# Presaccadic attention depends on eye movement direction

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## Abstract

With every saccadic eye movement, humans bring new information into their fovea to be processed with high visual acuity. Notably, perception is enhanced already before a relevant item is foveated: During saccade preparation, *presaccadic attention* shifts to the upcoming fixation location, which can be measured via behavioral correlates such as enhanced visual performance or modulations of sensory feature tuning. The coupling between saccadic eye movements and attention is assumed to be robust and mandatory, and considered a mechanism facilitating the integration of pre- and post-saccadic information. However, until recently it had not been investigated as a function of saccade direction. Here, we measured contrast response functions during fixation and saccade preparation and found that the pronounced response gain benefit typically elicited by presaccadic attention is selectively lacking before upward saccades – some observers even showed a cost. Individual observers' sensitivity before upward saccades was negatively related to their amount of surface area in primary visual cortex representing the saccade target, suggesting a potential compensatory mechanism that optimizes the use of the limited neural resources processing the upper visual field. Our results raise the question how perceptual continuity is achieved and upward saccades can be accurately targeted despite the lack of – theoretically required – presaccadic attention.

**Key words**: presaccadic attention, polar angle asymmetries, contrast response function

## Introduction

Given that the high acuity of the fovea markedly decreases with eccentricity, we constantly make saccadic eye movements – at a higher rate than our heart beats – to actively explore the visual world and gather information. To maintain a stable perception across saccades, the human visual system needs to seamlessly integrate blurry peripheral information with its high-acuity equivalent, once brought into the fovea by a saccade. To achieve this smooth transition, referred to as perceptual continuity, we preferentially and preemptively process visual information at the future eye fixation already before the eyes start moving: During saccade preparation, 'presaccadic attention' is automatically deployed to the saccade target[1,2], as evidenced, for example, by enhanced visual performance[3–6] or selective modulations of orientation[7,8] and spatial frequency tuning[7,9,10]. The scientific consensus is that the presaccadic shift of attention is robust and mandatory[11,12]. Sensitivity at locations other than the target –including the currently still foveated location[13] – inevitably decreases just before saccade onset[3,14,15]. Presaccadic attention even shifts to the saccade target when detrimental for the task at hand[1,9,16,17], demonstrating a strong functional coupling.

The effects of presaccadic attention on visual perception are assumed to rely on feedback signals projecting from oculomotor structures (e.g., frontal eye fields, FEF; superior colliculus, SC) back to early visual cortices[18,19]. Subthreshold micro-stimulation of FEF and SC (which would elicit a saccade if

stimulated above threshold) modulates activity in visual cortex[20] and enhances visual sensitivity at the movement field of the stimulated neurons[11,12] – resembling the typical behavioral correlates of presaccadic attention[1–6]. The coupling of oculomotor programming and attention is undisputed, but until recently[21] had not been investigated as a function of saccade direction. As a result, the neural and behavioral effects of presaccadic attention are thought to be ubiquitous throughout the visual field – independent of where the saccade is executed.

Visual performance, however, is heterogenous around the visual field: At fixed eccentricity, we perceive better along the horizontal than vertical meridian, and along the lower than upper vertical meridian. These two asymmetries, termed 'performance fields', emerge for various dimensions (e.g., contrast sensitivity, spatial resolution)[22–26] and are robust enough to not be attenuated by covert spatial exogenous[22,27–29] or endogenous attention[30], or by temporal attention[31]. Presaccadic attention –a major driver of everyday attentional orienting– can even exacerbate visual field asymmetries: Using an adaptive staircase procedure, we recently showed that saccade preparation enhances contrast sensitivity at threshold before horizontal and downward saccades, but not before upward saccades[21] (visualized in **Figure 1a**).

This finding is surprising for several reasons: (I) presaccadic attention is assumed to be mandatory: it automatically shifts before any saccade being made[1,17,32], via oculomotor feedback projections[11,12,18–20]; (II) presaccadic attention facilitates the integration of pre- and post-saccadic information[33] and thus has an important functional role, indispensable also for upward saccades: By rendering peripheral representations more fovea-like (e.g., via predictively enhancing contrast sensitivity[4,6] and spatial resolution at the saccade target[26], or shifting sensitivity at the saccade target to higher spatial frequencies[7,9]), presaccadic attention enables a smooth transition from presaccadic (peripheral) to post-saccadic (foveal) information – and thus perceptual continuity across saccades[6–9,34–36]; (III) visual sensitivity at the upper vertical meridian (during

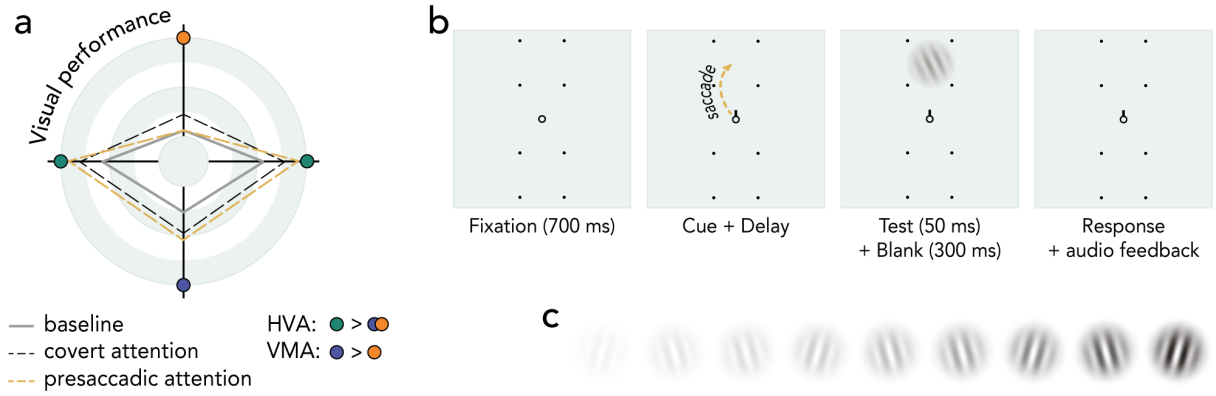


**Figure 1. Background and experimental design. (a)** Schematic representation of polar angle performance asymmetries. Points further from the center represent higher performance. Baseline visual performance (during fixation) is better along the horizontal than vertical meridian (HVA), and along the lower than upper vertical meridian (VMA). Covert attention equally benefits performance around the visual field[22,27–31]. Presaccadic attention, however, exacerbates the asymmetries by enhancing contrast sensitivity at all locations except the upper vertical meridian[21]. **(b)** Experimental task. Vertical *saccade* condition. After a fixation period, a central direction cue (black line) indicated the saccade target 8° above or below central fixation, marked by black dots (note that in the horizontal conditions stimuli were placed 8° left and right). ~100ms after direction cue onset (delay adjusted for each observer), a test Gabor was presented at the saccade target; observers reported its orientation after saccade offset. In the *fixation* condition, two lines cued both placeholder locations; observers were instructed to maintain fixation. See supplemental **Video S1** for a demonstration of the trials sequence. **(c)** Visualization of the different contrast levels (5-95%, log-spaced) tested to measure contrast response functions.

fixation) is generally lowest, thus could improve the most[22,27–30,37]. Our former study measured presaccadic attention at perceptual threshold[21], but recent findings show that presaccadic attention modulates performance via response gain[6], i.e., at higher stimulus contrasts where performance asymptotes. Thus, to systematically and optimally investigate the extent of presaccadic attention as a function of saccade direction, we evaluated sensitivity across the whole contrast response function.

