

Review

Polar angle asymmetries in visual perception and neural architecture

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Human visual performance changes with visual field location. It is best at the center of gaze and declines with eccentricity, and also varies markedly with polar angle. These perceptual polar angle asymmetries are linked to asymmetries in the organization of the visual system. We review and integrate research quantifying how performance changes with visual field location and how this relates to neural organization at multiple stages of the visual system. We first briefly review how performance varies with eccentricity and the neural foundations of this effect. We then focus on perceptual polar angle asymmetries and their neural foundations. Characterizing perceptual and neural variations across and around the visual field contributes to our understanding of how the brain translates visual signals into neural representations which form the basis of visual perception.

Visual perception throughout the visual field is linked to neural architecture

Information processing systems have limited capacity. Visual systems, whether artificial (e.g., cameras) or biological (e.g., the human visual system), are no exception. For example, both cameras and the visual system are limited in their spatial sampling of the visual field but differ in how they sample visual space. Cameras typically have a fixed resolution throughout visual space, whereas the visual system processes information at some locations in great detail but coarsely at other locations. The visual system has built-in location-specific sampling limits on the amount of information that is transmitted, extending from the eye to the brain. The location-specific differences become more pronounced due to the neural circuitry in the brain.

Location-dependent limits underlie non-uniformities in our perception throughout the visual field.

Visual performance (see [Glossary](#)) changes with **eccentricity** [1]; it is typically best at the **fovea** and decreases with distance towards the periphery. This eccentricity-dependent variation is consistent with retinal and neural features of the visual system that also vary with eccentricity [2–6]. Most of our knowledge and models of spatial vision account only for perceptual variation with eccentricity, even though at any given eccentricity a stimulus can appear anywhere around 360° of visual angle. The position of the stimulus around that 360° circle – **polar angle** – strongly affects visual performance; it is better along the horizontal than the vertical meridian, and along the lower than the upper vertical meridian of the visual field [7–18]. These polar angle asymmetries (or 'performance fields' [8,16]) also exist in the density of **photoreceptors** [2,5], **midget retinal ganglion cells (mRGCs)** [3,6], and the amount of surface area in **primary visual cortex (V1)** [19–23]. Advances in neuroimaging and computational modeling have enabled scientists to start linking these neural asymmetries to visual perception [20,21,23–25].

A core goal of neuroscience is to understand how the nervous system translates visual signals into an internal representation of visual space, which forms the basis of how we perceive and interact with our visual environment. Crucially, however, polar angle asymmetries are typically overlooked in both perceptual and neural measurements of vision. Integrating what has been

Highlights

Human visual performance typically declines with eccentricity; the neural bases of this effect exist at multiple stages of the visual system.

Visual performance also varies with polar angle: it is better along the horizontal than vertical meridian, and along the lower than upper vertical meridian.

Polar angle asymmetries exist at multiple stages of the visual system: in the density of photoreceptors and midget retinal ganglion cells, and in the distribution of tissue representing the visual field in visual cortex. Each subsequent stage explains more of the perceptual variability.

Polar angle asymmetries are rooted in the asymmetric distribution of tissue in visual cortex, but asymmetric differences in neural tuning properties (spatial frequency tuning, orientation tuning, and receptive field size) likely play a key role in the perceptual asymmetries.

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learnt about these perceptual and neural asymmetries with the well-established body of knowledge on eccentricity-dependent organization of the visual system would provide a more complete understanding of (i) how the visual field is represented in **retinotopic maps**, and (ii) how neural organization within retinotopic maps dictates perception as a function of visual field location.

In this review we bring together literature quantifying how visual performance varies with visual field location – across eccentricity and around polar angle – and how these differences relate to neural organization at multiple stages of the visual system.

Eccentricity effects across the visual field

Perception depends on eccentricity

Perceptual performance for many visual properties declines with eccentricity [1]; for example, **acuity**, **contrast sensitivity**, and temporal sensitivity. The eccentricity effect was first characterized for acuity [26–29], which is best at the fovea and steeply decreases with eccentricity.

The change in contrast sensitivity with eccentricity reflects a complex interplay among stimulus size, **spatial frequency**, and **temporal frequency**. Spatial contrast sensitivity is bandpass-filtered at the fovea, peaking at ~4 cycles per degree (cpd) [30,31] and monotonically decreasing with eccentricity [10,32]. The gradient of this decline depends upon spatial frequency [10,32,33], with a steeper decline for higher spatial frequencies [34]. **M-scaling** of a stimulus can account for differences in cortical magnification that occur as a function of eccentricity by adjusting the stimulus size at different eccentricities to produce equivalent cortical size representations [35,36]. M-scaling neutralizes the decline in contrast sensitivity [36] and acuity [37] with eccentricity. However, M-scaling does not always completely neutralize this decline for some visual dimensions (e.g., stereo acuity [38] and numerosity judgments [39]), implying that additional factors beyond cortical magnification contribute to eccentricity effects in perception [1,40].

In contrast to spatial properties, some temporal properties of vision improve with eccentricity – especially for low spatial frequencies. Temporal resolution, measured as **critical flicker frequency (CFF)**, follows a non-monotonic course, gradually increasing up to ~40° eccentricity before decreasing [41–43]. M-scaling stimulus area and luminance (to account for larger peripheral **receptive field** sizes) equalizes CFF across eccentricity [42]. Likewise, the speed of visual processing increases for stimuli presented at increasingly eccentric locations [44,45]; this effect is diminished – but is not eliminated – after M-scaling [44].

Eccentricity-dependent organization of the retina

There is a non-uniform spatial distribution of cells in the retina. In well-lit conditions, cone photoreceptors carry out the first steps of vision by capturing and transducing light into electrical signals. Cone density in the human retina peaks in the fovea (~15 000 cones/degree²) and sharply declines with eccentricity [2,6,46,47]. In dim light, vision begins with rod photoreceptors, which have a different eccentricity dependence. We focus here on cone-mediated vision.

