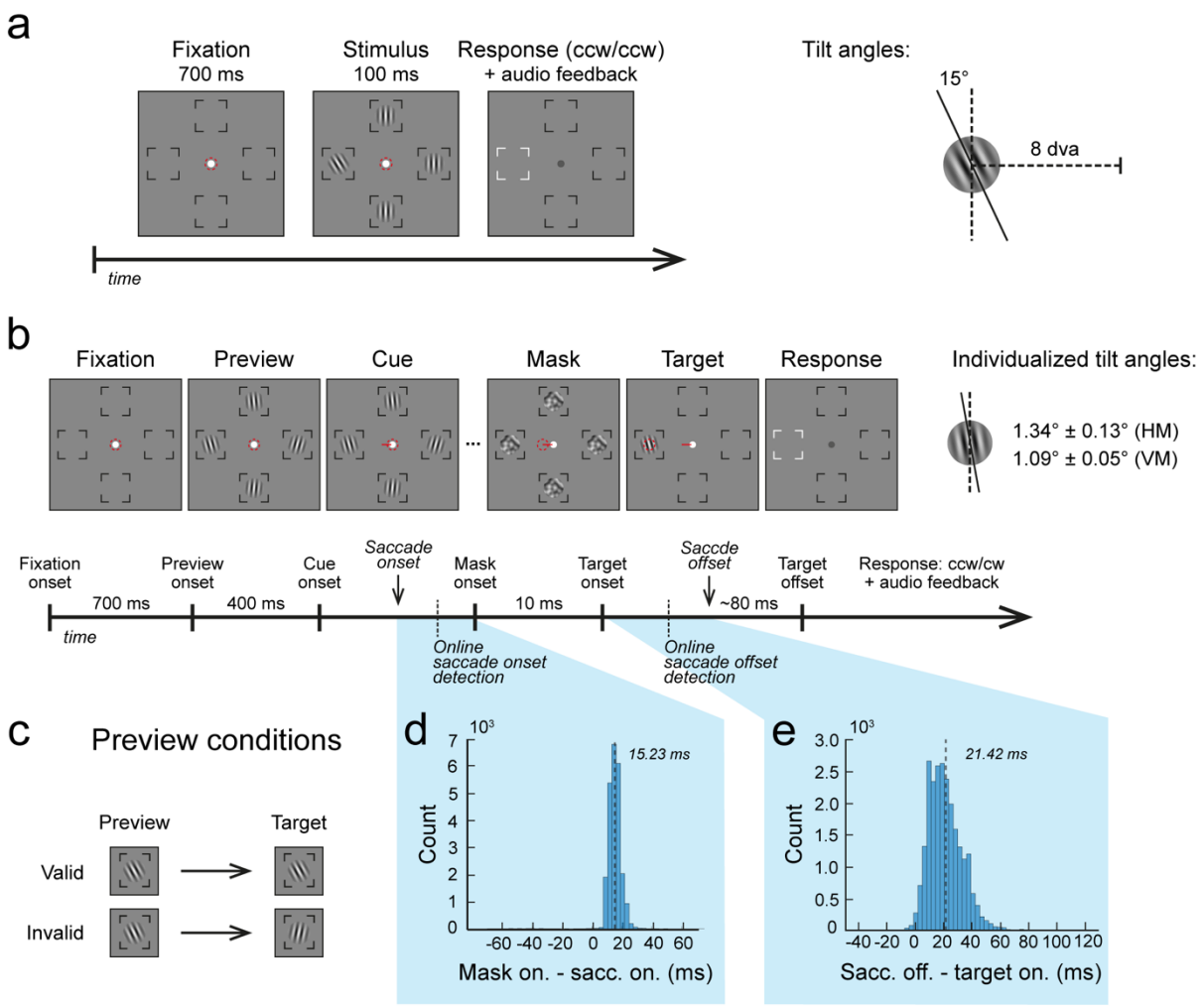

Fig 1. *Illustration of the task.* ***a****. Fixation task. Each trial started with a central fixation dot, followed by the stimuli. Participants indicated the tilt direction of a tilted Gabor (±15° relative to vertical) presented among distractors.* ***b****. Integration task. After fixation, participants previewed four slightly tilted Gabors, followed by a saccade cue for an immediate eye movement. Saccade onset, detected by an online algorithm (see Methods), triggered a 10ms mask, followed by the target. The target disappeared ~80ms after saccade offset. Participants then indicated the tilt direction of the second, foveated target. The tilt angles of Gabor stimuli were determined by a thresholding task (see Supplemental Material)* ***c****. Task conditions in the integration task.* ***d****. Temporal delay between offline detected saccade onset and mask onset.* ***e****. Temporal delay between target onset and offline detected saccade offset.*

they saw a saccade cue (the same overall fixation duration as in the integration task). Once a saccade was detected, we presented bandpass filtered noise at the target location for 10 ms, followed by a target Gabor at the saccade target. Again, the target Gabor disappeared 80 ms after we detected participants' gaze within 2 dva from saccade target center. The rest of the task was identical to the integration task.

The study comprised 3 experimental sessions. In the first session, participants completed, in order, the fixation task, the thresholding task (see Supplemental Material), and the first part of the integration task. The second session consisted of the postview task and the second part of the integration task (order counterbalanced among participants). In the third session, participants completed the last part of the integration task. Thus, participants completed the integration task in 3 sessions conducted on different days, with each session containing 2 staircases per condition. In total, there were 2592 trials: 432 trials in both the fixation and postview tasks, and 1728 trials in the integration task. Trials were aborted and repeated at the end of the session if participants 1) did not maintain central fixation during the preview, 2) made a saccade too fast (< 100 ms) or too slow (> 550 ms) after cue onset, or 3) looked toward a wrong stimulus in an eye-movement task.