We compared 2AFC orientation discrimination performance during fixation –a neutral cue instructed observers to maintain fixation throughout the trial– and saccade preparation –observers made an immediate saccade to a centrally cued target location 8° left, right, above, or below fixation (**Figure 1b & Video S1**; *Methods – Experimental design*). We varied the contrast of the test grating on a trial-by-trial basis across the full contrast range (**Figure 1c**), to measure presaccadic modulations of the contrast response function (CRF) at the saccade target. Observers' gaze positions were monitored continuously. Importantly, test presentation time was adjusted separately to each individual observer's horizontal and vertical saccade latencies (*Methods – Stimulus timing*), to ensure a measurement right before saccade onset, where presaccadic attention has its maximum effect[4,5,7,14,38]. Only trials in which the test was

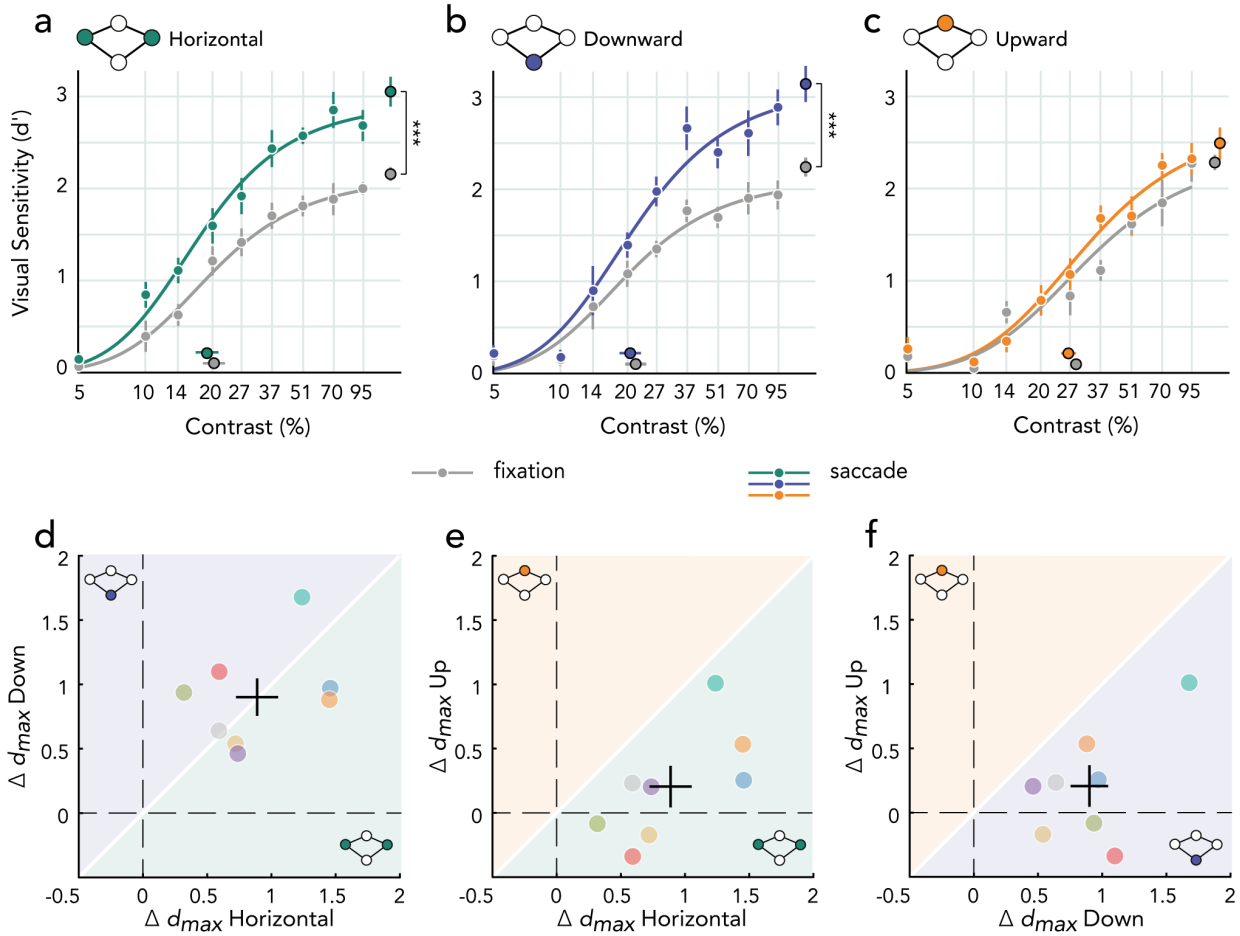


**Figure 2. Contrast responses depending on saccade direction.** Group-averaged psychometric contrast response functions (CRF; d′ versus contrast) measured during fixation (gray) or saccade preparation (colored) at the horizontal **(a)**, lower vertical **(b)**, and upper vertical **(c)** meridian. Group-averaged $d_{max}$ and $C_{50}$ extracted from individual observers' CRFs are plotted at the right and the bottom of the figure. Error bars depict ±1 SEM. ***$p$<0.001; **(d-f)** Pairwise comparison of individual observers' presaccadic benefit $\Delta d_{max}$ ($d_{max}$ *saccade* - $d_{max}$ *fixation*) at the horizontal (green background), lower (purple), and upper (orange) test locations. Black crosses depict the group average ±1 SEM.

presented during the last 100ms before saccade onset were included in the analysis. We adjusted the tilt angle (clockwise or counter-clockwise relative to vertical) in a pre-test (*Methods – Tilt titration*) to compensate for polar angle asymmetries and ensure equal task difficulty around the visual field during fixation – and thus equal room for a presaccadic benefit.

## Results

For each test location (*horizontal*, *lower*, *upper*) and condition (*fixation*, *saccade*), we fit performance (d') as a function of target contrast with a Naka-Rushton function[39] (*Methods – Quantification & Statistical analysis*). Contrast responses during fixation were highly comparable across test locations (**Figure 2a-c**; gray), also indicated by the absence of a difference between their asymptotic performance level $d_{max}$ ($F(2,14)=1.09$, $p=0.355$). We conducted repeated-measures ANOVAs with the factors test location and condition. In line with a previous study[6], presaccadic attention did not affect the semisaturation constant $C_{50}$ ($F(1,6)=1.81$; $p=0.221$), but significantly modulated the asymptotic performance level $d_{max}$ ($F(1,6)=29.63$, $p=0.001$), consistent with a response gain change. Importantly, this modulation interacted with saccade direction ($F(2,14)=15.63$, $p<0.001$). Bonferroni-corrected post-hoc comparisons showed that saccade preparation enhanced $d_{max}$ at the saccade target (relative to fixation) before horizontal ($p<0.001$; **Figure 2a**) and downward ($p<0.001$; **Figure 2b**) saccades. Crucially, there was no presaccadic response gain benefit before upward saccades ($p=0.217$; **Figure 2c**). Correspondingly, the presaccadic benefit $\Delta d_{max}$ ($d_{max}$ *saccade* - $d_{max}$ *fixation*) significantly varied with saccade direction ($F(2,14)=15.63$; $p<0.001$). Post-hoc