Signals from the cones are passed through the retinal circuitry and exit the eye via RGCs. The density of mRGCs representing the fovea peaks at ~33 000/degrees², roughly double the cone density, and declines with eccentricity [3,6,48]. mRGC cell body density peaks ~1 mm away owing to foveal displacement [3,6,48]. Accordingly, mRGC somal [49] and dendritic tree [50] sizes increase with eccentricity. Retinal temporal sensitivity varies substantially with eccentricity; peripheral cones [46] and mRGCs [46,51] show ~twofold faster response kinetics than those at the fovea, possibly contributing to the heightened temporal sensitivity of the periphery [41–43].

Glossary

Acuity: a measure of the ability of the visual system to distinguish between fine details.

Contrast sensitivity: a measure of the ability of the visual system to distinguish an object from its background.

Cortical magnification factor (CMF): the amount of cortical surface (mm²) representing 1 degree² of visual space.

Covert attention: the deployment of attention to a location without an accompanying eye movement.

Critical flicker frequency (CFF): the frequency (Hz) at which a flickering light is perceived as being continuous.

Eccentricity: distance (in degrees) from the center of the visual field (fovea).

Fovea: retinal region that processes the center of the visual field; this region has the greatest cone photoreceptor density.

Horizontal–vertical anisotropy

(HVA): the percent increase in a value (e.g., sensitivity, density, surface area) between the vertical and horizontal meridians. A perceptual HVA of 50% means that sensitivity is 50% greater along the horizontal than the vertical meridian.

M-scaling: magnifying stimulus size based on its eccentric location to compensate for differences in cortical magnification, often equalizing visual performance.

Midget retinal ganglion cells

(mRGCs): retinal cells receiving signals from the photoreceptors, with axons that transmit to V1 via the optic tract. mRGCs are the most numerous type of RGC.

Photoreceptors: retinal neurons that convert light to neural signal via phototransduction.

Polar angle: the angular distance (0–360°) between a location in visual space relative to an axis.

Population receptive field (pRF): an fMRI encoding model that captures the aggregate visual receptive field properties of the neural population within an fMRI voxel. This is possible because neurons with similar receptive field properties neighbor each other in cortex.

Presaccadic attention: a predictive attentional boost that occurs before saccadic eye movement onset at the target location.

Primary visual cortex (V1): the first visual map in the cortical hierarchy of visual areas, located (in humans) in the calcarine sulcus of the occipital lobe. V1

Thus, the eccentric organization of both cones and mRGCs shows a similar pattern to perceptual measurements; however, mRGC density declines with eccentricity more sharply than cone density. The decrease in cone density contributes modestly to the decrease in acuity with eccentricity [52], and computational models show that the decline in mRGC density explains some, but not all, aspects of eccentricity-dependent variation in acuity [53] and contrast sensitivity [54,55].

Eccentricity-dependent organization of early visual cortex

The change in visual performance with eccentricity is linked to cortical magnification in early visual cortex (V1–V3) [36,56]. The fovea is over-represented (Figure 1A) and has the largest **cortical magnification factor (CMF)**. Early visual cortex dedicates more tissue and neural resources to processing visual information appearing at the center of the visual field (i.e., wherever we are fixating). CMF decreases with eccentricity, thus there is less tissue (and less neural resources) devoted to sampling increasingly peripheral locations. Some, but not all, of the change in magnification with eccentricity is inherited from the eye; the eccentricity-gradient steepness increases from cones, to mRGCs, to V1 neurons [2,6,25,57]. Whereas the density of cones and mRGCs decreases with eccentricity, the density of V1 neurons is approximately uniform across visual

neurons code for location, contrast, orientation, spatial frequency, eye-of-origin, and temporal frequency.

Receptive field: the location in visual space that elicits a response from a visual neuron.

Retinotopic map: visual cortex is organized into multiple discrete retinotopic maps of visual space (i.e., visual field maps) where nearby neurons have receptive fields encoding nearby locations of the retinal image.

Spatial frequency: the number of repeating elements in a pattern (typically a sine wave grating), measured in cycles per degree of visual space.

Temporal frequency: the number of occurrences of repeating image in time, measured in Hz (cycles per second).

Vertical meridian asymmetry (VMA): the percent increase in a value (e.g., sensitivity, density, surface area) between the upper and lower vertical meridians. A perceptual VMA of 25% means that sensitivity is 25% greater along the lower than the upper vertical meridian.

Visual performance: how well an observer performs on a given visual task (e.g., accuracy in an orientation discrimination task).

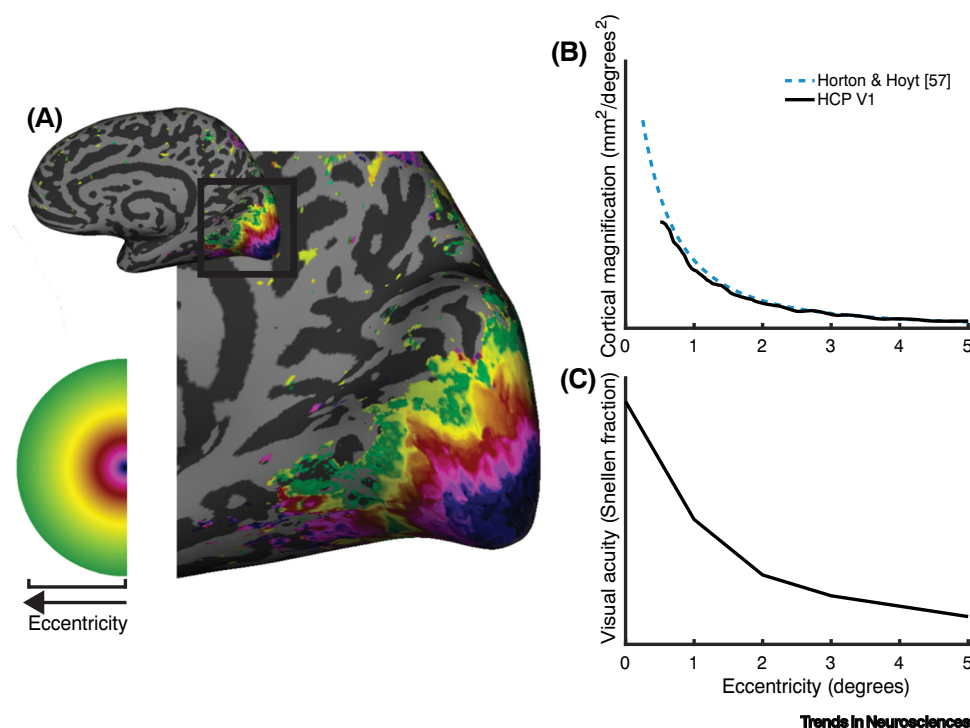


Figure 1. The amount of cortical tissue representing visual space decreases with increasing eccentricity.