Data analysis

Contrast sensitivity and saccade parameters were analyzed with R and MATLAB. Contrast thresholds and staircase exclusion were determined with a similar method as in Hanning et al. (2022a) (see Supplemental Material). On average, 12% of staircases were excluded for each subject. Contrast sensitivity was computed as the reciprocal of the average threshold estimate. We analyzed the recorded gaze samples with an offline algorithm that detects saccades based on gaze velocity, amplitude, and duration (Engbert & Mergenthaler, 2006; see Supplemental Material).

Unless otherwise noted, behavioral data were analyzed with repeated-measures analyses of variance (ANOVA) in R (package *ez*, version 4.4.0), with meridian (horizontal, vertical) and location (left and right, or upper and lower) as within-subject factors. Eye movement data were analyzed with 4 (saccade direction: left, right, upper, lower) × 3 (task condition: valid preview, invalid preview, postview) repeated-measures ANOVAs. For all repeated-measures ANOVAs in which the sphericity assumption was not met, we report Greenhouse-Geisser corrected *p*-values. Post-hoc tests for any significant effects were run with the package *emmeans* (version 1.7.4-1 in R). Multiple comparisons were corrected by controlling the false discovery rate. For effect size, we report η_p^2 for ANOVAs, along with 95% confidence interval (CI) for variance explained by each effect (CI_η). For post-hoc tests and the correlation analysis, we report the 95% CIs for difference and correlation coefficient.

Power analysis

We determined the sample size based on previous studies on polar angle asymmetries (e.g., Hanning et al., 2022a) or on the preview effect (e.g., Liu et al., 2022). A post-hoc power analysis confirmed that our sample size (n = 14) is associated with 100% power to detect an existing HVA and VMA, and 98% power to detect the preview effect (Cohen's d = 1.18, α = .005), and thus adequate to provide reliable results.

Results

Polar angle asymmetries during fixation

To measure horizontal-vertical anisotropy (HVA) and vertical-meridian asymmetry (VMA) in the fixation task, contrast sensitivity was analyzed using a 2 (meridian) × 2 (location) repeated-measures ANOVA. We found a main effect of meridian (**Fig. 2a**), $F(1, 13) = 11.56$, $p = .0047$, $\eta_p^2 = .47$, 95% CI_η = [.063, .68]. Consistent with the HVA, sensitivity along the HM (33.13 ± 4.08) (M ± SE) was significantly higher than that along the VM (21.73 ± 2.39). There was a significant interaction between meridian and location, $F(1, 13) = 4.97$, $p = .044$, $\eta_p^2 = .28$, 95% CI_η = [.00, .56]. Post-hoc contrasts showed no difference between the left (32.47 ± 4.09) and right (33.79 ± 4.4) HM, whereas sensitivity at the lower VM (24.96 ± 3.1) was significantly higher than the upper VM (18.49 ± 2.19), $t(25.9) = 2.70$, $p = .012$, 95% CI = [1.54, 11.40], consistent with the VMA.

To visualize the individual differences in HVA and VMA, we plotted each participant's contrast sensitivity along the HM against the VM (**Fig. 2b**), and along the LVM against the UVM (**Fig. 2c**). Diagonal lines indicate equivalent performance. HVA and VMA were found in all participants, except in two for HVA and four for VMA. The strength of the asymmetries was computed as the sensitivity difference between the two respective meridians divided by their average, with a positive number representing a typical HVA/VMA. The correlation between HVA and VMA was not significant ($r = .20$, $p = .50$), suggesting (at least partially) different origins (Himmelberg et al., 2020; Barbot et al., 2021).

