Visual field asymmetries vary between adolescents and adults

Marisa Carrasco[1,2]*, Caroline Myers[1] and Mariel Roberts[1]

[1] Department of Psychology, New York University, 6 Washington Place, New York, NY 10003, USA.
[2] Center for Neural Science, New York University, 4 Washington Place, New York, NY 10003, USA.

* Correspondence: marisa.carrasco@nyu.edu

ABSTRACT

For human adults, visual perception varies around isoeccentric locations (with polar angle at a constant distance from the center of gaze). The same visual information yields better performance along the horizontal than vertical meridian (horizontal vertical anisotropy, HVA) and along the lower than upper vertical meridian (vertical meridian asymmetry, VMA). For children, performance is better along the horizontal than vertical meridian (HVA) but does not differ between the lower and the upper vertical meridian. Here, we investigated whether the extent of the HVA varies and the VMA emerges and fully develops during adolescence, or whether the VMA only emerges in adulthood. We found that for adolescents, performance yields both HVA and VMA, but both are less pronounced than those for adults.

Visual perception in human adults varies throughout the visual field. It decreases across eccentricity –distance from the center of gaze– and changes around isoeccentric locations –with polar angle at a constant distance from the center of gaze. The same visual information yields better performance along the horizontal than vertical meridian (horizontal–vertical anisotropy, HVA) and along the lower than upper vertical meridian (vertical–meridian asymmetry, VMA). In adults, these perceptual polar angle asymmetries, and their retinal and cortical correlates, are well characterized (review **[1]**).

For adults, polar angle asymmetries are pervasive; they are present when stimuli are viewed monocularly or binocularly, for basic (e.g., acuity and contrast sensitivity), mid-level (e.g. texture segmentation), and higher-order (e.g., face perception) dimensions, and across stimulus properties (e.g., luminance, contrast, orientation, size, spatial frequency). These asymmetries become more pronounced as spatial frequency and eccentricity increase and when the target appears amidst distractors **[1]**. Optical quality and retinal factors (e.g., cone density and midget retinal ganglion cell density) account for a small percentage of the perceptual asymmetries **[2]**. These asymmetries are better accounted for by the distribution of cortical surface area in primary visual cortex (V1), which is larger for the horizontal than vertical meridian, as well as for the lower than upper vertical meridian **[3,4]**. Moreover, individual differences in contrast sensitivity at each of the cardinal meridians correlate with localized measures of the amount of V1 surface representing the same meridians **[5]**.

For children, visual performance yields an HVA, albeit less pronounced than that for adults, but not a VMA **[6]**. Correspondingly, children's cortical surface is larger for the horizontal than the vertical meridian but is similar for the upper and lower vertical meridian **[7]**.

Here, we investigated whether the extent of the HVA varies and the VMA emerges and fully develops during adolescence, or whether the VMA only emerges in adulthood.

Adolescents aged 12–17 years (n=128) and adults (n=112) performed an orientation discrimination task. A stimulus appeared briefly (~100 ms) at one of four isoeccentric locations (left- or right- horizontal meridian or upper or lower vertical meridian). Participants indicated whether the stimulus was tilted right or left from vertical, via key press (**Figure S1**). Performance (d') was calculated at each location according to signal detection theory.

Adolescents' performance revealed both an HVA and a VMA, as did adults' performance (**Figure 1A**). The HVA was more pronounced for adults than adolescents (**Figure 1C**). A 2X2 (age X location) analysis of variance (ANOVA) revealed an interaction ($F_{(1,238)}$=48.9, p<0.0001). The superior performance on the horizontal than vertical meridian was more pronounced for adults ($F_{(1,111)}$=142.89, p<0.0001) than adolescents ($F_{(1,127)}$=7.14, p<0.01).

The difference in the HVA magnitude between adolescents and adults is demonstrated when comparing the HVA ratios (Horizontal–Vertical)/(Horizontal+Vertical); $F_{(1,238)}$=60.37, p<0.0001) for both groups (**Figure 1D**).

