JNeurosci
THE JOURNAL OF NEUROSCIENCE

Research Articles: Systems/Circuits

Differential sampling of visual space in ventral and dorsal early visual cortex

Edward H. Silson[1], Richard C. Reynolds[2], Dwight J. Kravitz[3] and Chris I. Baker[1]

[1]*Sectional on Learning & Plasticity, Laboratory of Brain & Cognition, National Institute of Mental Health, Bethesda, MD, USA.*

[2]*Scientific and Statistical Computing Core, National Institute of Mental Health, Bethesda, MD, USA.*

[3]*Department of Psychology, The George Washington University, 2125 G St, NW, Washington DC 20052, USA.*

DOI: 10.1523/JNEUROSCI.2717-17.2018

Received: 20 September 2017

Revised: 8 January 2018

Accepted: 11 January 2018

Published: 30 January 2018

Author Contributions: E.H.S jointly designed the study, acquired and analyzed the neuroimaging data and wrote the manuscript. R.C.R designed the elliptical and circular pRF models in AFNI and analyzed the neuroimaging data. D.J.K jointly designed the study, analyzed the neuroimaging data and wrote the manuscript. C.I.B jointly designed the study and wrote the manuscript.

Conflict of Interest: The authors declare no competing financial interests.

We thank Iris Groen, Martin Hebert, Eli Merriam, Alexis Kidder and members of the Section on Learning and Plasticity for helpful comments on earlier versions of the manuscript.

Cite as: J. Neurosci ; 10.1523/JNEUROSCI.2717-17.2018

Differential sampling of visual space in ventral and dorsal early visual cortex

Edward H. Silson[1], Richard C. Reynolds[2], Dwight J. Kravitz[3]* & Chris I. Baker[1]*

1. Sectional on Learning & Plasticity, Laboratory of Brain & Cognition, National Institute of Mental Health, Bethesda, MD, USA.
2. Scientific and Statistical Computing Core, National Institute of Mental Health, Bethesda, MD, USA.
3. Department of Psychology, The George Washington University, 2125 G St, NW, Washington DC 20052, USA.

* Shared senior author.

Corresponding author: ed.silson@nih.gov

Abstract

A fundamental feature of cortical visual processing is the separation of visual processing for the upper and lower visual fields. In early visual cortex (EVC), the upper visual field is processed ventrally with the lower visual field processed dorsally. This distinction persists into several category-selective regions of occipitptemporal cortex, with ventral and lateral scene-, face-, and object-selective regions biased for the upper and lower visual fields, respectively. Here, using an elliptical population receptive field (pRF) model, we systematically tested the sampling of visual space within ventral and dorsal divisions of human EVC in both male and female participants. We

found that 1) pRFs tend to be ellipitical and oriented towards the fovea with distinct angular distributions for ventral and dorsal EVC, potentially reflecting a radial bias and 2) pRFs in ventral areas were larger (~1.5x) and more elliptical (~1.2x) than those in dorsal areas. These differences potentially reflect a tendency for receptive fields in ventral temporal cortex to overlap the fovea with less emphasis on precise localization and isotropic representation of space compared with dorsal areas. Collectively, these findings suggest that ventral and dorsal EVC sample visual space differently, likely contributing to and/or stemming from the functional differentiation of visual processing observed in higher level regions of the ventral and dorsal cortical visual pathways.

Significance Statement

The processing of visual information from the upper and lower visual fields is separated in visual cortex. Although ventral and dorsal early visual cortex (EVC) are commonly assumed to sample visual space equivalently, we demonstrate systematic differences using an elliptical population receptive field (pRF) model. Specifically, we demonstrate that 1) ventral and dorsal divisions of EVC exhibit diverging distributions of pRF angle, which are biased towards the fovea and 2) ventral pRFs exhibit higher aspect ratios and cover larger areas than dorsal pRFs. These results suggest that ventral and dorsal EVC sample visual space differently and such differential sampling likely contributes to different functional roles attributed to the ventral and dorsal pathways, such as object recognition and visually-guided attention, respectively.