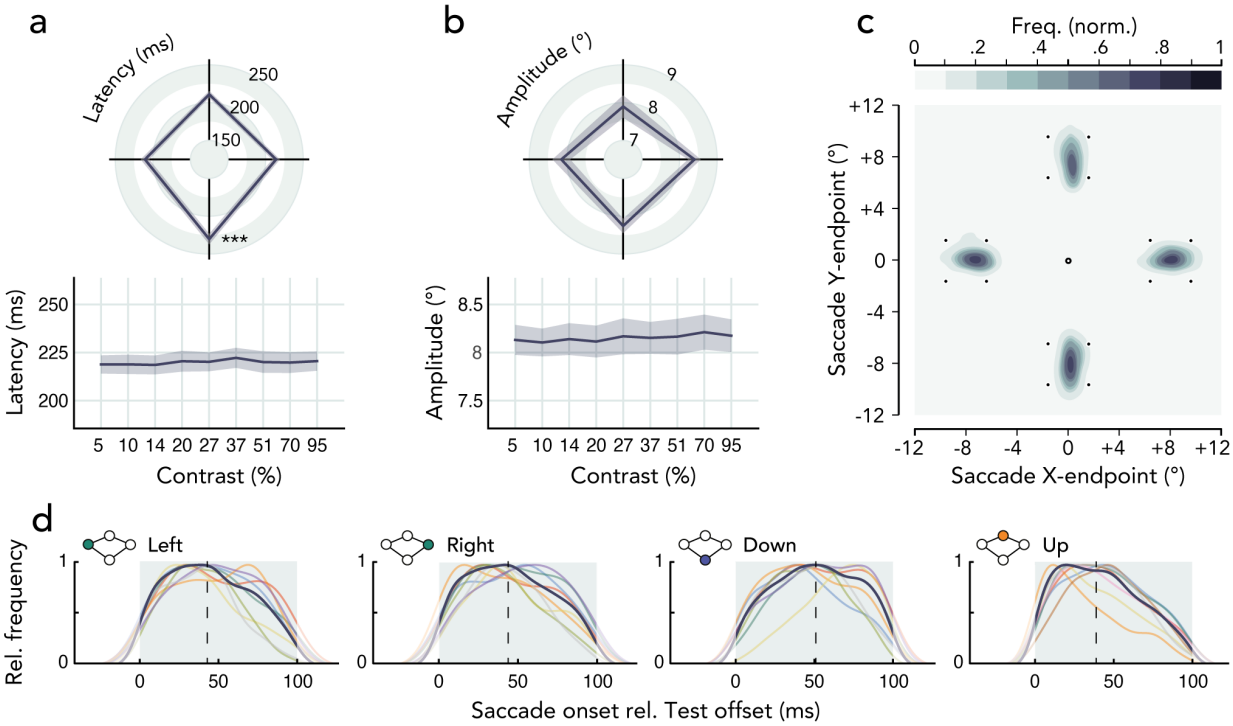


**Figure 3. Eye movement parameters.** Group average saccade latency (**a**) and amplitude (**b**) as a function of saccade direction (top) and test contrast level (bottom). Shaded error areas indicate ±1 SEM. (**c**) Normalized saccade endpoint frequency maps averaged across observers depicting saccade landing variance. (**d**) Density plots of saccade onset times relative to test offset, for each observer (thin colored lines) and across observers (bold line). Dashed vertical lines indicate the average saccade onset across observers; the gray background indicates the time window of trials included in the analysis (test offset ≤100ms before saccade onset).

comparisons demonstrated no statistical difference between the benefit caused by horizontal and downward saccades ($p$=1.00; **Figure 2d**), whereas the benefit before upward saccades (when present) was significantly reduced compared to both horizontal ($p$=0.003; **Figure 2e**) and downward ($p$=0.004; **Figure 2f**) saccades. Note that this differential effect was present for all observers.

We evaluated eye movement parameters to ensure that the missing presaccadic benefit before upwards saccades cannot be explained by differences in saccade latency or precision, e.g., comparatively slower or less precise upward saccade execution. A 2-way repeated-measures ANOVA with factors saccade direction and test contrast level showed a significant main effect of saccade direction ($F(3,21)=8.94$, $p=0.006$) on latency (**Figure 3a**), but no effect of stimulus contrast ($F(8,56)=1.50$, $p=0.248$) or an interaction effect between the two ($F(24,168)=2.15$, $p=0.116$). Post-hoc comparisons indicated significantly longer latencies for downward saccades compared to left ($p=0.006$), right ($p<0.001$), and upward ($p=0.037$) saccades. Given that this pattern was expected[21,26,40,41], we adjusted the delay between cue and test presentation to each observer's horizontal and vertical saccade latencies (*Methods – Stimulus timing*) so that test presentation time relative to saccade onset was matched across saccade directions (**Figure 3d**). Neither saccade amplitudes (**Figure 3b**) nor saccade landing errors (i.e., the mean Euclidean distance between saccade endpoints and saccade target center; **Figure 3c**) were affected by saccade direction (*amplitude*: $F(3,21)=1.585$, $p=0.241$; *landing error*: $F(3,21)=1.292$, $p=0.306$), stimulus contrast (*amplitude*: $F(8,56)<1$; *landing error*: $F(8,56)=1.41$, $p=0.259$), or their interaction (*amplitude*: $F(24,168)<1$; *landing error*: $F(24,168)=1.37$, $p=0.265$). In sum, latency and movement precision of upward saccades were comparable to those of horizontal and downward saccades, ruling out these parameters as source for the absent presaccadic benefit before upward saccades. In any case, the presaccadic shift of attention is not linked to the saccade landing position but to the *intended* saccade target[1,6,42–45].

Our data show that presaccadic attention not only varies around the visual field, but also considerably among individual observers. Whereas observers consistently showed a presaccadic benefit of similar magnitude before horizontal and downward saccades (**Figure 4a**), we observed a mixed pattern for upward saccades, ranging from moderate presaccadic benefits to even presaccadic costs (i.e., lower presaccadic sensitivity at the upward saccade target than during fixation; 37.5% of observers). Note that for those observers displaying a presaccadic benefit at all locations, the benefit before upward saccades was lower than before horizontal and downward saccades.

Notably, the visual field is non-uniformly represented in primary visual cortex (V1) – with greater surface area corresponding to the horizontal than vertical meridian, and lower than upper vertical meridian[46–49]. This directly reflects[50] – and likely, at least partially, underlies[49] – perceptual differences around the visual field (**Figure 1a**). Individual differences in contrast sensitivity around the visual field correlate with the amount of V1 surface dedicated to processing the respective region of visual space[49]. Thus, greater contrast sensitivity –during fixation– is a perceptual consequence of more dedicated V1 surface area. Could this relation also hold for presaccadic perceptual modulations? To explore whether presaccadic attention benefits are linked to V1 surface area, we correlated each observer's presaccadic benefit before horizontal, downward, and upward saccades with their amount of V1 surface area representing the respective saccade target region. Individual observers' surface estimates were obtained in a separate fMRI experiment[48] (*Methods – fMRI Retinotopy & Surface estimation*).

For horizontal and downward saccades, which showed the typical presaccadic sensitivity enhancement, we observed no correlation between presaccadic benefits and the amount of V1 surface area representing the saccade target (*horizontal* target: $r(6)=-0.03$, $p=0.947$; *downward* target: $r(6)=-0.17$, $p=0.681$). In contrast, inter-individual variations in the presaccadic effect preceding upward saccades were

negatively correlated with the amount of V1 surface dedicated to processing the upward saccade target (**Figure 4b**). Thus, the less cortical surface representing the saccade target, the larger the presaccadic attentional benefit (*upward* target: $r(6)=-0.79$, $p=0.019$). This finding documents a link between cortical anatomy and the magnitude of presaccadic perceptual modulations (or lack thereof) preceding upward saccades at the individual observer level.

