Presaccadic attention enhances contrast sensitivity, but not at the upper vertical meridian

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Abstract

Human visual performance is not only better at the fovea and decreases with eccentricity, but also has striking radial asymmetries around the visual field: At a fixed eccentricity, it is better along (1) the horizontal than vertical meridian and (2) the lower than upper vertical meridian. These asymmetries, known as *performance fields*, are pervasive –they emerge for many visual dimensions, regardless of head rotation, stimulus orientation or display luminance– and resilient –they are not alleviated by covert exogenous or endogenous attention, deployed in the absence of eye movements. Performance fields have been studied exclusively during eye fixation. However, a major driver of everyday attentional orienting is saccade preparation, during which visual attention automatically shifts to the future eye fixation. This presaccadic shift of attention is considered strong and compulsory, and relies on fundamentally different neural computations and substrates than covert attention. Given these differences, we investigated whether presaccadic attention can compensate for the ubiquitous performance asymmetries observed during eye fixation. Our data replicate polar performance asymmetries during fixation and document the same asymmetries during saccade preparation. Crucially, however, presaccadic attention enhanced contrast sensitivity at the horizontal and lower vertical meridian, but not at the upper vertical meridian. Thus, instead of attenuating polar performance asymmetries, presaccadic attention exacerbates them.

Introduction

Human visual performance is asymmetric around the visual field. At isoeccentric locations it is better along the horizontal than vertical meridian (horizontal-vertical anisotropy; HVA) and along the lower than upper vertical meridian (vertical-meridian asymmetry; VMA) (e.g., Carrasco et al., 2001; Cameron et al., 2002; Greenwood et al., 2017; Himmelberg et al., 2020; Barbot et al., 2021). These *performance fields* emerge across many perceptual dimensions (e.g., contrast sensitivity, spatial resolution) and are not alleviated by covert attention: Both involuntary *exogenous* (Carrasco et al., 2001; Cameron et al., 2002) and voluntary *endogenous* visual attention (Purokayastha et al., 2021), deployed in the absence of eye movements, uniformly improve performance around the visual field, thereby preserving the polar angle asymmetries (***Figure 1a***). Presaccadic attention, which automatically shifts to the future eye fixation during the preparation of saccadic eye movements (i.e., before the eyes start to move), also benefits visual performance (Kowler et al., 1995; Deubel & Schneider, 1996; Montagnini & Castet, 2007).