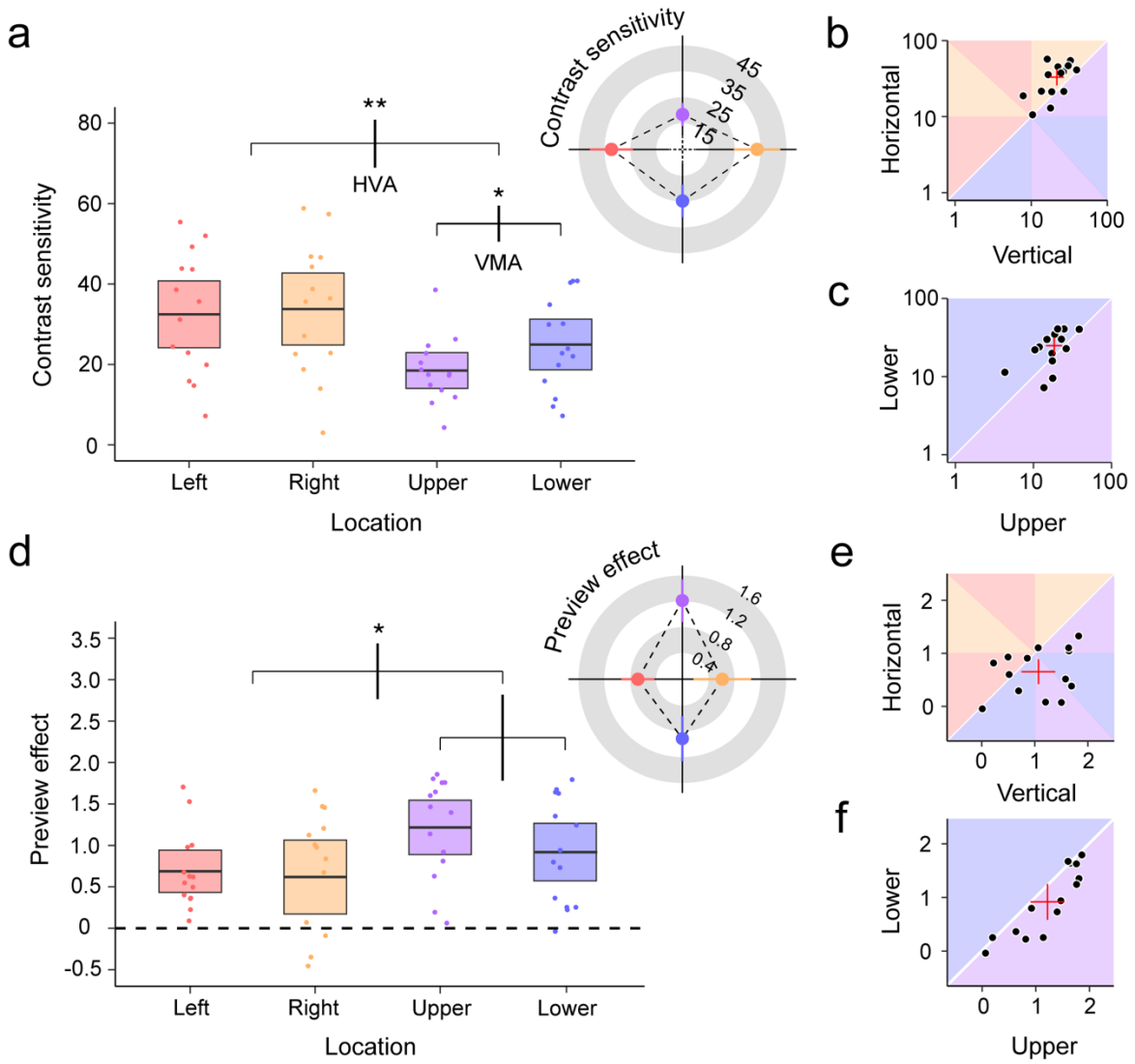

Fig. 2. *Behavioral results in the fixation and integration tasks.* ***a.d****. Contrast sensitivity in the fixation task computed as the reciprocal of the staircase threshold estimate (****a****) or preview effect in the integration task computed as the normalized difference in sensitivity between the valid and invalid conditions (****d****) as a function of target location. Boxes depict the 95% CIs around the mean, represented by the black lines. Horizontal brackets indicate comparisons between the horizontal vs. vertical meridian (HVA) and upper vs. lower vertical meridian (VMA); error bars on the brackets represent 95% CIs of the difference between compared conditions. * p < .05, ** p < .01 (after correcting for multiple comparisons). Polar plots depict the same data.* ***b.e****. Individual participants' contrast sensitivity (****b****) or preview effect (****e****) along the horizontal meridian plotted against the vertical meridian. Red error bars represent 95% Cis of group averages.* ***c.f.*** *Individual participants' contrast sensitivity (****c****) or preview effect (****f****) along the lower against the upper vertical meridian.*

Reversed asymmetries in the preview effect

To test whether the preview effect was consistent at all four locations, we performed a repeated-measures ANOVA with preview validity (valid, invalid) and target location (left, right, upper, lower) as within-subjects factors. We found a main effect of preview validity, $F(1, 13) = 44.00$, $p < .004$, $\eta_p^2 = .77$, 95% $CI_\eta = [.43, .86]$. Planned contrasts showed significant preview effects at all four locations (all $p < .001$) (**Fig. 2d**).

Next, we quantified the magnitude of the preview effect as the normalized difference between the valid and invalid conditions, which we then analyzed with a 2 (meridian) × 2 (location) repeated-measures ANOVA. We found a significant main effect of meridian, $F(1, 13) = 5.88$, $p = .031$, $\eta_p^2 = .31$, 95% $CI_\eta = [.00, .58]$. Interestingly, post-hoc contrasts revealed that the preview asymmetry was opposite to the polar angle asymmetry during fixation, with a larger preview effect at the VM (1.07 ± 0.16) than the HM (0.65 ± 0.12), $t(13) = -2.43$, $p = .031$, 95% CI = [-.79, -.045] (**Fig. 2d**). The reversed HVA in the preview effect was also evident at the individual level (**Fig. 2e**). Although the interaction between meridian and location was not significant, preview effect was slightly larger at the UVM (1.22 ± 0.16) than the LVM (0.92 ± 0.17), which was consistent in all but two participants (**Fig. 2f**).

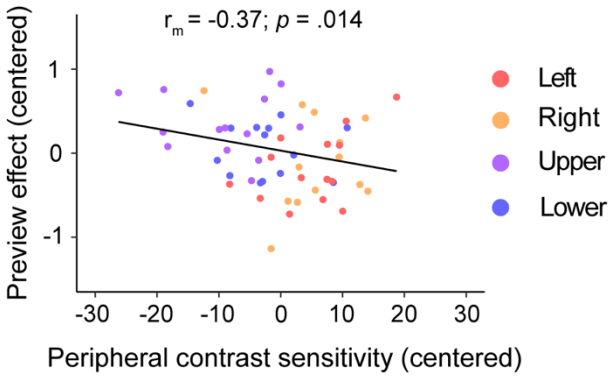

Fig. 3. *Individual participants' preview effect as a function of peripheral contrast sensitivity. Data centered to each participants' average across target locations. Dots represent individual data at the four cardinal locations. The regression line represents the intra-individual (repeated-measures) correlation.*

To further evaluate the relation between the peripheral contrast sensitivity during fixation and the magnitude of the preview effect at the individual level, we ran a repeated-measures correlation (Bakdash & Marusich, 2017), which accounts for the violation of independence in data due to repeated within-participant data points. This way we measured the variability across target locations by removing the inter-individual variability. Aligned with the reversed pattern of asymmetries indicated by the ANOVA, the repeated-measures

correlation showed a significant negative intra-individual correlation between peripheral contrast sensitivity and the preview effect, r_m = -.37, p = .014, 95% CI = [-0.61, -.074] (**Fig. 3**), i.e., within individuals, the preview effect was larger where peripheral sensitivity was smaller (e.g., UVM).