(A) Human fMRI retinotopy data showing an eccentricity map projected onto the inflated right hemisphere; more surface samples the fovea (purple) relative to the periphery (green). Thus, there is an over-representation of the center of the visual field in early visual cortex (V1, V2, and V3). (B) The change in surface area as a function of eccentricity can be quantified via the cortical magnification function (CMF) – the amount of cortical surface (mm²) representing 1° of visual space. The blue broken line shows the CMF prediction made by Horton and Hoyt [57] based on cortical lesion data. Surface area is greatest near the fovea and steeply decreases with eccentricity. The black line shows the median CMF derived from the Human Connectome Project (HCP) fMRI retinotopy dataset [4] which closely follows the predicted CMF from Horton and Hoyt [57]. This line starts at 0.5° because foveal fMRI data tend to be noisy. The HCP V1 data in panel B are replotted from [64]. (C) Studies of acuity show that it is greatest at the fovea and decreases with eccentricity. Data plotted are a cartoon to show the general pattern of results. Abbreviations: V1/2, primary/secondary visual cortex; V3, visual area 3.

space [58,59]. Therefore, the decline in V1 tissue with eccentricity reflects a decrease in neural count rather than a decrease in density.

In vivo measurements of early visual cortex, conducted in non-human primates, show that CMF is greatest at the fovea and decreases with eccentricity (e.g., [56,60–63]). In contrast, receptive field sizes are smallest at the fovea and increase with eccentricity [60].

The advent of fMRI has enabled similar measurements in human visual cortex. In V1, secondary visual cortex (V2), and visual area 3 (V3), CMF decreases (Figure 1B) [23,64–66] and **population receptive field (pRF)** size increases with eccentricity [4,67]; thus, these properties are negatively correlated [68]. Moreover, studies on the visual cortex of infants [69] and children [23,70], as well as of newborn non-human primates [71], have revealed adult-like fMRI measurements of neural properties that vary with eccentricity – pRF size, spatial frequency sensitivity, and cortical magnification. This early maturity suggests that a cortical blueprint underlies the retinotopic organization of eccentricity [71,72], at least in early visual cortex.

Neural properties of V1 vary with eccentricity in a way that predicts many aspects of perception. Electrophysiological recordings in macaque [73,74] and fMRI in humans [75,76] show that the spatial frequency preference in V1 decreases with eccentricity. These findings, alongside decreasing CMF and increasing receptive field sizes, parallel the decrease in perceptual spatial resolution with eccentricity (Figure 1C). Individual fMRI measurements of V1 cortical magnification correlate with Vernier acuity thresholds measured as a function of eccentricity [77], suggesting that Vernier acuity is limited by cortical magnification. Further, fMRI measurements of temporal sensitivity show that peripheral voxels prefer higher temporal frequencies [78,79], in accordance with perceptual measurements.

The eccentricity representation of higher-order visual field maps varies substantially with map selectivity. For example, human fMRI studies show that maps processing faces and words have a large fraction of their surface area representing the fovea, with little representation of the periphery; this physiological organization is presumably related to the tendency to foveate faces and words [70,80,81]. Conversely, peripherally presented stimuli drive stronger blood oxygen level-dependent (BOLD) responses in scene-selective maps [80], likely because accurate scene processing is driven by peripheral (rather than foveal) visual information. **Moreover, in the V6 map, which is involved with the perception of egocentric motion, foveal magnification is only slightly larger than that of the periphery; and thus the entire visual field is similarly represented** [82,83]. Overall, the eccentricity representation of higher-order maps does not simply follow the same gradient as V1 but is instead linked to the type of visual information that these maps encode.

Polar angle effects around the visual field

Polar angle asymmetries in visual perception

Perceptual variation with eccentricity and its relation to retinal and cortical organization has been well established but is typically considered without regard to polar angle. Perceptual measurements at different eccentricities are usually made along a single meridian – typically the horizontal – perhaps under the assumption that results will hold over other meridians. However, this is not the case: vision dramatically changes with polar angle.

Early work shows that in humans the gradient decline in contrast sensitivity with eccentricity is steeper along the vertical than the horizontal meridian [36,84,85]. However, differences between the vertical and horizontal meridians were not quantified in these early studies. It is now known that visual performance is better for stimuli presented along the horizontal than the vertical

meridian [**horizontal-vertical anisotropy (HVA)**] and along the lower than the upper vertical meridian [**vertical meridian asymmetry (VMA)**] of the visual field (Figure 2A). These perceptual polar angle asymmetries are pervasive: they have been identified in detection, discrimination, and/or localization tasks involving fundamental visual dimensions (Figure 2B) such as contrast sensitivity [7,10,17,18,33,86,87], contrast appearance [88], orientation [7,8,17,18,88,89], acuity [9,11,13,90–92], crowding [11,93], texture segmentation [94], motion perception [95–97], and hue discrimination [98]. Further, they exist for complex dimensions such as illusory contours [99], the line motion illusion [95], speed of information accrual [45], letter recognition [16,100], numerosity processing [14], visual short-term memory [101], face identification [102] and perception [103–105],