Introduction

One prominent feature of the cortical visual pathways is the segregated processing of input from the upper and lower visual field. In early visual cortex (EVC, V1-V3), the upper visual field is processed ventrally and the lower visual field is processed dorsally (Wandell et al., 2007). This distinction persists into higher-level visual areas with scene-, face- ,and object-selective regions in ventral occipitotemporal cortex biased for the upper visual field and those in lateral regions biased for the lower visual field (Arcaro et al., 2009; Kravitz et al., 2010; Silson et al., 2015; 2016a). While it is commonly assumed that ventral and dorsal EVC sample visual space equivalently, evidence suggests potential differences. First, functional differentiation between upper and lower visual fields has been reported in retinal ganglion-cell densities (Packer et al., 1989; Curcio et al., 1990; Curcio & Allen, 1990). Second, ventral and dorsal divisions of V2 and V3 contain different GABA receptor concentrations (Eickoff et al., 2008), perhaps reflecting different functional properties and helping to explain behavioral differences for the upper and lower visual fields. For example, stimulus discrimination and change detection advantages have been reported in the upper visual field (Levine & McAnany, 2005; Rutowski et al., 2002), whereas advantages in visually-guided pointing, spatial recollection memory and attentional resolution (Danckert & Goodale, 2001; Genzano et al., 2001; He, Cavanagh & Intriligator, 1996) have been reported in the lower visual field. Further, differential effects of attention between the upper and lower visual fields have been shown to reflect the

larger extent of the lower compared to upper visual field as well as individual differences in the shape and extent of those fields (Fortenbaugh et al., 2015). Here, using functional magnetic resonance imaging (fMRI), we examined differences in the sampling of visual space within ventral and dorsal divisions of human EVC using population receptive field (pRF) modeling. The majority of previous pRF studies model a voxel's pRF as a circular aperture defined by its centroid (x, y) and size (sigma) (e.g. Dumoulin & Wandell, 2008; Harvey et al., 2013; Silson et al., 2015; 2016a), although more recent studies also model suppressive surrounds (Zuiderbaan et al., 2012) and subadditive spatial summation (Kay et al., 2013). However, given evidence for elongated receptive fields of individual neurons (Hubel & Wiesel, 1962) and populations of neurons (Yoshor et al., 2007), a more biologically plausible model would allow for pRFs to take an elliptical shape - as a circular pRF assumes that orientations of neuronal receptive fields within a voxel are distributed evenly. Indeed, a model-free pRF approach (Greene et al., 2013), reported some deviation from circular pRFs with ~11% of EVC voxels (< 3.5 deg) exhibiting an aspect ratio >2.

First, we predicted that elliptical pRFs would be oriented towards fovea. Specifically, a radial bias has been reported within EVC (Sasaki et al., 2006), with fMRI activity ~20% higher in the retinotopic representations of polar angle (upper/lower quadrant maps) that corresponded to radial stimulus orientations. Further, a coarse-scale orientation map has been identified in V1 whereby the orientation sensitivity of a given voxel was largely commensurate with its preferred polar angle (Freeman et al., 2011).

Second, we predicted that pRFs in ventral EVC would be more elliptical (larger aspect ratio) and cover a larger area than those in dorsal EVC. Ventral EVC is strongly associated with the ventral visual pathway (Kravitz et al., 2013), which is often characterized by an over-representation of the fovea. For example, neurons in macaque inferotemporal cortex exhibit receptive fields that typically overlap the fovea (Op De Beeck & Vogels, 2000) regardless of eccentricity. In contrast, dorsal EVC is more associated with the dorsal visual pathway, which has a more isotropic representation of space (Gattass et al., 2005; Sheth and Young, 2016). While these differences in higher order areas could reflect a selective sampling of EVC, here we tested whether such differential sampling of space emerges within EVC.

Materials and Methods

Participants and testing

Twelve participants in total (five female; mean age, 29 years) completed the fMRI experiments. All participants had normal or corrected-to-normal vision, and gave written informed consent. The National Institutes of Health Institutional Review Board approved the consent and protocol. This work was supported by the Intramural Research program of the National Institutes of Health – National Institute of Mental Health Clinical Study Protocol 93-M-0170, NCT00001360.

fMRI scanning parameters

Participants were scanned on either a research-dedicated GE 3 Tesla Sigma scanner (8 participants) or a research-dedicated Siemens 7 Tesla Magnetom scanner (4 participants) in the Clinical Research Center on the National Institutes of Health campus (Bethesda, MD). In all scans and across scanners, oblique slices were oriented approximately parallel to the base of the temporal lobe and extended posteriorly through all of visual cortex.