The VMA differed between age groups (**Figure 1A**): a 2X2 (age x location) ANOVA revealed an interaction ($F_{(1,238)}$=15.65, p=0.0001). The superior performance on the lower than upper vertical meridian was more pronounced for adults ($F_{(1,111)}$=60.82, p<0.0001) than for adolescents ($F_{(1,127)}$=10.41, p 0.002) (**Figure 1C**).

The VMA age difference is illustrated in the VMA ratios (Lower Vertical – Upper Vertical/Lower Vertical + Upper Vertical) ($F_{(1,238)}$= 29.54, p<0.001) (**Figure 1D**). The HVA and VMA were more consistent across adults than adolescents (**Figure 1E,F**).

We divided the adolescent participants into 'older' (15-17 years, n=65) and 'younger' (12-14 years old, n=63) and analyzed whether the extent of the HVA or the VMA differed between these subgroups; they did not, either for accuracy (HVA: $F_{(1,126)}$=1.12, p>.1; VMA: F<1) or RT (both $Fs_{(1,126)}$<1).

The HVA and VMA were paralleled in response times (**Figure 1B**): For HVA, the age x location interaction ($F_{(1,238)}$=21.81, p<.005) resulted from a more pronounced HVA for adults ($F_{(1,111)}$=51.983, p<.001) than for adolescents ($F_{(1,127)}$ =3.584, p=.061). For VMA, the age x location interaction ($F_{(1,238)}$ =4.37, p<.05) resulted from faster RT at the lower than upper vertical meridian for adults ($F_{(1,111)}$=17.79, p<.005) but not for adolescents