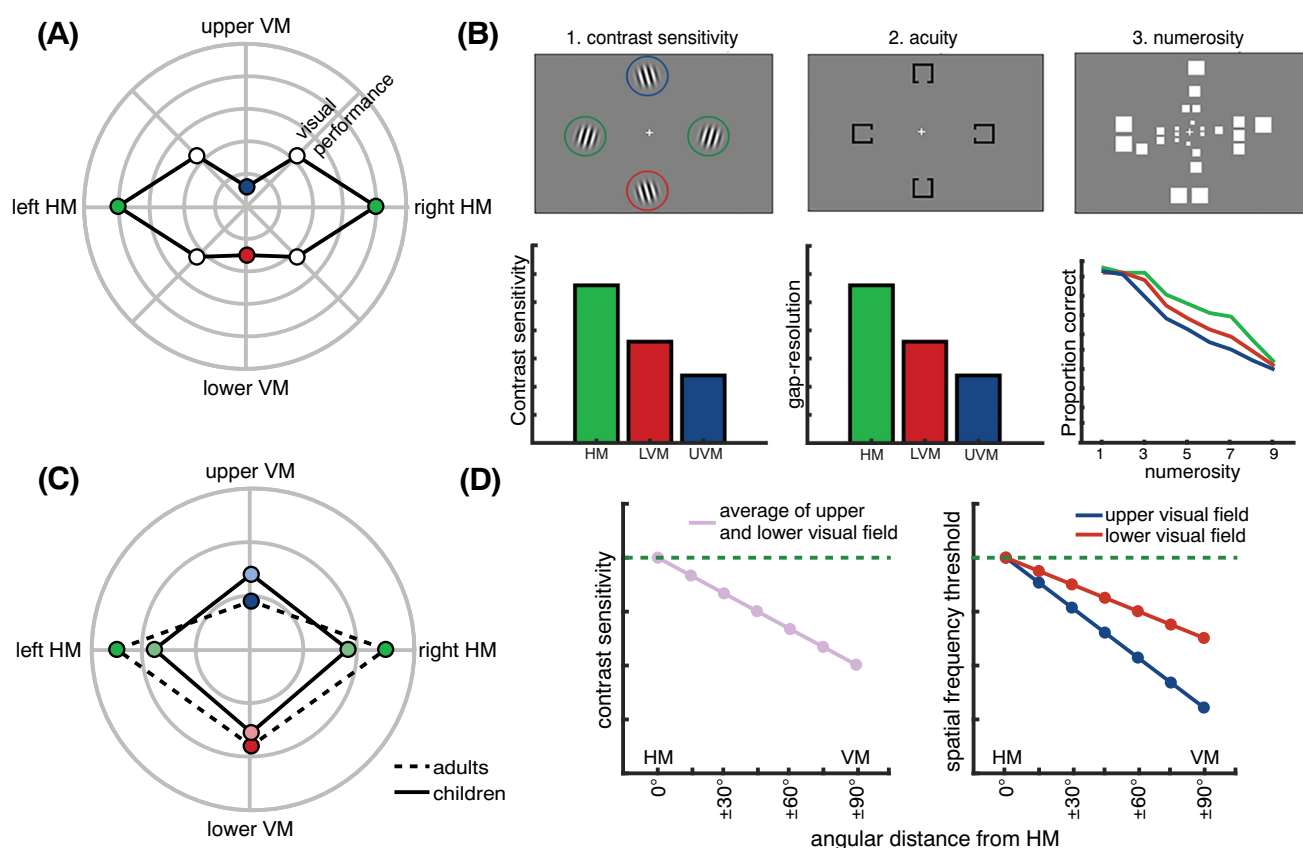


Figure 2. Polar angle asymmetries in visual perception. (A) In the schematic, points that are more eccentric from the center of the polar plot represent higher performance. Visual performance is best along the horizontal meridian, intermediate and similar at the intercardinal meridians, lower along the lower vertical meridian, and poorest along the upper vertical meridian. Adapted, with permission, from [8]. (B) Depiction of psychophysical tasks measuring polar angle asymmetries in (1) contrast sensitivity [7]: an observer is presented with an orientated Gabor patch at one of the four polar angle meridians and responds as to whether the Gabor was tilted left or right from vertical. The contrast of the Gabor is titrated using a staircase procedure until a contrast sensitivity (1/threshold) is found for each polar angle location. The colored circles used in the depiction indicate location and are for visualization, they are not presented during the experiment. (2) Acuity [11]: an observer is presented with a Landolt-C (size and gap titrated via a staircase) to measure gap resolution thresholds – the highest spatial scale at which stimulus differences (gap location) are visible. (3) Numerosity [14]: an observer is presented with white squares (1–9 squares) along one of the four polar angle meridians and enumeration accuracy is measured. (C) Perceptual asymmetries differ between adults (broken lines) and children (unbroken lines). Both display a horizontal-vertical anisotropy (HVA), whereas only adults have a vertical meridian asymmetry (VMA). Children have no VMA; their performance is similar at the lower and upper vertical meridians [109]. (D) Contrast sensitivity [18] and spatial frequency thresholds [9] decrease with increasing angular distance from the horizontal meridian, indicating that polar angle asymmetries are strongest at the meridians themselves rather than being hemifield effects. The green broken line indicates the measurement at the horizontal meridian. For all four panels, plots are cartoons showing the general pattern of results in these studies, several of which contained multiple conditions. Abbreviations: HM, horizontal meridian; LVM, lower vertical meridian; UVM, upper vertical meridian; VM, vertical meridian.

bistable image perception [106], perceived position [92] and size [15,92], and judgments of temporal order in distractor environments [107]. Evidence for polar angle asymmetries for basic visual dimensions and complex cognitive processes gives rise to the question – are asymmetries in higher-order function inherited from the low-level asymmetries? We return to this point later.

The magnitude of polar angle asymmetries varies with other stimulus properties. The magnitude of the HVA is large, similar to doubling [7,8] or even tripling [108] that of eccentricity. The magnitude of the VMA is typically smaller than that of the HVA [7] but can become similarly pronounced under some stimulus conditions [109]. Increasing stimulus spatial frequency exacerbates the magnitude of the HVA and VMA (i.e., visual performance becomes poorer along the vertical relative to the horizontal, and the upper relative to the lower vertical meridian) [7,8,17]. The few studies that have compared polar angle locations at more than one eccentricity show that increasing eccentricity exacerbates the HVA and VMA for measurements of acuity [11,90], crowding [11], apparent contrast [88], and contrast sensitivity [8,108], and this exacerbation is more pronounced for high spatial frequency stimuli [8]. However, for contrast sensitivity at intermediate spatial frequencies, the asymmetries increase slightly with eccentricity at $<10^\circ$ and more so at $>10^\circ$ [7,10]. Thus, comprehensive understanding of the visual field requires both that eccentricity measurements are made at multiple polar angles, and that polar angle measurements are made at multiple eccentricities (see [Outstanding questions](#)).