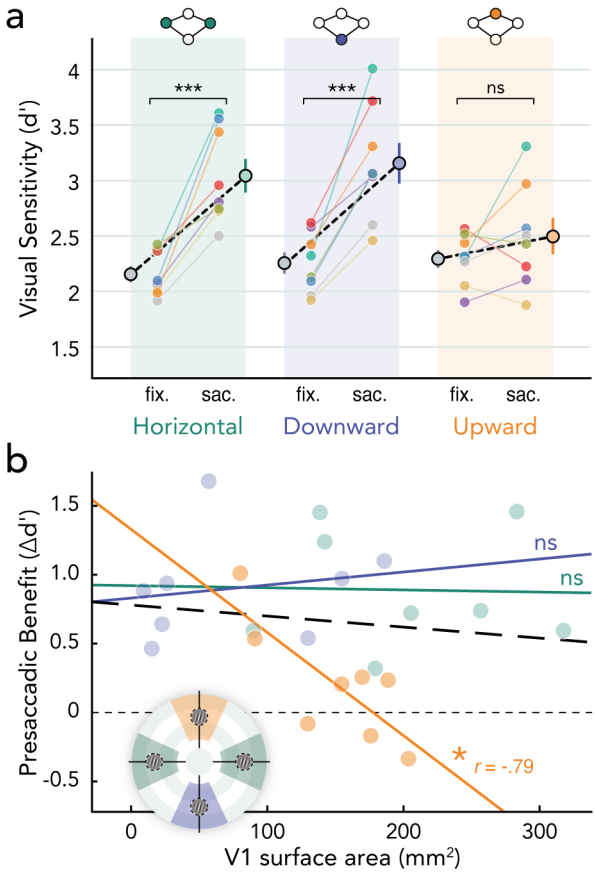


**Figure 4. Linking presaccadic attention to individual differences in the surface area of primary visual cortex. (a)** Individual observers' $d_{max}$ (extracted from their fitted CRF) for each test location and condition. Dashed black lines depict the group average, error bars depict ±1 SEM. **(b)** Individual observers' presaccadic benefit ($d_{max}$ saccade - $d_{max}$ fixation) before horizontal, downward, and upward saccades plotted as a function of their respective localized measurements of V1 surface area. The circular icon depicts the extracted area: 4°-12° eccentricity, ±35° of radial angle extending either side of each cardinal meridian (note that horizontal surface area was computed as the average of left and right). *$p<0.05$;

## Discussion

We investigated presaccadic attention for different saccade directions using a design optimized to detect presaccadic benefits: (I) We measured presaccadic contrast sensitivity across the full contrast range to capture the response gain effect by which presaccadic attention modulates contrast sensitivity[6]. (II) We adjusted overall task difficulty during fixation –which served as a baseline condition to quantity the effect of presaccadic attention– to compensate for performance field asymmetries (by separately titrating the tilt angle for observers and test locations). (III) We adjusted the test presentation time separately to each observer's direction-specific saccade latency to ensure a measurement right before saccade onset, where presaccadic attention has its maximum effect[4,5,7,14,38].

We found that horizontal and downward saccades caused a significant response gain, in line with the well-established and typically robust sensitivity benefit at the saccade target[1–3,5,6]. However, this response gain benefit was blatantly missing before upward saccades. At the upper vertical meridian, all observers showed either no or a markedly reduced presaccadic benefit across the contrast response function, some even showed a cost, which matches our previous findings on contrast sensitivity measured at perceptual threshold[21]. We ruled out that differences in saccade latency, amplitude or landing precision could explain the absent presaccadic benefit before upward saccades. Furthermore, we identified a neural correlate for this differential effect: Observers with a comparatively greater presaccadic benefit before upward saccades have relatively less V1 surface area dedicated to processing that target location.

The absent presaccadic benefit before upward saccades is at odds with the up-to-now uncontested view that presaccadic attention is automatically deployed before any saccade made (review[51]). However,

studies investigating presaccadic attention typically rely on measurements along the horizontal meridian[e.g.1,4,6–8,13,15,44] or place their saccade targets around the visual field but do not evaluate potential differences between among saccade directions[e.g.2,5,33,38,43,45]. The same applies to neurophysiological measurements of presaccadic attention, which likewise have not been obtained and evaluated as a function of saccade direction. These limitations have spurred the now debatable assumption that the effects of presaccadic attention are ubiquitous throughout visual space. Our current and recent[21] findings demonstrate that observations made for one saccade direction do not generalize to other directions; thus, measurements should not be collapsed around the visual field. Our findings call for a systematic investigation of presaccadic attention as a function of polar angle.

Although the strong coupling between saccade planning and visual attention –which we show does not hold for upward saccades– has been undisputed, the *direction* of this relation is still debated. Proponents of the *premotor theory of attention* argue that visual attention is a product of the motor system, and even covert shifts of attention, during fixation, results from (eye) movement planning[52,53] (review[54]). At a broad scale, brain structures active during saccadic eye movements (e.g., FEF, SC, precentral sulcus) are also selectively modulated during covert attention tasks in human- and non-human primates[55–57]. However, distinct neuronal populations within these regions are related to covert attention and saccade preparation activity[e.g.12,58–60]. In sum, recent research refutes the view that the control of spatial attention is dependent on oculomotor control circuits[6,7,9,17,44,60–62] (reviews[51,63]) and suggests the reverse: Attention does not result from motor programming but is a necessary predecessor, i.e., successful movements depend on preceding attentional selection to specify the motor coordinates for an upcoming movement – *selection-for-action*[1,64,65]. Our results are inconsistent with both accounts: (1) Eye movement parameters for upward saccades are no different from horizontal and downward saccades; given that upward saccade motor programming is “normal” (indicated by typical saccade latency and precision), it should – according to the premotor theory of attention – cause a regular shift of attention to the motor target; (2) According to the selection-for-action account, the presaccadic shift of attention functions as target marker and is a prerequisite for movement execution; the motor target has to be attentionally selected before the saccade is executed. Here we show regularly executed upward saccades without a measurable motor target selection marker.

Assuming presaccadic attention is required for motor target selection but absent prior to upward saccades, how can we nevertheless perform (accurate) upward saccades? Could presaccadic attention be deployed to upward saccade targets, without resulting in the typical corresponding perceptual advantages? This possibility could be tested by measuring neurophysiological rather than behavioral correlates of presaccadic attention. For example, event-related potentials (ERPs) in a dot-probe protocol reliably track attentional selection: stimuli presented at a covertly attended location[66,67], as well as attentionally selected motor targets[68], elicit larger sensory-evoked P1/N1 components than stimuli at unattended locations. It would be informative to probe the possibility of presaccadic attention shifting to upward saccade targets but not resulting in measurable perceptual benefits at a neurophysiological level.