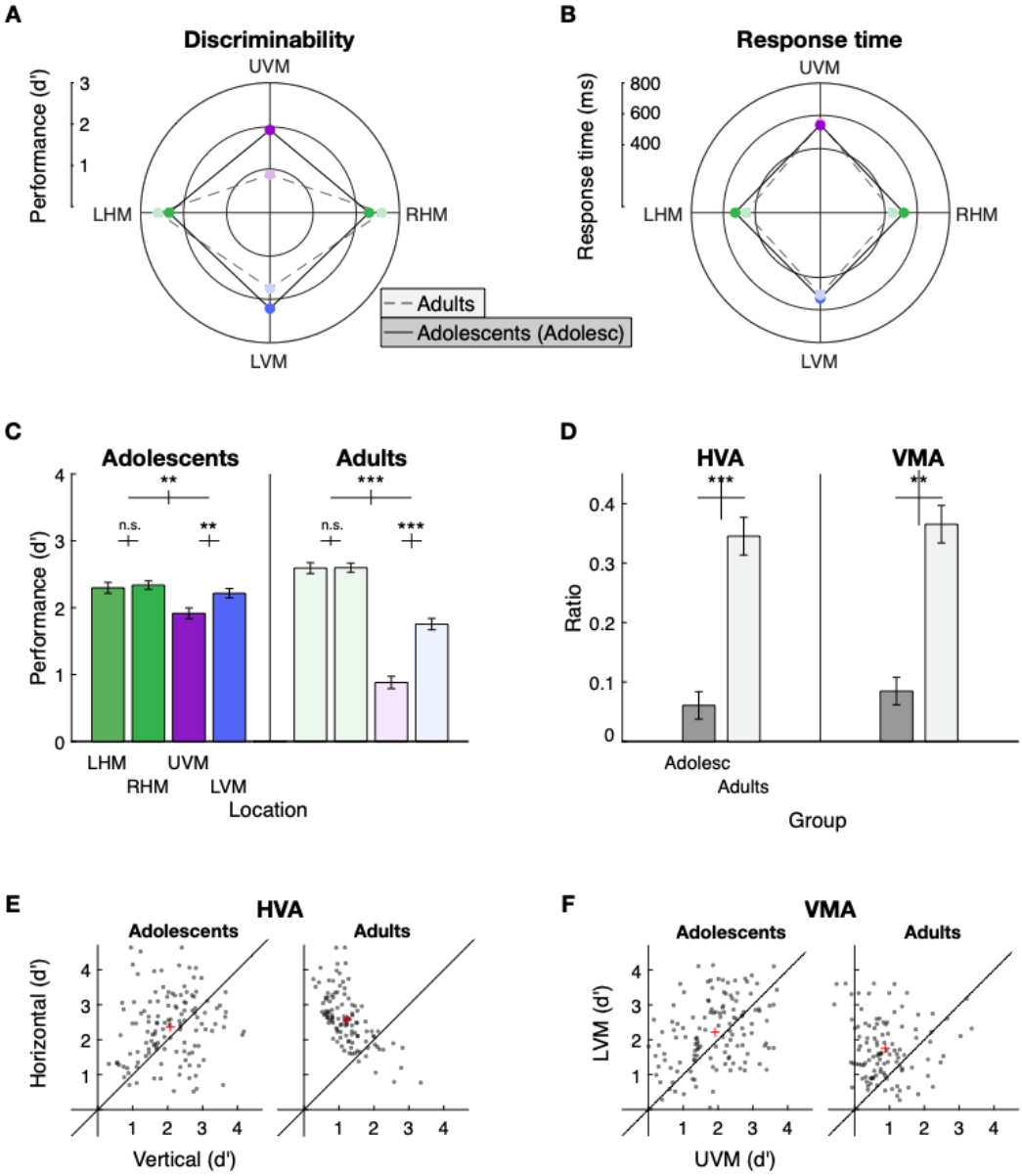

Figure 1. **Polar angle asymmetries differ between adolescents and adults.**

(**A**) Adults' (n=112) and adolescents' (n=128) polar angle asymmetries in visual performance (d'). The target was presented at the four isoeccentric cardinal locations. The center point represents chance performance and each of the four points represents discriminability (d') at those locations. For adults (dashed lines), performance shows the typical asymmetries: (1) horizontal–vertical anisotropy (HVA): better performance along the horizontal than vertical meridian; and (2) vertical–meridian asymmetry (VMA), better performance at the location directly below (LVM) than above (UVM) fixation. For adolescents (solid line), both asymmetries are present, but less pronounced.

(**B**) Adults' and adolescents' polar angle asymmetries in response time (ms). HVA is present in both groups, but more pronounced for adults than adolescents. VMA is present for adults but not for adolescents.
(**C**) Orientation discriminability (d') for each location.
(**D**) Magnitudes of the HVA and VMA ratios for adolescents and adults. HVA ratio indicated averaged performance between the horizontal and vertical meridian, and the VMA ratio between the lower and upper vertical meridian. Values ≥0 reveal better performance along the horizontal than vertical meridian (HVA) and along the lower than upper vertical meridian (VMA).
(**E**) The HVA for each adolescent (left) and adult (right). Data above the diagonal indicate better performance for the horizontal than vertical meridian and vice versa.
(**F**) The VMA for each adolescent (left) and adult (right). Data above the diagonal indicate better performance for the lower than upper vertical meridian and vice versa.
The center of the red cross in (**E**) and (**F**) indicates the mean value for each group. In all panels, error bars = ±1 within-subject SEM. ** = $p < 0.01$, *** = $p < 0.001$.
[data for adults previously published in Carrasco et al. [**6**]].

($F_{(1,127)} = 1.45$, $p > .1$). Thus, there were no speed-accuracy trade-offs in either adolescents or adults.

These systematic differences in visual performance around the visual field between adolescents and adults, and adolescents and children (**Figure S2)**, provide further evidence that some aspects of visual perception and the brain continue to develop throughout adolescence **[8,9]**. We plan to investigate whether the HVA and the emerging VMA in adolescence correspond to the distribution of cortical surface in early visual cortex for those locations.

A comprehensive account of visual development must explain how maturation interacts with environmental input. Asymmetries between the upper and lower hemifields may be related to the observation that the upper and lower visual fields may specialize for processing distant and near objects, respectively **[10]**. In the perceptual world of adults, stimuli for many tasks requiring manual manipulation naturally occur in the lower visual field. For children, in contrast, relevant visual information often appears above eye level, and as adolescents grow, the location where relevant information appears more frequently changes. However, the visual field asymmetries are mainly driven by the cardinal meridians **[1]**, and we found no correlation between height and the extent of the HVA or VMA (**Supplementary Information**).