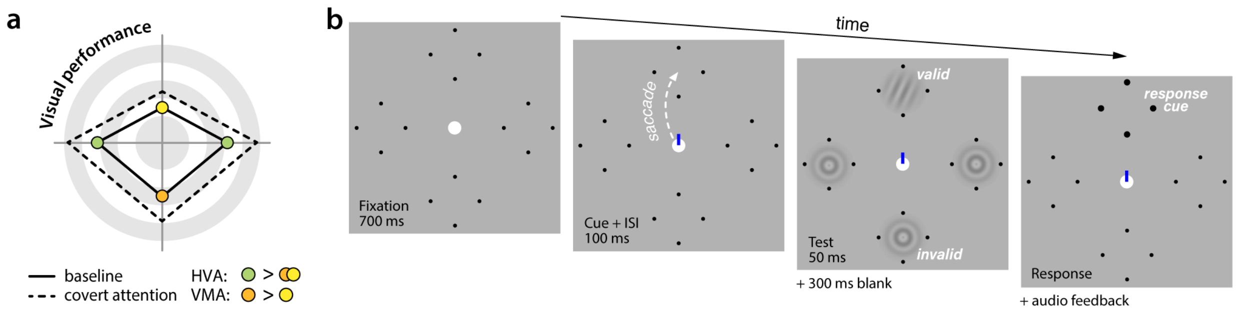

Figure 1. Background and experimental design. (**a**) Schematic representation of polar angle performance asymmetries reported in previous research. Points farther from the center represent higher performance. At matched eccentricity, visual performance is better on the horizontal than vertical meridian (HVA), and along the lower than upper vertical meridian (VMA) in several fundamental perceptual dimensions, including contrast sensitivity. (**b**) Experimental task. After a fixation period, a central direction cue (blue line) appeared. Observers were instructed to make a saccadic eye movement to the indicated target (8.5° left, right, above, or below central fixation, marked by black dots). 100 ms after direction cue onset, a test Gabor patch was presented at either the saccade target (*valid*) or at the opposing isoeccentric location (*invalid*). Radial frequency patterns with no orientation information were presented at the other three locations. At the end of the trial (after saccade offset), a response cue (bolded placeholder) indicated the location at which the test Gabor had appeared, and observers reported the Gabor orientation. Note that in the fixation condition the cue pointed to two opposing potential test locations (left and right or upper and lower) (supplemental ***Video S1*** demonstrates the trials sequence of each condition).

However, covert attention and presaccadic attention differentially modulate visual perception and the representation of features of basic visual dimensions (Li et al., 2016; Ohl et al., 2017), engage different neural computations (Li et al., 2021), and recruit partially distinct neural substrates (review: Li et al., 2021). Given these differences, can presaccadic attention compensate for the performance asymmetries established during eye fixation, thereby benefiting performance more where it is worse and thus diminish performance asymmetries? We hypothesized this may be the case given its automatic nature and prevalence in selective processing of visual information. Our data reproduced both the HVA and VMA during fixation (Carrasco et al., 2001; Cameron et al., 2002; Himmelberg et al., 2020; Purokayastha et al., 2021) and reveal the same polar asymmetries for contrast sensitivity during saccade preparation. Crucially, contrary to our initial hypothesis, presaccadic attention did not attenuate the cardinal polar angle asymmetries—quite the opposite: It enhanced contrast sensitivity at the horizontal and lower vertical meridian, but *not* at the upper vertical meridian. The surprising absence of a performance advantage preceding upwards saccades suggests a rigid perceptual limitation along the upper vertical meridian that cannot be allayed by presaccadic attention.

Results

We measured contrast sensitivity during saccade preparation using a two-alternative forced-choice orientation discrimination task (***Figure 1b***). Eleven observers performed horizontal or vertical saccades to a centrally cued peripheral target (8.5° eccentricity) and discriminated the orientation of a ±15° tilted Gabor grating presented briefly, just before eye movement onset, either at the saccade target (*valid*) or the opposite (*invalid*) isoeccentric location. In a fixation condition (*baseline*), observers performed the same orientation discrimination task without preparing saccades.