The asymmetries are ubiquitous across conditions used in psychophysical experiments; they persist across multiple types of attention ([Box 1](#)), whether measured binocularly or monocularly [8,9], across various luminance levels [8], when stimuli are masked or unmasked [90], when the target location is known or unknown [8,9,18,89], when the target is presented alone or with distractors [8,89,107], and regardless of stimulus orientation and tilt angle [8–10,89,110] and head orientation [110]. The asymmetries are retinotopic: when observers rotate their head the asymmetries shift in line with the stimulus retinal location – rather than with its location in space [110]. The prevalence of the asymmetries across so many conditions suggests that they are hard-wired into the visual system.

Polar angle asymmetries are most pronounced at the cardinal meridians and gradually weaken with increasing distance [9,18], often resulting in similar perception at intercardinal locations [8–10,18,94,100,110] ([Figure 2D](#)). Some studies have reported perceptual advantages for the lower over the upper visual hemifield, but it should be noted that, in most cases, stimuli were presented only along the upper and lower vertical meridians [98,99,107,111–117], and interpreting the findings in terms of perceptual differences across the upper and lower hemifields begs caution and further testing. Conversely, some studies presenting stimuli covering the upper or lower hemifield report a lower visual hemifield advantage [91,99,112,118,119], but this advantage may be specifically driven by the lower vertical meridian.

Polar angle asymmetries differ between children and adults ([Figure 2C](#)). Similar to adults, children have an HVA, but unlike adults they have no VMA. Instead, perception in children is similar between the lower and upper vertical meridians [109]. This difference during development might reflect the fact that a VMA would be particularly detrimental for children whose height places many behaviorally relevant aspects of their visual world in the upper visual field [109] (see [Outstanding questions](#)). In agreement with this interpretation, the VMA emerges during adolescence [120] as children grow taller. However, the asymmetries are driven by the meridians, and the VMA magnitude does not correlate with height [120].

Finally, in addition to visual performance varying systematically with polar angle, there are also idiosyncratic variations in performance. For example, for a given observer, an approximately gender-neutral

Box 1. Attention does not alleviate perceptual asymmetries

Attention improves performance for many basic and high-level visual tasks (reviewed in [135–139]). In principle, attentional benefits could differ with visual field location; for example, they could be more pronounced at locations where performance is poor (the upper vertical meridian) than at locations where performance is better (the horizontal meridian). A handful of studies have assessed whether attention preserves, alleviates, or exacerbates the polar angle asymmetries. Spatial endogenous (voluntary) and exogenous (involuntary) **covert attention** [8,17,18,89,94,140,141] and temporal covert attention [142] uniformly boost perceptual measurements (i.e., orientation discrimination, contrast sensitivity, texture segmentation) at the four polar angle meridians (Figure 1), thereby preserving the asymmetries. However, an exception is the effect of exogenous attention on the speed of information accrual, which is faster along the horizontal than the vertical meridian, and along the lower than the upper vertical meridian. Attention accelerates the speed of information accrual more at the upper than the lower vertical meridian, and the least along the horizontal meridian, providing a compensatory effect [45]. Another type of attention, **presaccadic attention**, boosts contrast sensitivity at the horizontal and lower vertical meridians, but not at the upper vertical meridian [12], thereby exacerbating the asymmetries. This finding specifically reflects a lack of response gain – that typically underlies presaccadic benefits to contrast sensitivity [143] – at the upper vertical meridian [144]. However, when stimuli are presented at high contrast, presaccadic attention uniformly boosts acuity at all cardinal meridians, including the upper vertical meridian [13]. This difference between contrast sensitivity and acuity is likely due to the dynamic range of the contrast sensitivity function at which acuity is measured. In short, neither covert attention nor presaccadic attention eliminates or attenuates the spatial perceptual asymmetries, suggesting that they may be resilient to other cognitive processes. The uniform benefit of attention on discriminability across the four polar angle meridians, and the finding that no type of attention alleviates the asymmetries, suggests that the intrinsic perceptual limitations for basic dimensions are rigid and cannot be mitigated. Asymmetries in higher-order dimensions might be inherited from these low-level dimensions in a ‘bottom-up’ fashion (see Outstanding questions).