The characterization of performance around the visual field in children, adolescents and adults is crucial for understanding functional plasticity of the human brain and how human vision develops and adapts to its environment. Consistent with the finding that overall contrast sensitivity continues to develop through adolescence **[9]**, we find that visual asymmetries in contrast sensitivity are still developing.

Supplemental Information

Supplemental information includes two figures, experimental procedures, supplementary analysis, author contributions, acknowledgments, declaration of interests and inclusion and diversity statements.

References

1. Himmelberg, M.M., Winawer, J., and Carrasco, M. (revised and resubmitted). Polar angle asymmetries in visual perception and neural architecture. TINS.
2. Kupers, E.R., Benson, N.C., Carrasco, M., and Winawer, J. (2022). Asymmetries around the visual field: From retina to cortex to behavior. PloS Comput. Biol., *18*, e1009771.
3. Benson, N.C., Kupers, E.R., Barbot, A., Carrasco, M., and Winawer, J. (2021). Cortical magnification in human visual cortex parallels task performance around the visual field. eLife, *10*, e67685.
4. Silva, M.F., Brascamp, J., Ferrerira, S., Castelo-Branco, M., Dumolin, S. and Harvery, B.M. (2018) Radial asymmetries in population receptive field size and cortical magnification factor in early visual cortex. Neuroimage, *167*, 41–52.
5. Himmelberg, M.M., Winawer, J., and Carrasco, M. (2022). Linking contrast sensitivity to cortical magnification in human primary visual cortex. Nat. Commun., *13*, 330.
6. Carrasco, M., Roberts, M., Myers, C., and Shukla, L. (2022) Visual field asymmetries vary between children and adults. Curr Bio, *32*(11): 509-510.
7. Himmelberg, M.M., Tünçok, E., Gomez, J., Grill-Spector, K., Carrasco, M. and Winawer, J. (in press). Comparing retinotopic maps of children and adults reveals a late-stage change in how V1 samples the visual field. Nat. Commun.
8. Toga, A.W., Thompson, P.M. and Sowel, E.R. (2006). Mapping brain maturation. TINS, *29*(3): 148-159.
9. Benedek, K., Janáky, M., Braunitzer, G., Rokszin, A., Kéri, S., and Benedek, G. (2010). Parallel development of contour integration and visual contrast sensitivity at low spatial frequencies. Neurosci. Lett. *472*, 175–178.
10. Previc, F.H. (1990). Functional specialization in the lower and upper visual fields in humans: Its ecological origins and neurophysiological implications. Behav. Brain Sci,. *13*, 519-542.

SUPPLEMENTARY

Supplemental Experimental Procedures

Observers. Two groups of observers participated in this study: 128 adolescents, 12-17 year-olds (median age = 15, mean = 15.01, sd = 1.41; 96 females, 32 males) and 112 adults (median age = 23.79, mean = 28.16, sd = 11.43; 76 females, 32 males, 4 unreported). [The data for adults have been previously reported in Carrasco et al.[S1]. All participants were recruited from New York City. The adults were undergraduate or graduate students at New York University and other New York City residents. The ethics committee of New York University approved the study.

Stimuli. Observers viewed a computer display from a distance of 57 cm on a 21-in. IBM P260 CRT monitor (1,280 x 960 pixel resolution, 90-Hz refresh rate), calibrated and linearized using a Photo Research (Chatworth, CA, USA) PR-650 SpectraScan Colorimeter. Viewing distance was maintained with a chin-and-forehead rest. On each trial, following either a 500-ms fixation point, a target stimulus appeared in one 4 isoeccentric locations centered at 6.2° eccentricity for 80-120 ms [**Figure S1**]. The stimulus was a 4 (80%) or 6 (20%) cycles/degree Gabor patch (a sinusoidal grating embedded in a Gaussian envelope), appearing by itself (41%) or amidst 3 distractors (59%), subtending 2º (23%), 3.2º (59.5%) or 4º (17.5%) of visual angle, oriented 20º (40%) or 30º (60%) from vertical. Previous studies with adults have revealed polar angle asymmetries with all these stimulus parameters[S1-11]. The stimulus contrast was ~25% for adults and ~30% for adolescents, adjusted individually before the experiment through an up-down staircase, to yield ~80% performance accuracy across all locations.