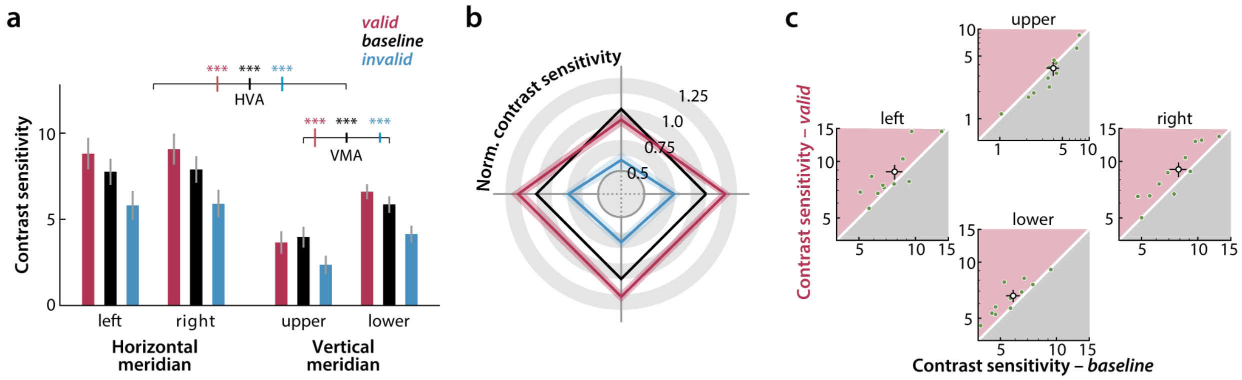

Figure 2. Main results. (**a**) Contrast sensitivity as a function of cardinal location for each experimental condition. Error bars depict ±1 standard error of the mean (SEM). Horizontal brackets indicate horizontal vs. vertical meridian (HVA) and vertical meridian upper vs. lower (VMA) comparisons, color coded error bars on the brackets indicate ±1 standard error of the difference between the compared conditions (SED). **p*<0.05, ***p*<0.01, ****p*<0.001. (**b**) Relative contrast sensitivity (normalized by respective baseline sensitivity) for each condition and cardinal location. Shaded error areas indicate ±1 SEM. (**c**) Individual observers' contrast sensitivity for each cardinal location. Green dots represent individual observers' sensitivity in valid trials plotted against their baseline sensitivity. White dots with black lines depict the group average and ±1 SEM. Note that the axes for the upper panel are different, to account for lower contrast sensitivity.

For each experimental condition (*valid*, *invalid*, *baseline*) we independently titrated Gabor contrast at four polar angle locations (*left*, *right*, *upper*, *lower*) using an adaptive psychometric "staircase" procedure [see Materials and methods - Titration procedure] and computed contrast sensitivity as the reciprocal of the titrated threshold value (***Figure 2a***). To test for the HVA, we conducted a 3 (condition: valid, invalid, baseline) X 2 (meridian: horizontal, vertical) repeated-measures ANOVA. The main effects for condition ($F(2,20)=41.78$, $p<0.001$) and meridian ($F(1,10)=74.51$, $p<0.001$), and their interaction ($F(2,20)=8.45$, $p=0.004$), were significant. Likewise, to test for the VMA, a 3 (condition: valid, invalid, fixation) X 2 (vertical meridian: upper, lower) repeated-measures ANOVA yielded significant main effects for condition ($F(2,20)=44.18$, $p<0.001$) and location ($F(1,10)=42.46$, $p<0.001$), and a significant interaction ($F(2,20)=7.46$, $p=0.018$). Post-hoc comparisons confirmed that for the fixation condition, contrast sensitivity changed around the visual field in accordance with the HVA (horizontal-vertical difference: 2.91±0.35 mean±SEM, $p<0.001$) and VMA (upper-lower vertical difference: 1.89±0.30, $p<0.001$), replicating previous findings (Carrasco et al., 2001; Cameron et al., 2002; Himmelberg et al., 2020; Purokayastha et al., 2021). Importantly, the same asymmetries emerged during saccade preparation, both when tested at the saccade target (*valid*) and opposite of it (*invalid*): HVA (*valid*: 3.81±0.47, $p<0.001$, *invalid*: 2.61±0.44, $p<0.001$) and VMA (*valid*: 2.95±0.56, $p<0.001$, *invalid*: 1.78±0.30, $p<0.001$).

To visualize the interaction between experimental condition and location, we plotted contrast sensitivity as a ratio of the baseline condition (***Figure 2b***). The 2 (condition: valid, fixation) X 4 (location: left, right, upper, lower) repeated-measures ANOVA to evaluate the relative benefit of presaccadic attention over the baseline yielded significant main effects for condition ($F(1,10)=7.05$, $p=0.024$) and location ($F(3,30)=7.24$, $p=0.001$) as well as their interaction ($F(3,30)=7.24$, $p=0.001$). Remarkably, post-hoc comparisons revealed the well-established perceptual advantage caused by presaccadic attention (e.g., Kowler et al., 1995; Deubel & Schneider, 1996; Montagnini & Castet, 2007; Hanning et al., 2019; Li et al., 2016, 2021) for all but one location: Relative to fixation (*baseline*), the preparation of horizontal and