This is a plausible scenario given that visual sensitivity at the upper vertical meridian is significantly lower than at other isoeccentric visual field locations due to anatomical constraints in retina and visual cortex. There is a relatively lower density of photoreceptor cones and midget retinal ganglion cells sampling along the upper vertical meridian of the visual field[69–71]. Whereas these retinal asymmetries only account for a small proportion of perceptual asymmetries[72,73], the distribution of cortical surface area in V1, which shows corresponding and more pronounced asymmetries[47,49,73], reliably predicts perceptual sensitivity differences around the visual field[47,49], even at the level of individual observers[49]. Could the reduced neural

resources devoted to processing the upper visual field likewise (partially) explain why saccade preparation does not improve sensitivity at the upper vertical meridian? The relation between cortical surface area and presaccadic benefit observed in the current study refutes this possibility: Individual observers' amount of V1 tissue representing the upward target location was negatively correlated with the magnitude of presaccadic benefit before upward saccades: those observers with comparatively less V1 surface representing the upward saccade target showed a relatively greater presaccadic benefit (however this benefit was still severely reduced compared to the other saccade directions). This negative correlation may point towards a compensatory mechanism –or computation– that is specific for the upper vertical meridian; no such relation was observed for horizontal and downward saccades. We speculate that presaccadic attention might help to make efficient use of cortical resources where they are most limited – at the upper vertical meridian[46–49,73].

To summarize, even when accounting for the known sensitivity differences around the visual field (during fixation) and testing in a contrast range optimized for detecting presaccadic sensitivity modulations, saccades made to the upper vertical meridian lack the typical presaccadic benefit. Neurophysiological studies need to test whether oculomotor feedback connections for upward saccades differ from those for other saccade directions. Our results challenge the mandatory nature of the link between saccade programming and attention, and raise the question how perceptual continuity –the smooth transition from presaccadic (peripheral) to post-saccadic (foveal) information– which is assumed to rely on predictive presaccadic sensitivity modulations to render peripheral representations at the saccade target fovea-like[6–9,34–36], is maintained also before upward saccades. Trans-saccadic integration has not been investigated as a function of saccade direction. Future studies need to test whether other behavioral correlates of presaccadic attention directly related to perceptual continuity across saccades –such as orientation tuning[7,8] or a selective shift of sensitivity to higher spatial frequencies[7–9]– are altered, or even absent prior to upward saccades.

## Materials & Methods

### *Observers*

Eight observers (4 female, aged 21–33 years, two authors: NMH and MMH) with normal or corrected-to-normal vision participated in the study. We chose a sample size in the typical range of studies investigating presaccadic attention[3,6,9,13,16,44,45]. All observers provided written informed consent, and (except for the two authors) were naive to the purpose of the experiment. 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 57cm 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 85 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[74,75] and EyeLink[76] toolboxes, controlled stimulus presentation and response collection.

### *Experimental design*

The experiment comprised two experimental conditions –*saccade* and *fixation*– tested at the two meridians –horizontal and vertical– in separate experimental blocks. Observers fixated a central fixation target (black ring; ~0 cd/m$^2$, diameter 0.35°, width 0.1° of visual angle) on gray (~26 cd/m$^2$) background (see **Figure 1b**). Two placeholders indicated the isoeccentric locations of the upcoming stimuli (and potential saccade targets), either 8° left and right, or above and below fixation (depending on the tested meridian). Each placeholder comprised four dark gray dots (diameter 0.1°), forming the corners of a square (diameter 4.5°). The trial started once we detected stable fixation within a 1.75° radius virtual circle centered on the fixation target.

In *saccade* blocks, after a 700ms fixation period, a central direction cue (black line; ~0 cd/m$^2$, length 0.175°, width 0.1°) pointed to one of the opposing 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. Approximately 100ms after cue onset (inter-stimulus interval adjusted based on each observer's direction specific movement latency, see *Stimulus timing*), a Gabor grating (4cpd, random phase, Gaussian envelope σ = 0.5°), which was slightly tilted relative to vertical (see *Tilt titration*), appeared for ~35ms at the cued saccade target. Gabor contrast was varied on a trial-by-trial basis following the methods of constant stimuli (Michelson contrast, 9 log-spaced steps from 5% to 95%, see **Figure 1c**). Note that the grating was presented within the movement latency, i.e., when gaze still rested at fixation. 400ms after stimuli offset (well after the eye had landed at the saccade target), we played a high- or low-pitch response sound to specify 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 were identical to the *saccade* blocks, with one difference: two (rather than one) black direction cue lines appeared, pointing to both placeholder locations and observers were instructed to keep eye fixation.

Observers performed multiple sessions of 12 experimental blocks each: 4 horizontal and 8 vertical blocks (counterbalanced within sessions), of which half were *fixation* and half were *saccade* blocks, randomly interleaved. Note that less experimental blocks were dedicated to testing the horizontal than vertical meridian because we collapsed data across the left and right test location (but separately analyzed upward and downward locations). Each block comprised 105 trials. We monitored gaze position online and controlled for correct eye fixation, i.e. gaze remaining within 1.75° from the central fixation target until (a) response cue onset (*fixation* blocks) or (b) direction cue onset (*saccade* blocks). Trials in which gaze deviated from fixation were aborted and repeated at the end of each block. In *saccade* blocks we also repeated trials with too short (<100ms) or long (>400ms) saccade latency, or incorrect eye movements (initial saccade landing beyond 2.5° from the indicated target). Overall data collection for an observer was stopped once at least 50 trials per stimulus contrast level and experimental condition were acquired after offline trial exclusion (see *Eye data preprocessing*).

### *Tilt titration*

To match overall task difficulty to each observers' visual sensitivity and to account for sensitivity differences around the visual field, we titrated the tilt angle (± 0.125° – 5° relative to vertical) separately for each observer and test position (horizontal, upper, lower) with best PEST[77] (using custom code [https://github.com/michaeljigo/palamedes_wrapper] that ran subroutines implemented in the Palamedes

toolbox[78]). Using the procedure of the *fixation* condition, we concurrently ran 3 independent adaptive procedures (each comprising 36 trials) for each test location, to determine the tilt angle at which observers ' orientation discrimination performance at the highest contrast level (95%) was ~d′ = 2. The location specific tilt angle used for the first main experimental session (same for *saccade* and *fixation* blocks) was computed by averaging medians of the last 5 trials of each individual staircase across the 3 staircases per location. Following each experimental session, the tilt angle for each location was adjusted as needed to ensure comparable accuracy across locations in the fixation condition. Note that the tilt angle for a given test location was the same for fixation and saccade blocks within an experimental session.

### *Eye data preprocessing*

We scanned the recorded eye-position data offline and detected saccades based on their velocity distribution[79] using a moving average over 20 subsequent eye position samples. Saccade onset and offset were detected when the velocity exceeded or fell below the median of the moving average by 3 standard deviations for at least 20ms. We included trials in which no blink occurred during the trial and correct eye fixation was maintained within a 1.75 radius centered on central fixation throughout the trial (*fixation* trials) or until cue onset (*saccade* trials). Moreover, we only included those eye movement trials in which the initial saccade landed within 2.5 from the required target location and in which the test signal was presented within 100ms before saccade onset (i.e., the saccade started only after test signal presentation, but not later than 100ms after signal offset). In total, we included 30,168 trials in the analysis of the behavioral results (on average 3,771 ± 114 (mean ± 1 SEM) trials per observer).

### *Stimulus timing*

The effect of presaccadic attention increases throughout saccade preparation and peaks shortly before saccade onset[4,5,7,14,38]. Saccade latencies, however, vary as a function of saccade direction[21,26,40,41], e.g., downward saccades are typically initiated ~25ms later than horizontal or upward saccades (also see **Figure 3d**). In order to measure and compare the effects of presaccadic attention equally close to saccade onset for all saccade directions, we matched the test presentation time relative to the saccade by adjusting the delay between saccade cue and test onset to each observer's direction specific saccade latency. For the initial experimental session, we randomly selected the stimulus onset asynchrony (SOA) between 141ms and 235ms on a trial-by-trial basis. After each session, we evaluated vertical and horizontal saccade latencies and adjusted the SOA-range to only include those SOAs for which test presentation fell in the desired presaccadic window (test offset -100 to 0ms relative to saccade onset) in at least 70% of trials. This adjusted SOA-range was used for both fixation and saccade blocks in the upcoming session.