Procedure. The experiment took place in a darkened and sound attenuated room to provide optimal viewing of the displayed stimuli. Observers viewed the display binocularly. We used a 2-alternative forced-choice orientation discrimination task; performance in this task is contingent upon the observers' contrast sensitivity and has been used to characterize performance at different locations[S5-9, S11-15]. The experimenter instructed observers to fixate on a central fixation point throughout each trial and to indicate whether the stimulus was tilted right (clockwise) or left (counterclockwise) from vertical with a keypress. A feedback tone indicated whether the response had been correct or incorrect after each trial. Instructions stressed accuracy, and there was no time pressure. Each observer performed 1-2 practice block(s) of 40 trials each, and on average, adults performed 77 and adolescents 45 trials per location.

Observers' eyes were tracked to ensure that they maintained fixation throughout the trial using an EyeLink 1000 Desktop Mount eyetracker (SR Research, Ontario,

Canada). If observers broke fixation, the trial would be not counted or aborted and replaced at the end of the block, to ensure that stimulus locations and retinal locations were equated.

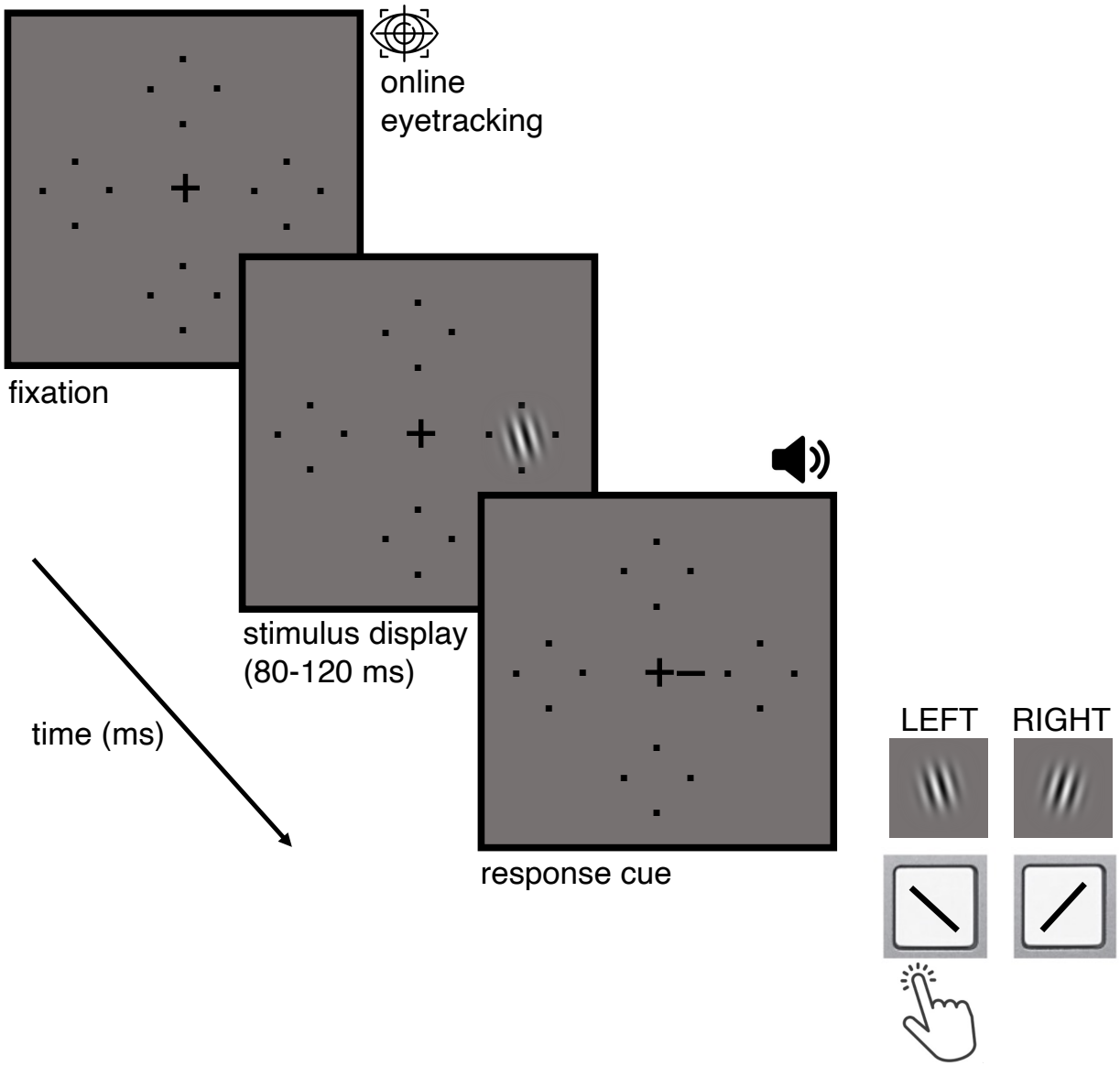

Figure S1. Experimental trial: orientation discrimination task.
Observers fixated at the plus sign in the center of the display. Stimuli were briefly presented at 4 isoeccentric locations. A response cue indicated the target location, and observers reported its orientation (left vs. right) with a key press. Observers' eyes were tracked to ensure stable fixation. A feedback tone indicated whether the response was correct or incorrect.

Analysis.