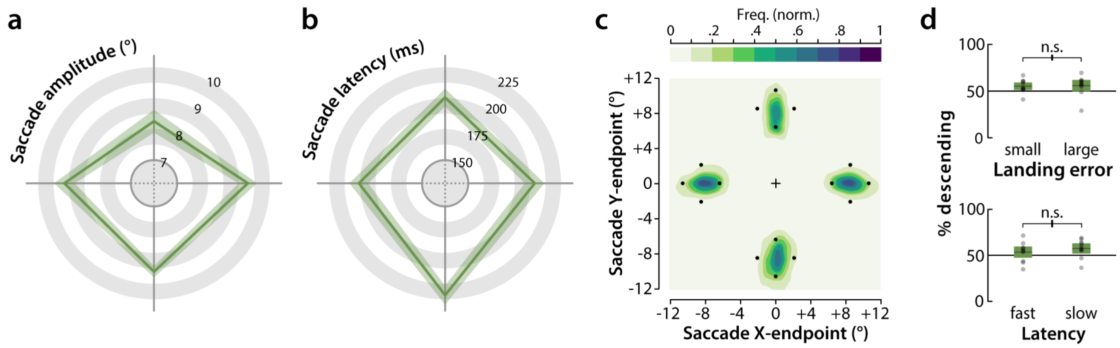

Figure 3. Eye movement parameters. Group average saccade amplitude (**a**) and saccade latency (**b**) as a function of saccade direction. Shaded error areas indicate ±1 SEM. (**c**) Normalized saccade endpoint frequency maps averaged across participants depicting saccade landing variance. (**d**) Percentage of trials contributing to staircase contrast decrement. Median-split for upper vertical meridian *valid* trials with comparably small or large saccade landing error (top plot) and low or high saccade latency (bottom plot). Horizontal lines within each whisker plot indicate the group average. Green bars depict the 95% confidence interval, black dots represent individual observer data. Error bars on horizontal brackets show the SED.

downward saccades increased contrast sensitivity at the target of the upcoming eye movement (*left*: p=0.040; *right*: p=0.007); *downward*: p=0.008). But upward saccades, consistent across individual observers (***Figure 2c***), did not yield a sensitivity benefit (p=0.114).

We evaluated eye movement parameters (***Figure 3***) to rule out that the absence of a performance advantage preceding upwards saccades can be explained by differences in saccade precision or latency. A repeated-measures ANOVA showed a significant main effect of cardinal saccade direction ($F(3,30)$=6.99, p=0.005) on amplitude. Post-hoc comparisons indicated that saccade amplitudes (***Figure 3a***) were significantly shorter for upward than leftward (p=0.041) and rightward (p=0.041) saccades. However, consistent with previous work (Deubel & Schneider, 1996; Van der Stigchel & de Vries, 2015; Wollenberg et al., 2018; Hanning et al., 2019), the presaccadic benefit was unaffected by landing precision (***Figure 3c***): More precise saccades (landing closer to the target center) were not more likely to contribute to a staircase contrast decrement than less precise saccades (p=0.837; ***Figure 3d***, top plot). Likewise, staircase contrast was not more likely to decrease with faster than slower saccade latency trials (p=0.346; ***Figure 3d***, bottom plot). The missing presaccadic benefit at the upper vertical meridian, therefore, cannot be explained by differences in eye movement parameters among polar angle locations.

Discussion

This study reveals that visual performance asymmetries are not compensated by presaccadic attention. The benefit was neither more pronounced at the vertical than the horizontal meridian, nor was there any benefit at the upper vertical meridian, where contrast sensitivity is the worst. The intrinsic perceptual limitation at the upper vertical meridian observer during fixation (Carrasco et al., 2001; Cameron et al., 2002; Greenwood et al., 2017; Himmelberg et al., 2020; Barbot et al., 2021) is rigid, and cannot be mitigated even by the typically robust effect of presaccadic attention (Kowler et al., 1995; Deubel & Schneider, 1996; Montagnini & Castet, 2007; Hanning et al. 2019; Li et al., 2016, 2021). This impervious constraint might be explained by anatomical constraints in the retina and visual cortex. There are similar polar angle asymmetries in the density of photoreceptor cones and midget retinal ganglion cells (Curcio & Allen, 1990; Song et al., 2011; Watson, 2014), for which cell density is lowest along the upper vertical meridian. However, a computational observer model has shown that these retinal asymmetries only account for a small proportion of behavioral contrast sensitivity asymmetries (Kupers et al., 2019, 2020). These asymmetries also exist, and are greatly amplified, in the cortical surface area of primary visual cortex, where there is substantially less surface dedicated to processing the upper vertical meridian (Benson et al., 2021; Himmelberg et al., 2021a,b).