### *Quantification & Statistical analysis*

Orientation discrimination performance, indexed by visual sensitivity (d-prime; d' = *z*(hit rate) - *z*(false alarm rate)), was measured as a function of stimulus contrast using the method of constant stimuli (9 log-spaced Michelson contrast levels: 5, 10, 14, 20, 27, 37, 51, 70, 95%). We arbitrarily defined counter-clockwise responses to counter-clockwise oriented gratings as hits and counter-clockwise responses to clockwise oriented gratings as false-alarms[6,80–83]. To avoid infinite values when computing d', we substituted hit and false alarm rates of 0 and 1 by 0.01 and 0.99, respectively[5,43,44,61].

As only *saccade* trials with test offset occurring within the last 100ms prior to saccade onset were included in the sensitivity analysis (see *Eye data preprocessing*), trials with certain SOAs (see *Stimulus timing*) were more likely to contribute to the averaged visual sensitivity per contrast level. To ensure identical timing parameters in the fixation condition (in which no trials were excluded based on temporal criteria), for

each observer we first calculated d' for each stimulus contrast level separately for each used SOA, before computing a weighted average per contrast level, that matched the respective contrast level's SOA distribution at the respective test location of the saccade condition.

To obtain contrast response functions for each condition and test location we fit each observer's data with Naka-Rushton functions[39], parameterized as $d'(C) = d_{max}C^n / (C^n + C^n_{50})$, where C is the contrast level, $d_{max}$ is the asymptotic performance, $C_{50}$ is the semi-saturation constant (contrast level corresponding to half the asymptotic performance), and n determines the slope of the function. The error was minimized using a least-squared criterion; $d_{max}$ and $c_{50}$ were free parameters, n was fixed. Contrast levels were log-transformed prior to fitting. A change in $d_{max}$ indicates a response gain change and a change of $C_{50}$ indicates a contrast gain change.

We used repeated measures ANOVAs to assess statistical significance, followed by paired t-tests for post-hoc comparisons. All post-hoc comparisons were Bonferroni-corrected for multiple comparisons. All p-values for repeated-measures ANOVAs in which the assumption of sphericity was not met were Greenhouse-Geisser corrected. Parameter estimates for psychometric functions and all statistical tests were computed in MATLAB.

***fMRI Retinotopy & V1 Surface computation***

Each observer's population receptive field (pRF) data[84] and anatomical data were taken from the NYU Retinotopy Database[48]. The pRF stimulus, MRI and fMRI acquisition parameters, MRI and fMRI preprocessing, the implementation of the pRF model, as well as the computation of V1 surface area representing wedge-ROIs along the cardinal meridians of the visual field are identical to those described in our previous work[48,49]. In brief, to calculate the V1 surface area representing each saccade target region, we defined wedge-ROIs in the visual field that were centered along each of the cardinal meridians. Each wedge-ROI was ±35° in width and extended 4°–12° of eccentricity. We calculated the amount of V1 surface area (in $mm^2$) encapsulated by each of these wedge-ROIs by first generating 9 sub-wedge-ROIs (that are later combined to form the full wedge-ROI). Each sub-wedge-ROI was constrained to a narrow eccentricity band (9 log-spaced bands from 4°–12°). For each sub-wedge-ROI, the 35° border on the cortex was calculated by identifying the average distance of a selected pool of vertices whose pRF polar angle coordinates lied around the 35° polar angle pRF centers from each respective meridian. All vertices between a meridian and the 35° boundary were included in the sub-wedge-ROI. The sub-wedge-ROI was then used as a mask and overlaid on the anatomical surface, for which each vertex has an assigned surface area value (in $mm^2$). The surface areas of the vertices within the sub-wedge-ROI mask were then summed to give a measurement of surface area for the respective sub-wedge-ROI. This was repeated for each sub-wedge ROI. Finally, the surface area of each sub-wedge-ROI was summed to compute the amount of surface area representing the full wedge-ROI representing a saccade target area in the visual field. This was repeated for each cardinal saccade target region. For the current study, the surface areas of the horizontal (left and right) saccade target wedge-ROIs were averaged together.

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## Additional information and files

### *Author contributions*

Conceptualization and methodology: NMH, MC; Software: NMH; Investigation: NMH; Overall analysis and visualization: NMH; fMRI analysis: 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 at https://osf.io/xrtbf/; preprocessed fMRI data is available from the openNeuro platform at https://openneuro.org/datasets/ds003787/versions/1.0.0;

### *Supplemental Video S1*

Demonstration of an exemplary vertical *saccade* trial (grating contrast 70%).

### *Declaration of interests*

The authors declare no competing interests.

## References


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

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

3. Montagnini, A., and Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. Journal of Vision *7*, 8–8. 10.1167/7.14.8.

4. Rolfs, M., and Carrasco, M. (2012). Rapid simultaneous enhancement of visual sensitivity and perceived contrast during saccade preparation. Journal of Neuroscience *32*, 13744 –13752. 10.1523/jneurosci.2676-12.2012.

5. Hanning, N.M., Deubel, H., and Szinte, M. (2019). Sensitivity measures of visuospatial attention. Journal of Vision *19*, 17–13. 10.1167/19.12.17.

6. Li, H.-H., Pan, J., and Carrasco, M. (2021). Different computations underlie overt presaccadic and covert spatial attention. Nature Human Behaviour, 1–16. 10.1038/s41562-021-01099-4.

7. Li, H.-H., Barbot, A., and Carrasco, M. (2016). Saccade Preparation Reshapes Sensory Tuning. Current Biology *26*, 1564–1570. 10.1016/j.cub.2016.04.028.

8. Ohl, S., Kuper, C., and Rolfs, M. (2017). Selective enhancement of orientation tuning before saccades. Journal of Vision *17*, 2–11. 10.1167/17.13.2.

9. Li, H.-H., Pan, J., and Carrasco, M. (2019). Presaccadic attention improves or impairs performance by enhancing sensitivity to higher spatial frequencies. Scientific Reports *9*, 1–9. 10.1038/s41598-018-38262-3.

10. Kroell, L.M., and Rolfs, M. (2021). The peripheral sensitivity profile at the saccade target reshapes during saccade preparation. Cortex *139*, 12–26. 10.1016/j.cortex.2021.02.021.

11. Moore, T., and Fallah, M. (2004). Microstimulation of the Frontal Eye Field and Its Effects on Covert Spatial Attention. Journal of Neurophysiology *91*, 152–162. 10.1152/jn.00741.2002.

12. Müller, J.R., Philiastides, M.G., and Newsome, W.T. (2005). Microstimulation of the superior colliculus focuses attention without moving the eyes. PNAS *102*, 524–529.

13. Hanning, N.M., and Deubel, H. (2022). The effect of spatial structure on presaccadic attention costs and benefits assessed with dynamic 1/f noise. J Neurophysiol *127*, 1586–1592. 10.1152/jn.00084.2022.

14. Deubel, H. (2008). The time course of presaccadic attention shifts. Psychological Research *72*, 630–640. 10.1007/s00426-008-0165-3.