Discriminability, d' = z(hit rate) minus z(false-alarm rate), was computed for each observer. A hit was (arbitrarily) defined as a left response to a left orientation and a false alarm as a left response to a right orientation[S11, S16-18]. The log-linear rule correction was applied while estimating d'[S19,20]. Response time (ms) was recorded from stimulus onset until participant's key press. This secondary dependent variable enabled us to assess any speed-accuracy tradeoff. We calculated the geometric mean for each participant.

For gender analyses, half of the adult participants whose gender was unreported (n=4) were randomly coded as females.

Supplementary Results

In all analyses presented, we collapsed across stimulus parameters, as there was no significant difference in the magnitude of the HVA and VMA for the different stimulus parameters for adults or adolescents. There were no significant interactions for the HVA. When there was a significant interaction for the VMA, it was due to the VMA being more pronounced for higher SF for both groups, $F_{(1,236)}=15.22$, $p=.0001$. This finding is consistent with previous studies[S5,9].

For the HVA, there were neither differences between the left and right locations of the horizontal meridian for adolescents or adults, nor an interaction with age ($Fs<1$). There was neither a gender effect nor an interaction of gender with age ($Fs<1$).

For the VMA, we analyzed differences between females and males and found neither a gender effect ($F<1$) nor an interaction with age ($F_{(1,236)}=2.04$, $p>1$).

We correlated the extent of the VMA and participants' heights and found no significant effect either for adolescents ($r(126)=0.115$, $p>0.1$), adults ($r(110) = -0.034$, $p>.1$), or for all participants taken together ($r(238) = -0.111$, $p=0.085$).