Lowest post-saccadic sensitivity at the UVM

We analyzed post-saccadic contrast sensitivity (measured in the postview-only task) with a 2 (meridian) × 2 (location) repeated-measures ANOVA. We expected to observe equivalent performance at the four cardinal locations, because in this task, participants made perceptual judgements about a brief, foveated target (i.e., polar angle asymmetries should not affect perception). Surprisingly, we found a main effect of location, $F(1, 13)$ = 5.46, p = .036, η_p^2 = .30, 95% CI_η = [.00, .57], and an interaction between meridian and location, $F(1, 13)$ = 10.08, p = .007, η_p^2 = .44, 95% CI_η = [.044, .66]. The effects were driven by a lower post-saccadic contrast sensitivity after upward saccades (15.00 ± 3.16) than after leftward (26.23 ± 3.64; p = .054, 95% CI = [-2.34, 24.80]; marginally significant), rightward (29.49 ± 4.76; p = .015, 95% CI = [0.91, 28.05]), or downward saccades (30.85 ± 2.77; p = .014, 95% CI = [2.28, 29.42]) (**Fig. 4**). Other post-hoc contrasts did not reach significance.

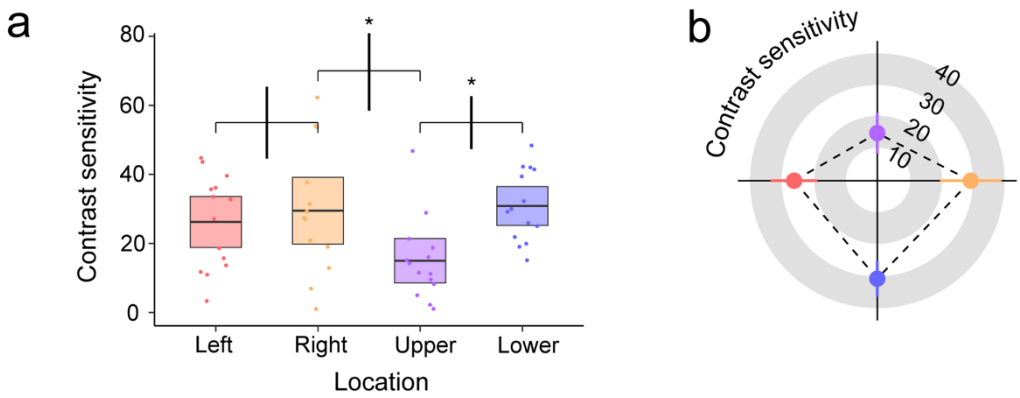

Fig. 4. *Contrast sensitivity in the postview task as a function of target location.* ***a.*** *Boxes depicts the 95% CIs around the mean, represented by black lines. Horizontal brackets indicate comparisons between the respective target location, with the error bars on the brackets representing 95% CIs of the difference between the compared conditions. * p < .05 (after correcting for multiple comparisons). b. Polar plots showing the same data.*

Saccade parameters cannot explain the preview effect asymmetries

To evaluate whether differences in saccade parameters could explain the observed preview asymmetries around the visual field, we analyzed the offline-computed saccade parameters (see Data Analysis section). A longer saccade latency and thus a longer preview duration, for example, could lead participants to rely more on the preview information, giving rise to a larger preview effect.

We found main effects of saccade direction, $F(3, 39) = 32.14$, $p < .001$, $\eta_p^2 = .71$, 95% CI_η = [.51, .79] and task condition, $F(2, 26) = 15.94$, $p < .001$, $\eta_p^2 = .55$, 95% CI_η = [.24, .69] (**Fig. 5a**) on saccade latency. Saccade latency was significantly longer for downward saccades (215.05 ± 2.6 ms) than saccades in the three other directions (left: 194.91 ± 1.98, 95% CI = [13.60, 26.69]; right: 197.81 ± 1.88, 95% CI = [10.64, 23.73]; upper: 196.22 ± 2.13 ms, 95% CI = [12.29, 25.38]; all $p < .001$), consistent with previous studies (Tzelepi et al., 2010; Hanning et al., 2022a,b; Kwak et al., 2023). Participants made faster saccades in the invalid (195.85 ± 1.87 ms) than in the valid preview (203.99 ± 2.21 ms; $p < .001$, 95% CI = [-12.21, -4.07]) and postview conditions (203.20 ± 2.24 ms; p

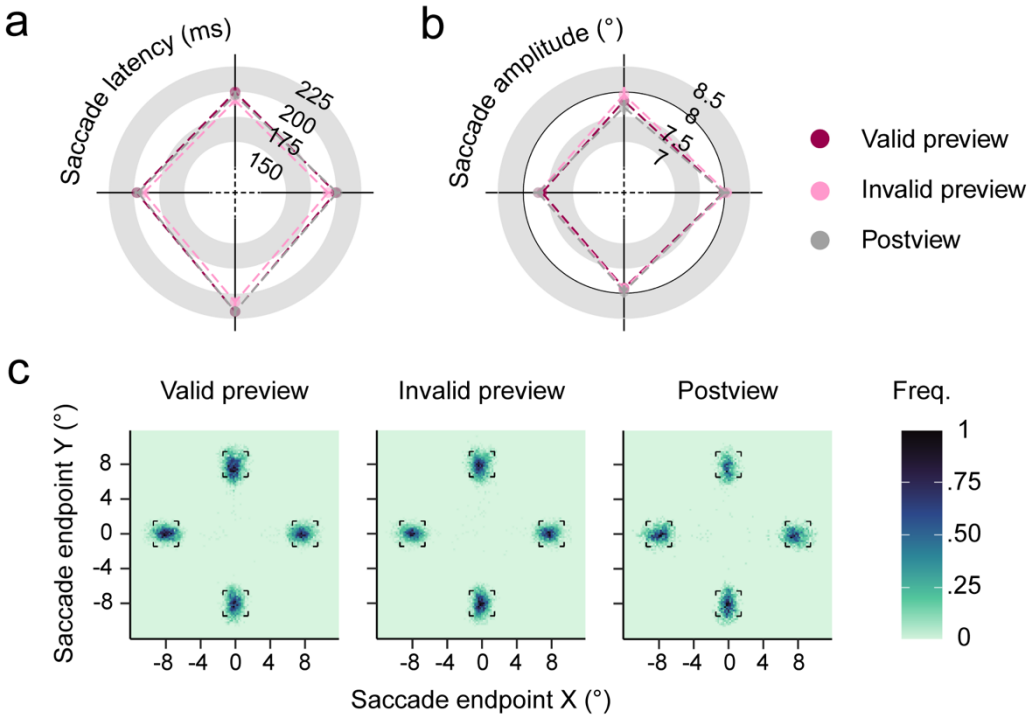

Fig. 5. *Group averaged saccade latency (**a**) and saccade amplitude (**b**) as a function of saccade direction and target location. Error bars indicate 95% CIs. **c**. Saccade endpoint frequency maps averaged across participants depicting saccade landing error. The outlined squares represent the placeholders.*