3T scanning parameters

Partial volumes of the occipital and temporal cortices were acquired using an eight-channel head coil (21 slices; 2x2x2mm; 10% interslice gap; TR, 2s; TE, 30ms; matrix size, 96x96; FOV, 192mm).

7T scanning parameters

Partial volumes of the occipital and temporal cortices were acquired using a 32-channel head coil (42 slices; 1.2x1.2x1.2 mm; 10% interslice gap; TR, 2s; TE, 27ms; matrix size, 170x170; FOV, 192mm).

Visual Stimuli and Tasks

Population receptive field mapping**.** During pRF mapping sessions, a bar aperture traversed gradually through the visual field while revealing randomly selected scene fragments from a total of 90 color images. During each 36s sweep the aperture took 18 evenly spaced steps every 2s (1 TR) to traverse the entire screen. During each bar position five scene fragments were displayed in rapid succession (400ms per image). Across the 18 aperture positions all 90 possible scene images were displayed once. A total of eight sweeps were made during each run (four orientations, two

directions). Specifically, the bar aperture progressed in the following order for all runs: Left – Right, Bottom Right – Top Left, Top – Bottom, Bottom Left –Top Right, Right – Left, Top Left – Bottom Right, Bottom –Top, and Top Right – Bottom Left. The bar stimuli covered a circular aperture (20° diameter 7T, individual bar width=1.6°**;** 15° diameter 3T, individual bar width=1.25°). Participants performed a color detection task at fixation, indicating via button press when the white fixation dot changed to red. Color fixation changes occurred semi-randomly, with approximately two color changes per sweep (Silson et al., 2015).

fMRI data preprocessing

All data were analyzed using the Analysis of Functional NeuroImages (AFNI) software package Cox (1996) (http://afni.nimh.nih.gov/afni). Prior to statistical and pRF analyses, all images for each participant were motion corrected to the first image of the first run, after removal of the appropriate 'dummy' volumes (8) to allow stabilization of the magnetic field.

pRF modelling

pRF analyses were conducted in AFNI. Unlike our own (Silson et al., 2015, 2016a; 2016b), and others previous work (Dumoulin & Wandell, 2008; Harvey et al., 2013), which employed variants of a 2-D Gaussian model, we employed a pRF implementation that models elliptical pRFs.

Given the position of the stimulus in the visual field at every time point, the model estimates the pRF parameters that yield the best fit to the data: pRF

center location (x, y), ratio of the major to minor widths (aspect ratio) and the orientation of the major axis (angle). Both Simplex and Powell optimization algorithms are utilized simultaneously to find the best time series/parameter sets (x, y, aspect ratio & angle) by minimizing the least-squares error of the predicted time series measured against the acquired time series in each voxel. All functions and programs are available in the current version of AFNI (3dNLfim AFNI_17.1.10, compiled Jun 6 2017).

Delineation of Visual Field Maps

To identify EVC in individual participants, the representations of polar angle and eccentricity were visualized on surface reconstructions of both hemispheres and inspected. Surface reconstructions of the gray and white matter boundary of individual participant hemispheres were made using the Freesurfer4 autorecon script (http://surfer.nmr.mgh.harvard.edu/). Retinotopically organized maps were visible and present in all tested hemispheres. Notwithstanding subtle inter-participant variability, the main features of the maps, in particular the reversals in visual field representation at the vertical and horizontal meridians were consistent across participants. In accordance with previous reports (Engel et al., 1994; Sereno et al., 1995; DeYoe et al., 1996; Larsson & Heeger, 2006; Wandell et al., 2007), visual field maps were delineated using the following criteria: (1) the polar angle representations displayed reversals. That is, representations of polar angle in neighboring visual areas were mirror reversals of one another, with a reversal in the representation along their shared boundary; (2) the polar angle and eccentricity components within each visual area were organized largely

orthogonal to one another. The following visual field maps were identified in each hemisphere and participant (V1, V2d, V2v, V3d, V3v). In order to divide V1 into ventral (V1v) and dorsal (V1d) divisions, we selected nodes with an angular position above and below the horizontal meridian, respectively. Importantly, these maps were defined relative to the polar coordinate of pRF centroids only, without reference to the size, eccentricity, aspect ratio, or angle of the pRF.