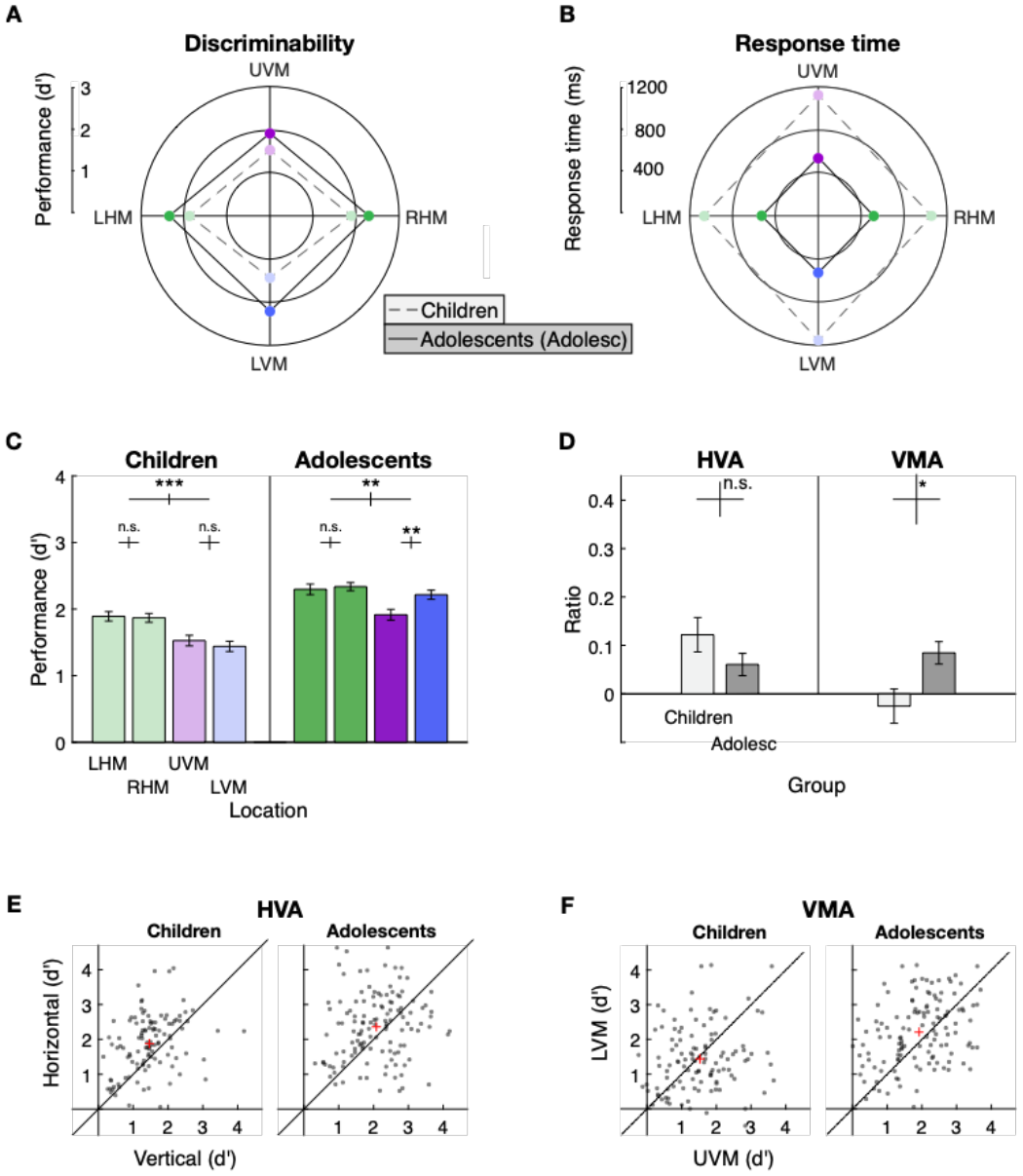

Figure S2. **Polar angle asymmetries differ between children and adolescents.**
(**A**) Children's and adolescents' polar angle asymmetries in visual performance (d'). Children's data correspond to those reported in Carrasco et al., 2022 (5-12 year-olds, mean age = 9.49). For children the HVA emerged but not the VMA. For adolescents (solid line), both asymmetries are present; (1) horizontal–vertical anisotropy (HVA) and (2) vertical–meridian asymmetry (VMA).
(**B**) Children's and adolescents' polar angle asymmetries in response time (ms). HVA is present in both groups.
(**C**) Orientation discriminability (d') for each location.

(**D**) Magnitudes of the HVA and VMA ratios for children and adults. HVA ratio indicated averaged performance between the horizontal and vertical meridian, and the VMA ratio between the lower and upper vertical meridian. Values ≥0 reveal better performance along the horizontal than vertical meridian (HVA) and along the lower than upper vertical meridian (VMA.
(**E**) The HVA for each child (left) and adolescent (right). Data above the diagonal indicate better performance for the horizontal than vertical meridian and vice versa.
(**F**) The VMA for each child (left) and adolescent (right). Data above the diagonal indicate better performance for the lower than upper vertical meridian and vice versa. The center of the red cross in (**E**) and (**F**) indicates the mean value for each group. In all panels, error bars = ±1 within-subject SEM. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.
[data for children previously published in Carrasco et al.[S1]].