15. Collins, T., Heed, T., Doré-Mazars, K., and Röder, B. (2010). Presaccadic attention interferes with feature detection. Exp Brain Res *201*, 111–117. 10.1007/s00221-009-2003-2.

16. Kreyenmeier, P., Deubel, H., and Hanning, N.M. (2020). Theory of visual attention (TVA) in action: Assessing premotor attention in simultaneous eye-hand movements. Cortex *133*, 133–148. 10.1016/j.cortex.2020.09.020.

17. Hanning, N.M., Wollenberg, L., Jonikaitis, D., and Deubel, H. (2022). Eye and hand movements disrupt attentional control. PLOS One *17*, e0262567. 10.1371/journal.pone.0262567.

18. Ekstrom, L.B., Roelfsema, P.R., Arsenault, J.T., Bonmassar, G., and Vanduffel, W. (2008). Bottom-Up Dependent Gating of Frontal Signals in Early Visual Cortex. Science *321*, 414–417. 10.1126/science.1153276.

19. Bisley, J.W., and Mirpour, K. (2019). The neural instantiation of a priority map. Current Opinion in Psychology *29*, 108–112. 10.1016/j.copsyc.2019.01.002.

20. Moore, T., and Armstrong, K.M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. Nature *421*, 370–372. 10.1038/nature01285.

21. Hanning, N.M., Himmelberg, M.M., and Carrasco, M. (2022). Presaccadic attention enhances contrast sensitivity, but not at the upper vertical meridian. Iscience *25*, 103851. 10.1016/j.isci.2022.103851.

22. Carrasco, M., Talgar, C.P., and Cameron, E.L. (2001). Characterizing visual performance fields: effects of transient covert attention, spatial frequency, eccentricity, task and set size. Spatial Vision *15*, 61–75. 10.1163/15685680152692015.

23. Corbett, J.E., and Carrasco, M. (2011). Visual Performance Fields: Frames of Reference. Plos One *6*, e24470. 10.1371/journal.pone.0024470.

24. Abrams, J., Nizam, A., and Carrasco, M. (2012). Isoeccentric locations are not equivalent: The extent of the vertical meridian asymmetry. Vision Res *52*, 70–78. 10.1016/j.visres.2011.10.016.

25. Barbot, A., Xue, S., and Carrasco, M. (2021). Asymmetries in visual acuity around the visual field. Journal of Vision *1*, 1–23. 10.1167/jov.21.1.2.

26. Kwak, Y., Hanning, N.M., and Carrasco, M. (2022). Presaccadic attention sharpens visual acuity. bioRxiv. https://doi.org/10.1101/2022.11.02.514935.

27. Cameron, E.L., Tai, J.C., and Carrasco, M. (2002). Covert attention affects the psychometric function of contrast sensitivity. Vision Research, 949–967.

28. Talgar, C.P., and Carrasco, M. (2002). Vertical meridian asymmetry in spatial resolution: Visual and attentional factors. Psychon B Rev *9*, 714–722. 10.3758/bf03196326.

29. Roberts, M., Cymerman, R., Smith, R.T., Kiorpes, L., and Carrasco, M. (2016). Covert spatial attention is functionally intact in amblyopic human adults. J Vision *16*, 30. 10.1167/16.15.30.

30. Purokayastha, S., Roberts, M., and Carrasco, M. (2021). Voluntary attention improves performance similarly around the visual field. Attention, Perception, & Psychophysics, 1–11. 10.3758/s13414-021-02316-y.

31. Fernández, A., Denison, R.N., and Carrasco, M. (2019). Temporal attention improves perception similarly at foveal and parafoveal locations. Journal of Vision *19*, 12–10. 10.1167/19.1.12.

32. Shepherd, M., Findlay, J.M., and Hockey, R.J. (1986). The Relationship between Eye Movements and Spatial Attention. Q J Exp Psychol *38*, 475–491. 10.1080/14640748608401609.

33. Kwon, S., Rolfs, M., and Mitchell, J.F. (2019). Presaccadic motion integration drives a predictive postsaccadic following response. J Vision *19*, 12. 10.1167/19.11.12.

34. Herwig, A. (2015). Transsaccadic integration and perceptual continuity. Journal of Vision *15*, 1–6. 10.1167/15.

35. Herwig, A., and Schneider, W.X. (2014). Predicting object features across saccades: Evidence from object recognition and visual search. Journal of Experimental Psychology: General *143*, 1903–1922. 10.1037/a0036781.

36. Rolfs, M. (2015). Attention in Active Vision: A Perspective on Perceptual Continuity Across Saccades. Perception *44*, 900–919. 10.1177/0301006615594965.

37. Kristjánsson, Á., and Sigurdardottir, H.M. (2008). On the Benefits of Transient Attention across the Visual Field. Perception *37*, 747–764. 10.1068/p5922.

38. Hanning, N.M., Aagten-Murphy, D., and Deubel, H. (2018). Independent selection of eye and hand targets suggests effector- specific attentional mechanisms. Scientific Reports *8*, 1–8. 10.1038/s41598-018-27723-4.

39. Naka, K.I., and Rushton, W.A.H. (1966). S-potentials from luminosity units in the retina of fish (Cyprinidae). J Physiology *185*, 587–599. 10.1113/jphysiol.1966.sp008003.

40. Honda, H., and Findlay, J.M. (2010). Saccades to targets in three-dimensional space: Dependence of saccadic latency on target location. 1–8.

41. Tzelepi, A., Laskaris, N., Amditis, A., and Kapoula, Z. (2010). Cortical activity preceding vertical saccades: A MEG study. Brain Research *1321*, 105–116. 10.1016/j.brainres.2010.01.002.

42. Stigchel, S.V. der, and Vries, J.P. de (2015). There is no attentional global effect: Attentional shifts are independent of the saccade endpoint. Journal of Vision *15*, 17–12. 10.1167/15.15.17.

43. Wollenberg, L., Deubel, H., and Szinte, M. (2018). Visual attention is not deployed at the endpoint of averaging saccades. PLoS Biol *16*, e2006548-23. 10.1371/journal.pbio.2006548.

44. Hanning, N.M., Szinte, M., and Deubel, H. (2019). Visual attention is not limited to the oculomotor range. PNAS *39*, 201813465–201813466. 10.1073/pnas.1813465116.

45. Wollenberg, L., Hanning, N.M., and Deubel, H. (2020). Visual attention and eye movement control during oculomotor competition. Journal of Vision *20*, 16–16. 10.1167/jov.20.9.16.

46. Silva, M.F., Brascamp, J.W., Ferreira, S., Castelo-Branco, M., Dumoulin, S.O., and Harvey, B.M. (2018). Radial asymmetries in population receptive field size and cortical magnification factor in early visual cortex. Neuroimage *167*, 41–52. 10.1016/j.neuroimage.2017.11.021.

47. Benson, R, K.E., A, B., M, C., and J, W. (2021). Cortical magnification in human visual cortex parallels task performance around the visual field. eLife, e67685.

48. Himmelberg, M.M., Kurzawski, J.W., Benson, N.C., Pelli, D.G., Carrasco, M., and Winawer, J. (2021). Cross-dataset reproducibility of human retinotopic maps. Neuroimage *244*, 118609. 10.1016/j.neuroimage.2021.118609.

49. Himmelberg, M.M., Winawer, J., and Carrasco, M. (2022). Linking individual differences in human primary visual cortex to contrast sensitivity around the visual field. Nat Commun *13*, 3309. 10.1038/s41467-022-31041-9.