Reliability Analyses

Before comparing differences between ventral and dorsal EVC, we tested the reliability of our elliptical pRF parameter estimates by splitting the eight pRF runs for each participant into odd and even runs (4 runs each) and analyzing these now independent data-sets with both circular and elliptical pRF models.

Initially, we compared the reliability of our elliptical estimates with those derived from the circular pRF method in a cross-validated approach. For each participant and split (odd/even) we compared how well the estimated time-series predicted the time-series in the independent data set. For each voxel, we correlated (Pearson's) the predicted time-series from the odd runs with the actual time-series in the even runs and squared the resulting correlation value. This process was reversed and the average computed. We then computed the difference in cross-validated explained variance (R^2) for each participant between elliptical and circular pRF models.

Next, the elliptical pRF parameter estimates (x, y, aspect ratio and angle) derived for each set of runs in our elliptical model were compared on a node-wise basis in each participant, collapsing across visual field maps V1-V3. Initially, we selected significantly modulated nodes (R^2 >.2) in the odd runs and correlated the parameters of interest with the parameters extracted from the exact nodes in the even runs. This process was reversed to avoid any bias in node selection, and the average computed. Of note, due to the circular nature of angle estimates we computed the odd/even correlation of angle using a circular correlation coefficient method.

Statistical Analyses

Statistics were calculated using the SPSS software package (IBM version 24). For our analyses, we employed repeated-measures ANOVAs to examine differences in our pRF parameters between ventral and dorsal EVC. For each analysis, we established initially whether the ANOVA adhered to the assumptions of sphericity using Mauchly's test. When the assumption of sphericity was violated, the degrees of freedom for the offending main-effect or interaction were corrected using the Greenhouse-Geisser correction to allow appropriate interpretation of the F-value resulting from the ANOVA.

Results

We employed an elliptical pRF model to test the prediction that ventral and dorsal divisions of EVC differentially sample visual space (see **Figure 1** for group average pRF parameters on the cortical surface). Before systematically

comparing ventral and dorsal EVC, we established the reliability of the elliptical pRF estimates.

Reliability of elliptical pRF estimates

Initially, we compared the explained variance between the elliptical and circular pRF models using a cross-validated approach (see *Reliability Analyses* above). On average, we observed a significant advantage for the elliptical model ($t_{(11)}$=3.19, p=0.01), with an elliptical advantage in all but one participant, reflecting that our elliptical pRF model captures significantly more of the variance in the time-courses than the circular model.

Next, we examined the reliability of our elliptical pRF parameters. For each parameter, we compared both the correlation (Pearson's) as well as the absolute differences between independent estimates (see *Reliability Analyses* above). For each parameter, there were no significant differences in either Pearson's correlation between hemispheres (paired *t*-test (two-tailed), x ($t_{(11)}$=0.88, p=0.40); y ($t_{(11)}$=.0.87, p=0.40); aspect ratio ($t_{(11)}$=0.57, p=0.58); angle ($t_{(11)}$ =0.89, p=0.39)) or the absolute differences between hemispheres (paired *t*-test (two-tailed), x ($t_{(11)}$=0.60, p=0.56); y ($t_{(11)}$ =0.34, p=0.73); aspect ratio ($t_{(11)}$=0.88, p=0.34); angle ($t_{(11)}$=1.28, p=0.22)), so for further analyses we collapsed across hemispheres.

We observed significant positive correlations for all parameters, (*t*-test relative to zero (two-tailed), (x ($t_{(11)}$=50.58, p=2.21^{-14}); y ($t_{(11)}$=48.7, p=3.36^{-14}); aspect

ratio ($t_{(11)}$=15.02, p=1.12^{-8}); angle ($t_{(11)}$=15.33, p=9.00^{-9})) **(Figure 2A)**. The lowest correlation was for pRF angle, but it is important to consider the influence of aspect ratio. A pRF with an aspect ratio near 1 will result in an unstable estimate of angle, as the principle axis could take a different orientation with little loss in explained variance. We therefore tested the prediction that our estimates of angle would become increasingly reliable with increasing aspect ratio. Accordingly, we computed the correlation between odd and even angle estimates for pRFs that fell into one of four aspect ratio bins (1-2, 2-3, 3-4 & 4-5) **(Figure 2B)**. With increasing aspect ratio, the correlation of the angle estimates increased. A one-way repeated measures ANOVA with Aspect Ratio as a within-subjects factor revealed a significant main effect of Aspect Ratio ($F_{(1.67, 18.36)}$=5.24, p=0.005), reflecting the increase in reliability as a function of increasing aspect ratio.