Author Contributions
MC conceptualized the study, acquired the funding, and supervised and administered the study. CM and MR collected the data. CM analyzed the data and created the figures. MC wrote the original draft. All authors reviewed and edited the manuscript and reviewed the figures.

Acknowledgments
NIH Grant ODSS/NEI RO1 EY027401 to MC supported this research. We thank the participants in this study, members of the Carrasco Lab for assistance with subject recruitment, data collection and for helpful comments.

Declaration of interests. The authors declare no competing interests.

Inclusion and diversity statements. We worked to ensure gender balance and ethnic diversity in the recruitment of human subjects. While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list.

Supplemental References

S1. Carrasco, M., Roberts, M., Myers, C., and Shukla, L. (2022) Visual field asymmetries vary between children and adults. Curr Bio, *32*(11): 509-510.

S2. Rovamo, S1. Rovamo, J., and Virsu, V. (1979). An estimation and application of the human cortical magnification factor. Exp. Brain Res. *37*, 495-510.

S3. Rijsdijk, J., Kroon, J., and Van der Wildt, G. (1980). Contrast sensitivity as a function of position on the retina. Vision Res. *20*, 235-241.

S4. Pointer, J., and Hess, R. (1989). The contrast sensitivity gradient across the human visual field: With emphasis on the low spatial frequency range. Vision Res. *29*, 1133-1151.

S5. Carrasco, M., Talgar, C., and Cameron, E.L. (2001). Characterizing visual performance fields: effects of transient covert attention, spatial frequency, eccentricity, task and set size. Spatial Vis. *15*, 61-75.

S6. Cameron, E.L., Tai, J.C., and Carrasco, M. (2002). Covert attention affects the psychometric function of contrast sensitivity. Vision Res. *42*, 949-967.

S7. 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.

S8. Roberts, M., Ashinoff, B.K., Castellanos, F.X., and Carrasco, M. (2018). When attention is intact in adults with ADHD. Psychon. B. Rev. *25*, 1423-1434.

S9. Himmelberg, M.M., Winawer, J., and Carrasco, M. (2020). Stimulus-dependent contrast sensitivity asymmetries around the visual field. J. Vis. *20*, 18-18.

S10. Barbot, A., Xue, S., and Carrasco, M. (2021). Asymmetries in visual acuity around the visual field. J. Vis. *21*, 2-2.

S11. Purokayastha, S., Roberts, M., and Carrasco, M. (2021). Voluntary attention improves performance similarly around the visual field. Atten. Percept. Psychophys. *83*, 2784-2794.

S12. Skottun, B.C., Bradley, A., Sclar, G., Ohzawa, I., and Freeman, R.D. (1987). The effects of contrast on visual orientation and spatial frequency discrimination: a comparison of single cells and behavior. J. Neurophysiol. *57*, 773-786.

S13. Tomassini, A., Spinelli, D., Jacono, M., Sandini, G., and Morrone, M.C. (2015). Rhythmic oscillations of visual contrast sensitivity synchronized with action. J. Neurosci. *35*, 7019-7029.

S14. White, A.L., Boynton, G.M., and Yeatman, J.D. (2019). The link between reading ability and visual spatial attention across development. Cortex *121*, 44-59.

S15. Ramirez, L.D., Foster, J.J., and Ling, S. (2021). Temporal attention selectively enhances target features. J. Vis. *21*, 6-6.

S16. Hanning, N.M., Deubel, H., and Szinte, M. (2019). Sensitivity measures of visuospatial attention. J. Vis. *19*, 17-17.

S17. Szinte, M., Jonikaitis, D., Rangelov, D., and Deubel, H. (2018). Pre-saccadic remapping relies on dynamics of spatial attention. eLife *7*, e37598.

S18. Jigo, M., and Carrasco, M. (2020). Differential impact of exogenous and endogenous attention on the contrast sensitivity function across eccentricity. J. Vis. *11*, 1-25.

S19. Hautus, M.J. (1995). Corrections for extreme proportions and their biasing effects on estimated values of d′. Behav. Res. Meth. Ins. C. *27*, 46-51.

S20. Brown, G.S., and White, K.G. (2005). The optimal correction for estimating extreme discriminability. Behav. Res. Methods *37*, 436-449.