< .001, 95% CI = [-11.42, -3.28]). Note that as the perceptual task was relatively harder for the invalid preview condition, Gabor contrast (adjusted by the staircase) accordingly was higher (invalid preview: 21.24% ± 3.42%; valid preview: 4.58% ±0.56%; postview: 9.49% ±2.45%), which might explain the latency difference. Neither saccade amplitudes (on average of 7.86 ± 0.03 dva; **Fig. 5b**) nor saccade precision (on average of 0.97 ± 0.01 dva; **Fig. 5c**) differed as a function of target location or task condition.

Post-saccadic eye movements. Shortly after a saccade, gaze is instable. The eyes may drift or participants may perform tiny (corrective) saccades. As any post-saccadic movement shifts the image on the retina and thereby directly affects foveal perception (Rucci & Victor, 2015), we evaluated participants' post-saccadic eye movements and its potential effect on the preview effect. To consider any ocular movements after saccade landing, including post-saccadic oscillations (i.e., ocular instability due to pupil movements; Nyström et al., 2013), fixational eye movements (micro-saccades) and ocular drift, we analyzed eye movement rate and distance gaze covered (see Supplemental Material) during the post-saccadic target presentation with repeated-measures ANOVAs. Post-saccadic movement distance did not differ between saccade directions or task conditions, with gaze samples covering an average range of 0.51 dva (± 0.03 dva) (**Fig. 6a**).

There was a main effect of saccade direction on post-saccadic eye movement rate, $F(3, 39) = 3.11$, $p = .037$, $\eta_p^2 = .19$, 95% CI_η = [.00, .35], driven by a higher movement rate after upward (6.02 ± 0.07 Hz) than leftward (5.56 ± 0.08 Hz, $p = .025$, 95% CI = [.040, .87]) saccades (**Fig. 6b**). Because other post-hoc contrasts did not reach significance, differences in post-saccadic ocular instability can only partially explain the observed asymmetries in preview effect and post-saccadic sensitivity.

Post-saccadic target viewing duration. Another potential source of the observed preview asymmetries could be post-saccadic target viewing duration. A shorter viewing time could bias trans-saccadic integration toward the preview, leading to a larger preview effect. Even though we timed stimulus offset based on the estimated saccade offset (using an online criterion, see Methods), the actual target viewing time could vary as a function of target location due to differences in saccade velocity or post-saccadic instability that could not be detected online. Indeed, there was a main effect of saccade direction, $F(3, 39) = 4.31$, $p = .010$, $\eta_p^2 = .25$, 95% CI_η = [.018, .41]. However, target viewing duration was slightly but significantly *longer* after upward saccades (69.78 ± 0.63ms) than leftward (67.18 ± 0.77ms; $p = .039$,

95% CI = [-.17, 5.37]) and downward (66.34 ± 0.73ms; p = .0082, 95% CI = [.67, 6.21]) saccades (**Fig. 6c**), ruling out the possibility that a *shorter* post-saccadic target duration time contributed to the larger preview effect at the UVM. There was also a main effect of task condition, $F(2, 26) = 3.58$, $p = .042$, $\eta_p^2 = .22$, 95% CI_η = [.00, .42], with a shorter target viewing found in the invalid preview (67.18 ± 0.64ms) than postview condition (68.25 ± 0.69ms; p = .041, 95% CI = [.033, 2.11]).

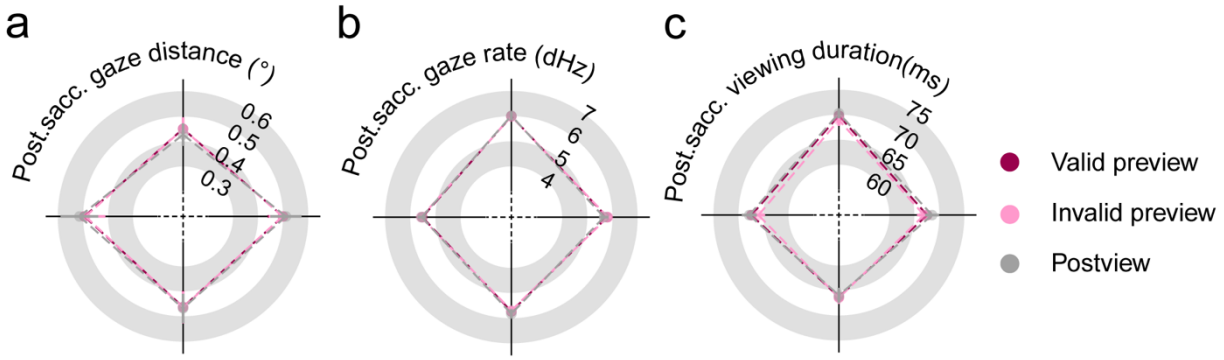

Fig. 6. *Group averaged post-saccadic gaze distance (a), saccade rate (b), and target viewing duration (c) as a function of task condition and saccade direction. Error bars indicate 95% CIs.*

Discussion

We investigated trans-saccadic integration around the visual field, by testing whether and how the extrafoveal preview effect is modulated by polar angle asymmetries in peripheral vision. We replicated the typical polar angle asymmetries during fixation –higher contrast sensitivity at the horizontal than vertical meridian (HVA) and at the lower than upper vertical meridian (VMA)– and found a robust preview effect at all cardinals: Post-saccadic foveal sensitivity was higher after a valid than invalid preview. Importantly, the magnitude of this preview effect was inversely related to the polar angle asymmetries: larger at locations with lower peripheral sensitivity. These preview asymmetries could not be explained by differences in saccade parameters. Our novel findings suggest that the visual system actively predicts and compensates for asymmetries in peripheral vision across saccadic eye movements.