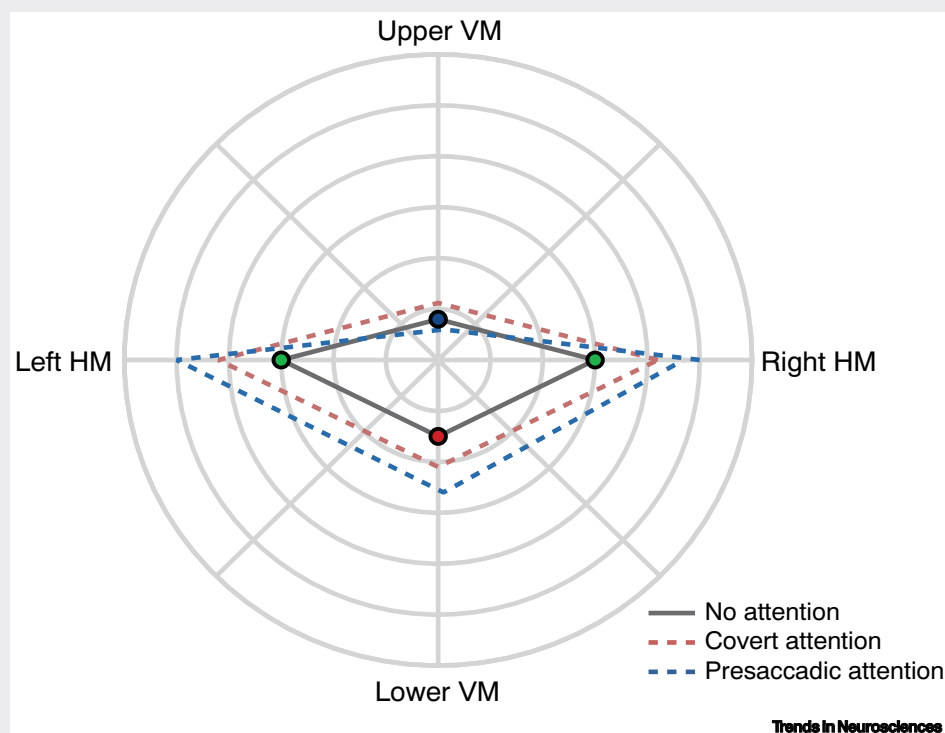


Figure 1. Differential effects of attention on perceptual polar angle asymmetries. Spatial endogenous and exogenous attention [8,17,89,140,141] and temporal attention [142] provide a uniform boost to perception (i.e., orientation discrimination, contrast sensitivity) at each of the polar angle meridians, as shown by the red plot relative to the baseline (gray) plot. Presaccadic attention (broken blue line) similarly provides a uniform boost in performance, but not for the upper vertical meridian [12,144]. Thus, endogenous and exogenous attention preserve polar angle asymmetries in perception, whereas presaccadic attention can increase the asymmetries. The data plotted are cartoons showing the general pattern of results in the aforementioned studies. Abbreviations: HM, horizontal meridian; VM, vertical meridian.

face might be perceived as male when presented in some locations in the visual field and as female in others [121]. Some observers have also been shown to have stereo-motion scotomas at idiosyncratic locations that are spatially consistent over time [122]. These effects differ from polar angle effects in that the locations are unpredictable and vary from person to person.

Polar angle asymmetries in the organization of retina

Work in the early 1990s measuring the density of cones and mRGCs as a function of eccentricity concurrently quantified their density along the cardinal polar angle meridians, confirming that polar angle asymmetries exist in the organization of the retina in humans and monkeys [2,3,47]. Paradoxically, many subsequent perceptual and cortical measurements did not evaluate polar angle asymmetries.

There is an HVA in the density of cones in the human retina: cone density is ~30% greater along the horizontal than the vertical meridian, consistent with up to ~20° eccentricity [2,5]. However, cone density shows no VMA, inconsistent with perception. Instead, there is a slightly greater cone density along the upper than the lower vertical meridian within the central 10° [2,5,47].

There is both an HVA and a VMA in the density of mRGCs. mRGC density is ~40% greater along the horizontal than the vertical meridian, and the asymmetry in density increases with eccentricity [3,6]. Thus, the magnitude of the HVA is amplified from the cones to the mRGCs. mRGC density is ~20% greater along the lower than the upper vertical meridian, reflecting a VMA, and the asymmetry in density again increases with eccentricity [3,6]. The existence of a VMA in the mRGCs, but not in the cones, indicates that the mRGC asymmetries are not simply inherited from prior processing stages.

Although the polar angle asymmetries in cell density are amplified from the cones to the mRGCs, these retinal asymmetries only partially explain the asymmetries seen in perception. A computational observer model based on photon absorptions in the cones – incorporating asymmetries in optics and cone density – accounts for ~10% of the variation in perceptual asymmetries measured psychophysically [24]. Extending this model to include cone phototransduction and mRGC spatial filtering explains more variation, but still only accounts for ~40% of the HVA and ~10% of the VMA measured psychophysically [25]. Thus, neither cone nor mRGC density is the limiting factor for the perceptual asymmetries (see Outstanding questions).

Polar angle asymmetries in the cortical organization of V1

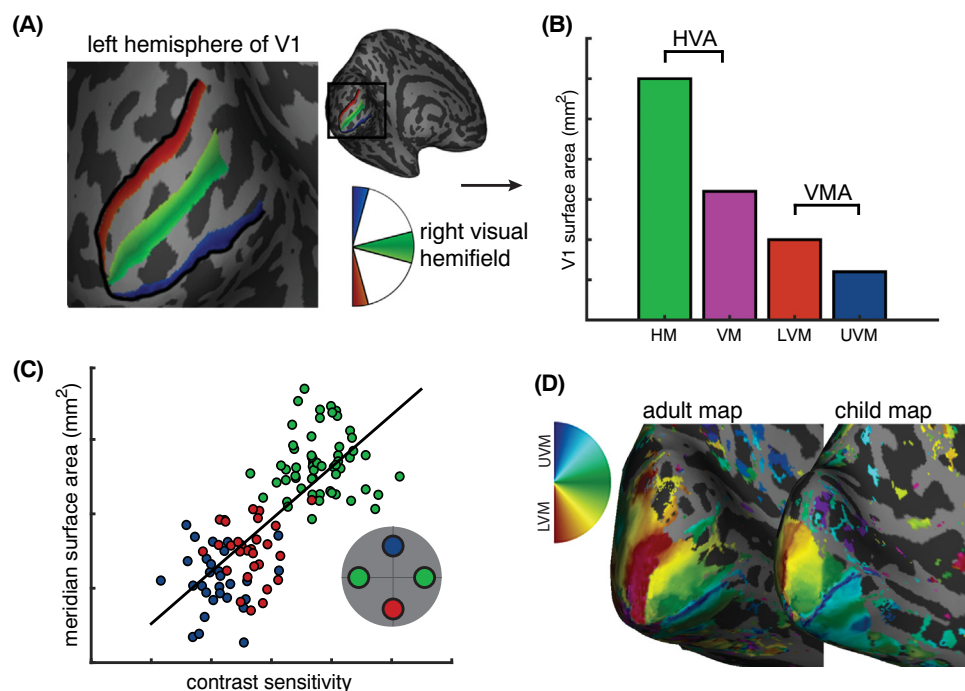
Early measurements of macaque and baboon V1 reported that CMF was independent of the visual field meridians [56], suggesting that cortical tissue might be invariant with polar angle. However, further histological work in non-human primates [60,62] and, more recently, fMRI research in humans [19–23] have revealed an asymmetric distribution of cortical tissue with polar angle that parallels perceptual measurements.

Histological work in macaque shows that there is an HVA and a VMA in the distribution of cortical surface in V1; more tissue is devoted to the horizontal than the vertical meridian, and to the lower than the upper vertical meridian of the visual field [60,62]. However, in squirrel monkey, about the same amount of surface area is devoted to all four meridians [63]. These studies also report that the linear cortical distance from fovea to periphery is ~1.5-fold longer along the V1 vertical than the horizontal meridian [56,62,63].