To summarize, saccade preparation surprisingly did not enhance contrast sensitivity at the upper vertical meridian, where contrast sensitivity is poorest and could benefit the most. Consequently, instead of diminishing contrast sensitivity asymmetries around the visual field, presaccadic attention actually exacerbates them and modifies the shape of visual performance fields.

Materials and methods

Observers

We report data of eleven observers (6 female, aged 19–32 years, two authors: NMH and MMH). All had normal or corrected-to-normal vision, provided written informed consent, and (except for two authors) were naive to the purpose of the experiment. Three additional observers were not considered in the final analysis because they did not meet our inclusion criteria[1] (note that none of them showed a presaccadic benefit at the upper vertical meridian). The protocols for the study were approved by the University Committee on Activities involving Human Subjects at New York University and all experimental procedures were in agreement with the Declaration of Helsinki.

Setup

Observers sat in a dimly illuminated room with their head stabilized by a chin and forehead rest and viewed the stimuli at 57 cm distance on a gamma- linearized 20-inch ViewSonic G220fb CRT screen (Brea, CA, USA) with a spatial resolution of 1,280 by 960 pixels and a vertical refresh rate of 100 Hz. Gaze position of the dominant eye was recorded using an EyeLink 1000 Desktop Mount eye tracker (SR Research, Osgoode, Ontario, Canada) at a sampling rate of 1 kHz. Manual responses were recorded via a standard keyboard. An Apple iMac Intel Core 2 Duo computer (Cupertino, CA, USA) running Matlab (MathWorks, Natick, MA, USA) with Psychophysics (Brainard, 1997; Pelli, 1997) and EyeLink toolboxes (Cornelissen, 2002), controlled stimulus presentation and response collection.

Experimental design

The experiment comprised two eye movement conditions and a fixation condition. Eye movement conditions (*valid* and *invalid*) were randomly intermixed within blocks, whereas the fixation condition (*baseline*) was run in separate experimental blocks. At the beginning of each trial, observers fixated a central white dot (~52 cd/m^2; diameter 0.45° of visual angle) on gray background (~26 cd/m^2). Four

[1] One observer did not show the characteristic performance asymmetries during the fixation baseline condition (sensitivity horizontal meridian > lower vertical meridian > upper vertical meridian). Another observer did not show higher contrast sensitivity for *valid* trials than *invalid* trials. A third observer was excluded due to technical issues with eye movement recording.

placeholders indicated the isoeccentric locations of the upcoming stimuli (and potential saccade targets) 8.5° left, right, above, and below fixation. Each placeholder comprised four black dots (~0 cd/m², diameter 0.1°), forming the corners of a squared diamond (diameter 4.2°). Once we detected stable fixation within a 2.25° radius virtual circle centered on this fixation, the beginning of the trial was indicated by a sound.

In eye movement blocks (*valid* and *invalid* trials), after 700 ms fixation period, a central direction cue (blue line, ~4 cd/m², length 0.45°) pointed to one of the four cardinal placeholders (randomly selected), cueing the saccade target. Observers were instructed to look as fast and precisely as possible to the center of the indicated placeholder. 100 ms after cue onset (i.e., within the movement latency – gaze still rests at fixation), a Gabor grating (tilted ±15° relative to vertical; spatial frequency 5 cpd; 2.8° diameter Gaussian envelope diameter, σ = 0.43°) appeared for 50 ms either at the cued saccade target (*valid* trials; 50%) or at the location opposing the saccade target (*invalid* trials; 50%). Gabor contrast was titrated using an adaptive psychometric "staircase" procedure [see *Titration procedure*] and thus varied from trial to trial. Together with the Gabor, three radial frequency patterns with no orientation information (same spatial frequency, envelope, and contrast as the Gabor) were presented at the other placeholders to avoid biasing eye movements to a single sudden-onset stimulus. 300 ms after stimuli offset (once the eye movement had been performed), the dots of one placeholder increased in size (diameter 0.16°), functioning as a response cue to indicate the location that had contained the Gabor patch. Observers indicated their orientation judgement via button press (clockwise or counterclockwise, two-alternative forced choice) and were informed that the orientation report was non-speeded. They received auditory feedback for incorrect responses.