What could give rise to these preview asymmetries? There are three stages in the preview effect (Huber-Huber et al., 2019; Fabius et al., 2020; Jensen et al., 2021): (1) A prediction about the saccade target is made based on peripheral inputs. (2) Pre- and post-

saccadic information are then integrated, as evident by an interaction of post-saccadic fixation-related potentials (FRPs) amplitude and experimental conditions. (3) Post-saccadic inputs dominate the FRPs and influence behavior. Changes in the magnitude of the preview effect could be attributed to any combination of these stages.

At the first stage, a stronger prediction about the peripheral saccade target could cause its (relative) up-weighting, leading to a larger preview effect. Strength and content of pre-saccadic predictions are learned over time: The repeated exposure to consistently invalid previews (e.g., an orange always changes to a basketball during a saccade), causes participants to make predictions about the saccadic target in the learnt direction, reducing the preview effect in response to statistical regularity (Huber-Huber et al., 2021; Osterbrink & Herwig, 2021). According to predictive processing, the preview effect is a measure of how much post-saccadic perception is biased toward a pre-saccadic prediction about the target. In comparison to real-world visual inputs on the upper vertical meridian (e.g., high buildings), visual signals on the horizontal axis (e.g., faces or body parts) tend to be more transient, and these transient changes are more relevant to us (Stigliani et al., 2015). Thus, despite a higher contrast sensitivity, people might make comparatively weaker predictions about objects along the HM due to their transient nature, which would result in a smaller preview effect at the HM than the VM.

Around the time of the second stage (i.e., integration), right before saccade onset, contrast sensitivity rapidly increases at the saccade target (Rolfs & Carrasco, 2012; Hanning et al., 2022a,b; Li et al., 2021) and renders the peripheral information more fovea-like already before the eyes start moving (Li et al., 2016, 2019; 2022; Kwak et al., 2023). This pre-saccadic shift of attention could lead to an up-weighting of the peripheral preview and thus modulate the preview effect (De Pisapia et al., 2010; Melcher, 2007). However, because pre-saccadic attention either improves performance equally around the visual field (Kwak et al., 2023) or less for upward saccades (Hanning et al., 2022a,b), it cannot be responsible for the observed preview asymmetries.

A potential source of asymmetries during the third stage of the preview effect is the heterogeneity of post-saccadic visual sensitivity. Participants' foveal discrimination after upward saccades was worse than after saccades in other directions. This is in line with a higher post-saccadic instability (eye movement rate), which could explain the impaired post-saccadic sensitivity after upward saccades. The reduced sensitivity following upward

saccades could also be related to the absent or reduced pre-saccadic attention benefit at this location (Hanning et al., 2022a,b). Without attention shifting prospectively to the saccade target –easing trans-saccadic integration by rendering the peripheral visual input more fovea-like– visual sensitivity might recover more slowly after saccade offset.

Regardless of the mechanism underlying the worsened post-saccadic sensitivity following upward saccades, the visual system might have given more decision weight to the peripheral preview when a less reliable post-saccadic percepts was expected, consistent with the optimal integration framework (Ganmor et al., 2015; Wolf & Schütz, 2015). This, however, cannot explain the reverse VMA in the preview effect, as the here observed post-saccadic contrast sensitivity were equivalent between the LVM and HM.

Our study is the first to investigate how in homogenously perceived peripheral information is integrated across saccadic eye movements. On the one hand, these asymmetries are so robust that they cannot be overridden by any attention mechanism studied so far (e.g., Carrasco et al., 2001; Fernández et al., 2019; Purokayastha et al., 2021; Hanning et al., 2022a,b; Kwak et al., 2023). On the other hand, the current results indicate that our brain over-compensates for these asymmetries during trans-saccadic integration, by relying more on previewed peripheral information for which it is less sensitive (at the UVM), but which might be more stable and thus predictable.

These results have significant implications in real-world applications. When driving, for example, people tend to fixate on one point while covertly monitoring the periphery. Polar angle asymmetries in peripheral vision suggest that drivers will be the most sensitive to objects along the HM (e.g., pedestrians), followed by the LVM (e.g., signals on the instrument panel), and lastly the UVM (objects in the distance/the sky). The observed preview asymmetries show that when drivers make saccadic eye movements to different locations, integrating information across these saccades results in more homogenous performance for locations around the visual field.

This study highlights the need in future work to study pre-, post-, and trans-saccadic perception for different saccade directions. Most studies investigating perceptual modulations around saccades, such as pre-saccadic attention (Melcher, 2007; De Pisapia et al., 2010; Li et al., 2016; Buonocore et al., 2017), predictive remapping (Duhamel et al., 1992; Jonikaitis et al., 2013; Wang et al., 2016), and trans-saccadic integration (Ganmor et al.,

2015; Wolf & Schütz, 2015; Huber-Huber et al., 2019; Huber-Huber & Melcher, 2021; Liu et al., 2022) are based on horizontal eye movements. The here observed preview asymmetries, in line with polar angle differences in pre-saccadic attention (Hanning et al., 2022a,b) call into question the generalizability of these findings from one saccade angle to another.

In summary, the extrafoveal preview effect, as a measure of trans-saccadic integration, follows a reverse pattern of peripheral polar angle asymmetries during fixation. This finding suggests that the visual system actively compensates for polar angle asymmetries in peripheral visual perception by selectively facilitating the use of less-well perceived preview information around the time of a saccade. Future neurophysiological studies should investigate how and where such compensation is implemented in the human brain

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References

Abrams, J., Nizam, A., & Carrasco, M. (2012). Isoeccentric locations are not equivalent: The extent of the vertical meridian asymmetry. *Vision Research*, *52* (1), 70–78.