In humans, fMRI has confirmed the decline in CMF with eccentricity in multiple human datasets over the past 30 years [64–66,68], but only recent studies have investigated whether cortical polar angle asymmetries are present in human V1.

Indeed, fMRI-derived measurements of retinotopic maps of human adults reveal a cortical HVA and VMA; greater V1 surface area represents the horizontal than the vertical meridian, and the lower than the upper vertical meridian of the visual field [19–21] (Figure 3A,B). The strengths of these asymmetries are larger than those in the cones and mRGCs [25], confirming that the mapping of the retina to the cortex is non-uniform for both eccentricity and polar angle. These studies are also the first to report an asymmetry between the upper and lower vertical meridians [19–23] rather than a hemifield asymmetry as described in the earlier primate work [60,62]. Both the cortical HVA and VMA weaken with distance from the respective meridians, to the extent that surface area [21] and BOLD amplitude [123] at the four obliques are similar, in accordance with perception [8–10,18,94,100,110]. Thus, any difference in hemifield surface area must be primarily driven by the cardinal meridians themselves, at least in humans.

Notably, the largest asymmetries stem from the vertical meridian where there are discontinuities in the V1 map. The V1 polar angle representation is most compressed along the vertical meridian,



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Figure 3. Polar angle asymmetries in the organization of human primary visual cortex (V1). (A) The V1 representation of the lower vertical (red), upper vertical (blue), and right horizontal (green) meridians projected onto an inflated cortical mesh. The black lines represent the V1/V2 boundary. Adapted, with permission, from [20]. (B) Measuring V1 surface area for the cardinal meridians (i.e., the amount of tissue within each of the colored masks in panel A) shows that greater surface area (about double) represents the horizontal than the vertical meridian. Further, greater surface area represents the lower than the upper vertical meridian. Plots are cartoons to capture the patterns observed in several studies [19–23]. (C) Individual measurements of V1 surface area correlate with contrast sensitivity measurements localized to the polar angle meridians. Those with greater surface area representing a meridian have greater contrast sensitivity at that meridian relative to someone with less surface area representing the same meridian. Modified, with permission, from [20]. (D) Polar angle maps projected onto the left hemisphere of inflated cortical surfaces for an adult and a child from [23], zoomed in to show the V1 representation of the right visual hemifield (see inset). The adult map has a thick red stripe along the dorsal V1/V2 border, representing the lower vertical meridian, whereas the child map has a thin red stripe, indicating that the cortical representation of the lower vertical meridian is narrower in children. Abbreviations: HM, horizontal meridian; HVA, horizontal-vertical anisotropy; LVM, lower vertical meridian; UVM, upper vertical meridian; VM, vertical meridian; VMA, vertical meridian asymmetry.

where V1 is cleaved into the left and right hemispheres of the cortex [124,125]. It is unclear whether the relation is deeper than coincidental. The polar angle asymmetries originate in the retina, where there is no discontinuity along the vertical meridian [2,47]. Moreover, the cortical VMA cannot be explained by map discontinuities because there is a discontinuity at both the upper and lower vertical meridians. One potential link between map discontinuities and polar angle asymmetries comes from duplicated projections from the eye to the brain: there are more bilateral projections of RGCs to V1 along the lower than the upper vertical meridian [126]. Overall, however, the relation between the perceptual asymmetries and the partitioning of visual cortex into hemifields (V1) and quarterfields (V2, V3) remains largely unknown.

Other V1 properties also change with polar angle. pRF sizes are larger along the vertical than the horizontal meridian [22,23]. These results were interpreted to support a link between pRF size and perceived object size: objects are perceived as smaller along the vertical than the horizontal meridian owing to larger pRFs, resulting in poorer encoding and read-out in higher-order regions [15,92,127]. BOLD amplitude is larger along the horizontal than the vertical meridian [128] and along the lower than the upper vertical meridian [123,129]. These cortical asymmetries have been used to assess the non-neural factors that might contribute to the BOLD response [128,130]. Further, spatial frequency preference is greater for voxels within quadrants centered along the horizontal than the vertical meridian [75,76], and slightly greater for voxels within quadrants centered along the lower than the upper vertical meridian [76]. Were such spatial frequency measurements more finely tailored to the cardinal meridians (rather than quadrants), it is likely that they would be consistent with the finding that perceptual spatial resolution and acuity vary with polar angle [9,11,13,94].

There is substantial variability in the magnitude of the cortical HVA and VMA across observers [20,21], and individual differences have been used to link perceptual asymmetries to cortical asymmetries [20]. Across individuals, those with more V1 surface representing one of the four polar angle meridians have greater contrast sensitivity at that meridian (Figure 3C); moreover, a stronger cortical HVA correlates with a stronger perceptual HVA [20]. These findings suggest that perceptual polar angle asymmetries are largely attributable to the asymmetric distribution of V1 surface area (see Outstanding questions) and support the hypothesis that contrast sensitivity is limited by the pooled activity of V1 neurons [131]. This is not to say that contrast sensitivity is limited by V1 surface area alone; behavioral work shows that additional factors (e.g., different sensory tuning or neuronal computations) may contribute to the perceptual asymmetries [108].

Genetic and developmental factors also contribute to the polar angle asymmetries. Retinotopy data show that the magnitudes of the cortical HVA and VMA are more similar for monozygotic than dizygotic twins [21], indicating that the cortical asymmetries are, in part, heritable. Further, as noted above, children have a perceptual HVA, but no VMA [109]. Comparisons of retinotopic maps from children and adults show that this perceptual difference is reflected in a difference in the distribution of V1 surface area. Children, in accordance with their perception [109], have a cortical HVA but no cortical VMA [23]. The cortical HVA is evident in children as young as 5 years of age, and is likely to be part of a cortical blueprint, similar to the prenatally defined eccentric representation of the visual field [69,71]. However, children do not have a cortical VMA; retinotopic maps show that the adult cortical VMA reflects an increase in the amount of V1 tissue representing the lower vertical meridian [23] (Figure 3D). These results imply that V1 continues to develop through adolescence and into adulthood (see Outstanding questions).