50. Himmelberg, M.M., Winawer, J., and Carrasco, M. (2020). Stimulus-dependent contrast sensitivity asymmetries around the visual field. Journal of Vision *20*, 18–19. 10.1167/jov.20.9.18.

51. Li, H.-H., Hanning, N.M., and Carrasco, M. (2021). To look or not to look: dissociating presaccadic and covert spatial attention. Trends in neurosciences, 1–18. 10.1016/j.tins.2021.05.002.

52. Rizzolatti, G., Riggio, L., Dascola, I., and Umiltá, C. (1987). Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. Neuropsychologia *25*, 31–40.

53. Craighero, L., Fadiga, L., Rizzolatti, G., and Umiltà, C. (1999). Action for Perception: A Motor–Visual Attentional Effect. J Exp Psychology Hum Percept Perform *25*, 1673–1692. 10.1037/0096-1523.25.6.1673.

54. Smith, D.T., and Schenk, T. (2012). The Premotor theory of attention: Time to move on? Neuropsychologia *50*, 1104–1114. 10.1016/j.neuropsychologia.2012.01.025.

55. Nobre, A.C., Gitelman, D.R., Dias, E.C., and Mesulam, M.M. (2000). Covert Visual Spatial Orienting and Saccades: Overlapping Neural Systems. Neuroimage *11*, 210–216. 10.1006/nimg.2000.0539.

56. Bollimunta, A., Bogadhi, A.R., and Krauzlis, R.J. (2018). Comparing frontal eye field and superior colliculus contributions to covert spatial attention. Nature Communications *9*, 1961–11. 10.1038/s41467-018-06042-2.

57. Bogadhi, A.R., Bollimunta, A., Leopold, D.A., and Krauzlis, R.J. (2018). Brain regions modulated during covert visual attention in the macaque. Scientific Reports, 1–15. 10.1038/s41598-018-33567-9.

58. Ignashchenkova, A., Dicke, P.W., Haarmeier, T., and Thier, P. (2003). Neuron-specific contribution of the superior colliculus to overt and covert shifts of attention. Nat Neurosci *7*, 56–64. 10.1038/nn1169.

59. Gregoriou, G.G., Gotts, S.J., and Desimone, R. (2012). Cell-Type-Specific Synchronization of Neural Activity in FEF with V4 during Attention. Neuron *73*, 581–594. 10.1016/j.neuron.2011.12.019.

60. Messinger, A., Cirillo, R., Wise, S.P., and Genovesio, A. (2021). Separable neuronal contributions to covertly attended locations and movement goals in macaque frontal cortex. Sci Adv *7*, eabe0716. 10.1126/sciadv.abe0716.

61. Hanning, N.M., and Deubel, H. (2020). Attention capture outside the oculomotor range. Current Biology *30*, R1353–R1355. 10.1016/j.cub.2020.09.054.

62. Masson, N., Andres, M., Pereira, S.C., Pesenti, M., and Vannuscorps, G. (2020). Exogenous covert shift of attention without the ability to plan eye movements. Current Biology *30*, R1032–R1033. 10.1016/j.cub.2020.07.074&domain=pdf.

63. Carrasco, M., and Hanning, N.M. (2020). Visual Perception: Attending beyond the Eyes' Reach. Curr Biol *30*, R1322–R1324. 10.1016/j.cub.2020.08.095.

64. Schneider, W.X. (1995). VAM: A neuro-cognitive model for visual attention control of segmentation, object recognition, and space-based motor action. Vis Cogn *2*, 331–376. 10.1080/13506289508401737.

65. Baldauf, D., and Deubel, H. (2010). Attentional landscapes in reaching and grasping. Vision Research *11*, 999–1013.

66. Luck, S.J., Hillyard, S.A., Mouloua, M., Woldorff, M.G., Clark, V.P., and Hawkins, H.L. (1994). Effects of Spatial Cuing on Luminance Detectability: Psychophysical and Electrophysiological Evidence for Early Selection. J Exp Psychology Hum Percept Perform *20*, 887–904. 10.1037/0096-1523.20.4.887.

67. Luck, S.J., and Yard, S.A.H. (1995). The role of attention in feature detection and conjunction discrimination: An electrophysiological analysis. Int J Neurosci *80*, 281–297. 10.3109/00207459508986105.

68. Baldauf, D., and Deubel, H. (2009). Attentional Selection of Multiple Goal Positions Before Rapid Hand Movement Sequences: An Event-related Potential Study. J Cognitive Neurosci *21*, 18–29. 10.1162/jocn.2008.21021.

69. Curcio, C.A., and Allen, K.A. (1990). Topography of ganglion cells in human retina. J Comp Neurol *300*, 5–25. 10.1002/cne.903000103.

70. Song, H., Chui, T.Y.P., Zhong, Z., Elsner, A.E., and Burns, S.A. (2011). Variation of Cone Photoreceptor Packing Density with Retinal Eccentricity and Age. Investigative Opthalmology Vis Sci *52*, 7376. 10.1167/iovs.11-7199.

71. Watson, A.B. (2014). A formula for human retinal ganglion cell receptive field density as a function of visual field location. J Vision *14*, 15. 10.1167/14.7.15.

72. Kupers, E.R., Carrasco, M., and Winawer, J. (2019). Modeling visual performance differences 'around' the visual field: A computational observer approach. Plos Comput Biol *15*, e1007063. 10.1371/journal.pcbi.1007063.

73. Kupers, E.R., Benson, N.C., Carrasco, M., and Winawer, J. (2022). Asymmetries around the visual field: From retina to cortex to behavior. PLoS Computational Biology *18*, e1009771.

74. Brainard, D.H. (2000). The Psychophysics Toolbox. 1–7.

75. Pelli, D.G. (2003). The VideoToolbox software for visual psychophysics: transforming numbers into movies. Spatial Vision *10*, 437–442.

76. Cornelissen, F.W., Peters, E.M., and Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. Behavior Research Methods, Instruments, & Computers *34*, 613–617. 10.3758/bf03195489.

77. Pentland, A. (2010). Maximum likelihood estimation: The best PEST. Percept Psychophys *28*, 377–379. 10.3758/bf03204398.

78. Prins, N., and Kingdom, F.A.A. (2018). Applying the Model-Comparison Approach to Test Specific Research Hypotheses in Psychophysical Research Using the Palamedes Toolbox. Front Psychol *9*, 1250. 10.3389/fpsyg.2018.01250.

79. Engbert, R., and Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. Proc National Acad Sci *103*, 7192–7197. 10.1073/pnas.0509557103.

80. Huihui, Z., Concetta, M.M., and David, A. (2019). Behavioural oscillations in visual orientation discrimination reveal distinct modulation rates for both sensitivity and response bias. Scientific Reports *1*, 1–11.

81. Jigo, M., and Carrasco, M. (2020). Differential impact of exogenous and endogenous attention on the contrast sensitivity function across eccentricity. Journal of Vision *20*, 1–25. 10.1167/jov.20.6.11.

82. Fernández, A., and Carrasco, M. (2020). Extinguishing Exogenous Attention via Transcranial Magnetic Stimulation. Current Biology *30*, 4078–4084. 10.1016/j.cub.2020.07.068.

83. Fernández, A., Hanning, N.M., and Carrasco, M. (2022). Transcranial magnetic stimulation to frontal but not occipital cortex disrupts endogenous attention. bioRxiv. https://doi.org/10.1101/2022.11.01.514715.

84. Dumoulin, S.O., and Wandell, B.A. (2008). Population receptive field estimates in human visual cortex. NeuroImage *2*, 647–660.