Angele, B., & Rayner, K. (2011). Parafoveal processing of word n+ 2 during reading: Do the preceding words matter? *Journal of Experimental Psychology: Human Perception and Performance*, *37* (4), 1210.

Bakdash, J. Z., & Marusich, L. R. (2017). Repeated measures correlation. *Frontiers in Psychology*, *8*, 456.

Baldwin, A. S., Meese, T. S., & Baker, D. H. (2012). The attenuation surface for contrast sensitivity has the form of a witch's hat within the central visual field. *Journal of Vision*, *12* (11), 23–23.

Barbot, A., & Carrasco, M. (2017). Attention modifies spatial resolution according to task demands. *Psychological Science*, *28* (3), 285–296.

Barbot, A., Xue, S., & Carrasco, M. (2021). Asymmetries in visual acuity around the visual field. *Journal of Vision*, *21* (1), 2–2.

Buonocore, A., Dimigen, O., & Melcher, D. (2020). Post-saccadic face processing is modulated by pre-saccadic preview: Evidence from fixation-related potentials. *Journal of Neuroscience*, *40* (11), 2305–2313.

Buonocore, A., Fracasso, A., & Melcher, D. (2017). Pre-saccadic perception: Separate time courses for enhancement and spatial pooling at the saccade target. *PLoS One*,*12* (6), e0178902.

Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51* (13), 1484–1525.

Carrasco, M., Talgar, C. P., & Cameron, E. L. (2001). Characterizing visual performance fields: Effects of transient covert attention, spatial frequency, eccentricity, task and set size. *Spatial Vision*, *15* (1), 61–75.

Caruso, V. C., Pages, D. S., Sommer, M. A., & Groh, J. M. (2018). Beyond the labeled line: variation in visual reference frames from intraparietal cortex to frontal eye fields and the superior colliculus. *Journal of Neurophysiology, 119*(4), 1411-1421.

Cornelissen, F. W., Peters, E. M., & Palmer, J. (2002). The eyelink toolbox: Eye tracking with matlab and the psychophysics toolbox. *Behavior Research Methods, Instruments, & Computers*, *34* (4), 613–617.

De Pisapia, N., Kaunitz, L., & Melcher, D. (2010). Backward masking and unmasking across saccadic eye movements. *Current Biology*, *20* (7), 613–617.

Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision research, 36*(12), 1827-1837.

Deubel, H. (2008). The time course of presaccadic attention shifts. *Psychological Research*, *72* (6), 630–640.

Duhamel, J.-R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation

of visual space in parietal cortex by intended eye movements. *Science*, *255* (5040), 90–92.

Edwards, G., VanRullen, R., & Cavanagh, P. (2018). Decoding trans-saccadic memory. *Journal of Neuroscience*, *38* (5), 1114–1123.

Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. *Proceedings of the National Academy of Sciences, 103*(18), 7192-7197.

Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415* (6870), 429–433.

Ernst, M. O., & Bülthoff, H. H. (2004). Merging the senses into a robust percept. *Trends in cognitive Sciences*, *8* (4), 162–169.

Fabius, J. H., Fracasso, A., Acunzo, D. J., Van der Stigchel, S., & Melcher, D. (2020). Low-level visual information is maintained across saccades, allowing for a postsaccadic handoff between visual areas. *Journal of Neuroscience*, *40* (49), 9476–9486.

Fernández, A., Denison, R. N., & Carrasco, M. (2019). Temporal attention improves perception similarly at foveal and parafoveal locations. *Journal of Vision, 19*(1), 12-12.

Ganmor, E., Landy, M. S., & Simoncelli, E. P. (2015). Near-optimal integration of orientation information across saccades. *Journal of Vision*, *15* (16), 8–8.

Greenwood, J. A., Szinte, M., Sayim, B., & Cavanagh, P. (2017). Variations in crowding, saccadic precision, and spatial localization reveal the shared topology of spatial vision. *Proceedings of the National Academy of Sciences*, *114* (17), E3573–E3582.

Hanning, N. M., Deubel, H., & Szinte, M. (2019). Sensitivity measures of visuospatial attention. *Journal of Vision, 19*(12), 17-17.

Hanning, N. M., Himmelberg, M. M., & Carrasco, M. (2022a). Presaccadic attention enhances contrast sensitivity, but not at the upper vertical meridian. *iScience*, *25* (2), 103851.

Hanning, N. M., Himmelberg, M. M., & Carrasco, M. (2022b). Presaccadic attention depends on eye movement direction. *bioRxiv*, 2022-12.

Himmelberg, M. M., Winawer, J., & Carrasco, M. (2020). Stimulus-dependent contrast sensitivity asymmetries around the visual field. *Journal of vision*, *20* (9), 18–18.

Huber-Huber, C., Buonocore, A., Dimigen, O., Hickey, C., & Melcher, D. (2019). The peripheral preview effect with faces: Combined eeg and eye-tracking suggests multiple stages of trans-saccadic predictive and non-predictive processing. *NeuroImage*, *200*, 344–362.

Huber-Huber, C., Buonocore, A., & Melcher, D. (2021). The extrafoveal preview paradigm as a measure of predictive, active sampling in visual perception. *Journal of Vision*, *21* (7), 12–12.

Huber-Huber, C., & Melcher, D. (2021). The behavioural preview effect with faces is susceptible to statistical regularities: Evidence for predictive processing across the saccade. *Scientific Reports*, *11* (1), 942.

Hutzler, F., Schuster, S., Marx, C., & Hawelka, S. (2019). An investigation of parafoveal masks with the incremental boundary paradigm. *PLoS One*, *14* (2), e0203013.

Jensen, O., Pan, Y., Frisson, S., & Wang, L. (2021). An oscillatory pipelining mechanism supporting previewing during visual exploration and reading. *Trends in Cognitive Sciences*, *25* (12), 1033–1044.

Jonikaitis, D., Szinte, M., Rolfs, M., & Cavanagh, P. (2013). Allocation of attention across saccades. *Journal of Neurophysiology, 109*(5), 1425-1434.

Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in psychtoolbox-3?

Körding, K. P., & Wolpert, D. M. (2004). Bayesian integration in sensorimotor learning. *Nature*, *427* (6971), 244–247.

Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research, 35*(13), 1897-1916

Kwak, Y., Hanning, N. M., & Carrasco, M. (2023). Presaccadic attention sharpens visual acuity. *Scientific Reports*, *13* (1), 2981.

Li, H.-H., Barbot, A., & Carrasco, M. (2016). Saccade preparation reshapes sensory tuning. *Current Biology*, *26* (12), 1564–1570.

Li, H. H., Hanning, N. M., & Carrasco, M. (2021). To look or not to look: dissociating presaccadic and covert spatial attention. *Trends in Neurosciences*, 44(8), 669-686.

Li, H. H., Pan, J., & Carrasco, M. (2019). Presaccadic attention improves or impairs performance by enhancing sensitivity to higher spatial frequencies. *Scientific Reports*, 9(1), 1-9.

Li, H.-H., Pan, J., & Carrasco, M. (2021). Different computations underlie overt presaccadic and covert spatial attention. *Nature Human Behaviour*, *5* (10), 1418–1431.

Liu, X., Huber-Huber, C., & Melcher, D. (2022). The trans-saccadic extrafoveal preview effect is modulated by object visibility. *2022 Symposium on Eye Tracking Research and Applications*, 1–7.

McDonald, S. A. (2005). Parafoveal preview benefit in reading is not cumulative across multiple saccades. *Vision Research*, *45* (14), 1829–1834.

Melcher, D. (2007). Predictive remapping of visual features precedes saccadic eye movements. *Nature Neuroscience*, *10* (7), 903–907.

Melcher, D., & Colby, C. L. (2008). Trans-saccadic perception. *Trends in Cognitive Sciences*, *12* (12), 466–473.

Montaser-Kouhsari, L., & Carrasco, M. (2009). Perceptual asymmetries are preserved in short-term memory tasks. *Attention, Perception, & Psychophysics*, *71* (8), 1782–1792.

Nyström, M., Hooge, I., & Holmqvist, K. (2013). Post-saccadic oscillations in eye movement data recorded with pupil-based eye trackers reflect motion of the pupil inside the iris. *Vision Research*, *92*, 59–66.

Osterbrink, C., & Herwig, A. (2021). Prediction of complex stimuli across saccades. *Journal of Vision*, *21* (2), 10–10.

Pentland, A. (1980). Maximum likelihood estimation: The best pest. *Percept. Psychophys.*, *28*, 377–379.

Prins, N., & Kingdom, F. A. (2018). Applying the model-comparison approach to test specific research hypotheses in psychophysical research using the palamedes toolbox. *Frontiers in Psychology*, *9*, 1250.

Purokayastha, S., Roberts, M., & Carrasco, M. (2021). Voluntary attention improves performance similarly around the visual field. *Attention, Perception, & Psychophysics*, *83* (7), 2784–2794.

Rayner, K., McConkie, G. W., & Zola, D. (1980). Integrating information across eye movements. *Cognitive Psychology*, *12* (2), 206–226.

Rijsdijk, J., Kroon, J., & Van der Wildt, G. (1980). Contrast sensitivity as a function of position on the retina. *Vision Research*, *20* (3), 235–241.

Roberts, M., Ashinoff, B. K., Castellanos, F. X., & Carrasco, M. (2018). When attention is intact in adults with ADHD. *Psychonomic Bulletin & Review*, 25, 1423-1434.

Rolfs, M., & Carrasco, M. (2012). Rapid simultaneous enhancement of visual sensitivity and perceived contrast during saccade preparation. *Journal of Neuroscience*, *32* (40), 13744–13752a.

Ross, J., Morrone, M. C., Goldberg, M. E., & Burr, D. C. (2001). Changes in visual perception at the time of saccades. *Trends in Neurosciences*, *24* (2), 113–121.

Rucci, M., & Victor, J. D. (2015). The unsteady eye: an information-processing stage, not a bug. *Trends in Neurosciences, 38*(4), 195-206.

Sadeh, M., Sajad, A., Wang, H., Yan, X., & Crawford, J. D. (2015). Spatial transformations between superior colliculus visual and motor response fields during head-unrestrained gaze shifts. *European Journal of Neuroscience*, *42* (11), 2934–2951.

Schall, J. D., & Hanes, D. P. (1993). Neural basis of saccade target selection in frontal eye field during visual search. *Nature*, *366* (6454), 467–469.

Sharp, P., Melcher, D., & Hickey, C. (2018). Endogenous attention modulates the temporal window of integration. *Attention, Perception, & Psychophysics*, *80*, 1214–1228.

Stigliani, A., Weiner, K. S., & Grill-Spector, K. (2015). Temporal processing capacity in high-level visual cortex is domain specific. *Journal of Neuroscience*, *35* (36), 12412–12424.

Talgar, C. P., & Carrasco, M. (2002). Vertical meridian asymmetry in spatial resolution: Visual and attentional factors. *Psychonomic Bulletin & Review*, *9*, 714–722.

Tzelepi, A., Laskaris, N., Amditis, A., & Kapoula, Z. (2010). Cortical activity preceding vertical saccades: A meg study. *Brain Research*, *1321*, 105–116.

Vallines, I., & Greenlee, M. W. (2006). Saccadic suppression of retinotopically localized blood oxygen level-dependent responses in human primary visual area v1. *Journal of Neuroscience*, *26* (22), 5965–5969.

Wang, X., Fung, C. A., Guan, S., Wu, S., Goldberg, M. E., & Zhang, M. (2016). Perisaccadic receptive field expansion in the lateral intraparietal area. *Neuron*, *90* (2), 400–409.

Wolf, C., & Schütz, A. C. (2015). Trans-saccadic integration of peripheral and foveal feature information is close to optimal. *Journal of Vision*, *15* (16), 1–1.