The existence of an HVA, but no VMA, in children demonstrates that the two phenomena are separate entities that develop independently. This is supported by studies showing that (i) the

magnitudes of the HVA in mRGC density [3,6], V1 surface area [19–21,23], and perception [9,12,89] are more pronounced than those of the corresponding VMA; (ii) across individuals, the HVA and VMA magnitudes are uncorrelated for cortical [20] and perceptual [7,9,89] measurements; and (iii) cone density shows an HVA, but no VMA [2,5]. The reasons why the HVA is stronger than the VMA at multiple stages of the visual system remain to be unveiled.

As with the eccentricity representation, the polar angle representation in higher-order maps may differ from that in V1. For example, human fMRI studies have shown that the transverse occipital sulcus (TOS) [132] and lateral occipital (LO) cortex [133] over-represent the lower visual field, whereas parahippocampal place area (PPA) over-represents the upper visual field [132]. These hemifield asymmetries may underlie the organization of lateral and ventral occipitotemporal cortex. To our knowledge, these effects have to date only been investigated at the granularity of hemifields (upper vs. lower). Thus, it is unknown whether these hemifield effects are primarily driven by representations near the cardinal meridians, as in V1 [21] (see Outstanding questions).

In sum, the existence of polar angle asymmetries has been documented in the organization of cones, mRGCs, and V1. The presence of these asymmetries at different stages of the early visual system gives rise to the question of how far up the visual hierarchy they extend. fMRI measurements of polar angle representation in higher-order maps involved with complex vision can be ambiguous, and the angular organization of some maps remains to be confirmed. One possibility is that the perceptual asymmetries observed for higher-order visual dimensions are inherited from signals from early visual field maps, as suggested by work linking visual field differences in perceived object size [15,92,127] and bistable image perception [106] to visual field sampling in V1 (see Outstanding questions).

Concluding remarks

We have reviewed evidence for location-dependent limits in perception that are paralleled by the organization of cones, mRGCs, and V1 tissue, with a focus on polar angle asymmetries. Each subsequent stage of processing explains more of the variability in visual performance around the visual field, and the hard-wiring of these asymmetries into multiple stages of the visual system may underlie their prevalence across many visual dimensions and tasks. These limits have been studied using an array of techniques, in human and non-human primates, and in different age groups. Together, this literature shows that perceptual quality around the visual field is limited by asymmetric neural structures within the visual system.

Perceptual performance can change by 2–3-fold with polar angle, as can the cortical asymmetries [20,108]. However, polar angle asymmetries have been often overlooked by vision scientists. To understand, model, and predict how perception changes with visual field location, it is essential to consider both eccentricity and polar angle, their interaction, and whether these effects vary for different visual dimensions.

At the group level, behavioral, electrophysiological, histological, and neuroimaging studies yield parallel findings regarding polar angle. The variation in perception with polar angle, like eccentricity, is rooted in the organization of the visual system – the density of photoreceptors and mRGCs [2,3,47] and the distribution of neurons in visual cortex [19–23,60,74]. The ubiquitous and resilient nature of the perceptual asymmetries for the basic visual dimensions that have been studied is likely due to the existence of the asymmetries at the early, fundamental stages of visual processing.

These asymmetries provide a way to more directly link brain and behavior. Computational models have assessed the contribution of retinal asymmetries to perception [24,25], and brain–behavior

Outstanding questions

Why are perceptual and cortical polar angle asymmetries strongest at the cardinal meridians rather than occurring as hemifield effects?

What computations underlie the variation in visual performance throughout the visual field?

The perception of dynamic visual dimensions (e.g., flicker, speed) varies with eccentricity; do these dimensions also vary with polar angle?

How steeply does performance change with eccentricity along polar angle locations? Does this differ for different visual dimensions?

Perceptual polar angle asymmetries are found for complex visual dimensions which likely involve visual maps beyond V1. Do cortical asymmetries exist in higher-order maps?

Computational models show that optical and retinal factors only account for a small fraction of the perceptual asymmetries, whereas V1 accounts for much more. If cortical asymmetries were to exist in extrastriate maps, could they provide a better account of the perceptual asymmetries?

Individual differences in localized measurements of V1 surface area and contrast sensitivity taken from the polar angle meridians are correlated. Do other visual properties linked to V1 (e.g., orientation tuning) vary with polar angle? Do these properties also correlate with V1 surface area measurements?

Some properties of the cortical polar angle asymmetries do not quantitatively match perceptual asymmetries (e.g., perceptual HVA in children is half the size of that in adults, but their cortical HVA is the same size as that of adults). Would this discrepancy be resolved if the brain and behavior measures came from the same individuals rather than from separate studies, or are additional neural properties not yet accounted for necessary to fully explain the perceptual asymmetries?

Are there ecological reasons for polar angle asymmetries? Have these

correlations have linked individual differences in cortical surface measurements to perception [20]. Moreover, the striking difference in the vertical meridian between children and adults in perception [109] and the cortical representation [23], and the difference between adolescents and adults in perception [120], implies that V1 continues to develop beyond childhood.

There are many benefits to investigating how visual performance varies with location and the neural substrates of this variation. Characterizing the organization of retinotopic maps brings us closer to understanding how the brain translates visual signals into a neural representation of visual space. This neural representation influences our perception: what we see and what we cannot see, which information we can discern and which we cannot discern, and where we localize visual information precisely and where we cannot. In turn, this representation forms the basis of how we interact with our visual environment. Moreover, quantifying the perceptual heterogeneity throughout the visual field has implications for psychophysical experimental design and the interpretation and generalization of findings in vision science studies. Finally, the ability to predict human performance both across and around the visual field has implications for human factors such as the development and design of real-world displays and interfaces [134] that are an increasingly integral part of our everyday lives.

Acknowledgments

The authors thank Antoine Barbot, Rania Ezzo, Nina Hanning, Hsing-Hao Lee, Ekin Tünçok, and Shutian Xue for their feedback. This work was supported by National Institutes of Health grant ODSS/NEI R01EY027401 to M.C. and J.W.

Declaration of interests

The authors declare no competing interests.

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asymmetries evolved to exist at multiple stages of the visual system as a result of environmental or task demands (if so, what demands?), or are they ingrained properties of the visual system?

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