Stimulus parameters and timing for the fixation blocks (*baseline* condition) were identical to the eye movement blocks, with one difference: two (rather than one) blue direction cue lines appeared, pointing to opposing locations (left and right or upper and lower, randomly selected). Participants were instructed to keep eye fixation. As in the eye movement blocks, the Gabor appeared at one of two possible locations (indicated by the two direction cues) – thus location uncertainty as to where the test Gabor would appear was constant across experimental conditions.

Observers performed 3 sessions of 3 experimental blocks each (one fixation block followed by two eye movement blocks). Each block comprised 144 trials. We monitored gaze position online and controlled for correct eye fixation, i.e. gaze remaining within 2.25° from the central fixation target until (a) response cue onset (fixation blocks) or (b) direction cue onset (eye movement blocks). Observers maintained precise eye fixation during the pre-cue interval in fixation trials (0.80°±0.089° average distance from fixation target center ±1 SEM) as well as eye movement trials (0.72±0.077°). Trials in which gaze deviated from fixation were aborted and repeated at the end of each block. In eye movement blocks we also repeated trials with too short (<150 ms) or long (>350 ms) saccade latency, or incorrect eye movements (initial saccade landing beyond 2.25° from the indicated target). We collected a total of 1296 trials per observer – 432 fixation (*baseline*) trials and 864 eye movement trials (432 *valid*, 432 *invalid*).

Titration procedure

We titrated contrast separately for each experimental condition (*valid*, *invalid*, *baseline*) and cardinal location (left, right, upper, lower) with best PEST (Pentland, 1980), an adaptive psychometric procedure, using custom code (https://github.com/michaeljigo/palamedes_wrapper) that ran subroutines implemented in the Palamedes toolbox (Prins & Kingdom, 2018). We concurrently ran 36 independent adaptive procedures (3 for each condition-location combination) targeting 80% orientation discrimination accuracy throughout the experiment. One psychometric procedure comprised 36 trials. We calibrated each procedure by presenting fixed levels of contrast that spanned the range of possible values (1% - 100%) for the first 9 trials. To derive the contrast thresholds, we took the median across the last 5 trials of each individual staircase. Then, before averaging across the 3 staircases per condition-location combination, we excluded outliers (3.03% of all procedures) for which the derived threshold deviated more than 0.5 log-contrast units from the other thresholds of the respective condition-location combination.

Data analysis

We computed contrast sensitivity for each condition-location combination as the reciprocal of the average contrast threshold (CS = 1 / threshold). To evaluate the effect of saccade precision and latency on visual performance at the upper vertical meridian in the *valid* condition, we conducted two median splits and computed the percentage of trials causing the staircase procedure to decrease the contrast for (1) upward saccades with smaller vs. larger landing error and (2) upward saccades with faster vs. slower latencies (***Figure 3d***). Note that across the compared conditions, an average 55.5% of trials decreased the staircase contrast. Had saccade landing precision or latency affected the presaccadic attention benefit, trials with (1) smaller / larger landing errors or (2) faster / slower saccade latencies would have differentially affected staircase direction. This was not the case (see main text). For the conducted repeated-measures ANOVAs in which the sphericity assumption was not met, we report Greenhouse-Geisser corrected *p*-values; all *p*-values of post-hoc comparisons were Bonferonni corrected for multiple-comparisons.

Additional information and files

Author contributions

Conceptualization and methodology: NMH, MC; Software: NMH; Investigation: NMH, MMH; Formal analysis: NMH; Visualization: NMH, MMH; Writing—original draft: NMH; Writing—review & editing: NMH, MMH, MC; Funding acquisition: NMH, MC.

Data availability

Raw eye tracking and behavioral data are available from the OSF database URL: https://osf.io/9a36u/.

Supplemental Video S1

Demonstration of stimuli and experimental design. Shown are one *valid*, one invalid, and one *baseline* trial. For demonstration purposes, all three trials test contrast sensitivity at the upper vertical meridian (contrast here fixed to 35%).

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