We also computed the distribution of the absolute differences in each parameter between odd and even runs. In each case, the absolute differences were small [mean (sd): x=0.67° (± 0.01°); y=0.63° (± 0.01°); aspect ratio=0.02 (± 0.004); angle=10.8° (± 1.71°), across all aspect ratio bins; (AR), AR1-2=10.1° (± 1.33°), AR2-3=11.52° (± 0.93°), AR3-4=11.14° (± 0.81°), AR4-5=11.37° (± 1.14°)], which reflects the reliability of our pRF parameter estimates across independent runs **(Figure 2C)**.

Ventral and dorsal pRFs are orientated towards the fovea

Our first prediction was that due to the restricted representations within ventral (upper visual field) and dorsal (lower visual field) divisions of EVC, and

the presence of both a coarse-scale orientation map (Freeman et al., 2011) and radial biases (Sasaki et al., 2006), pRFs would exhibit a general orientation bias toward the fovea. In particular, if 0 degrees represents the horizontal axis with positive angles toward the upper vertical meridian and negative angles toward the lower vertical meridian, we hypothesized that ventral regions (V1v, V2v & V3v), would show a positively biased distribution of pRF angles, with dorsal regions (V1d, V2d & V3d) exhibiting the opposite bias, largely commensurate with their visual field representations. Our results reveal a striking difference in the distributions of pRF angle within ventral and dorsal divisions of V2 and V3 consistent with these predictions **(Figure 3)**. Initially, we tested for hemispheric differences in the distribution of pRF angle within each visual field map division using two-sample Kolmogorov-Smirnov (KS) tests (two-tailed). There were no significant differences between hemispheres for any visual field map division (V1v (ks=0.05, p=0.99); V1d (ks=0.07, p=0.98); V2v (ks=0.08, p=0.93); V2d (ks=0.07, p=0.98); V3v (ks=0.06, p=0.99); V3d (ks=0.07, p=0.98)), thus distributions of pRF angle were averaged across hemispheres. Next, we compared directly the ventral and dorsal divisions for each visual field map separately using two-sampled KS tests. There were significant differences between the pRF angle distributions of ventral and dorsal V2 (ks=0.23, p=0.01) and V3 (ks=0.27, p=0.002), respectively, although ventral and dorsal V1 were not significantly different (ks=0.04, p=1.00). In the case of V2 and V3, ventral maps exhibited a positively biased angle distribution with dorsal maps exhibiting a negatively biased angle distribution largely commensurate with their visual field representations **(Figure 3)**.

Ventral pRFs are more elliptical than dorsal pRFs

Along with diverging orientations, we also predicted that ventral pRFs would be more elliptical than their dorsal counterparts. Potentially reflecting the importance of the fovea often attributed to anterior regions of the ventral pathway and of a more even and precise representation of space in the dorsal pathway. Both of which receive major input from ventral and dorsal EVC divisions, respectively (Kravitz et al., 2013). To test this, we initially computed the distribution of aspect ratios in each participant and visual field map division. First, we tested for hemispheric differences within each visual field map division using two-sample KS tests (two-tailed). There were no significant differences between hemispheres for any visual field map (V1v (ks=0.04, p=1.00); V1d (ks=0.06, p=1.00); V2v (ks=0.04, p=1.00); V2d (ks=0.04, p=1.00); V3v (ks=0.06, p=1.00); V3d (ks=0.08, p=0.99)), thus distributions of aspect ratio were averaged across hemispheres **(Figure 4)**. Next, we compared directly each ventral and dorsal division separately using two-sampled KS tests. There were significant differences between the aspect ratio distributions of ventral and dorsal V2 (ks=0.25, p=0.03) and V3 (ks=0.25, p=0.03), but not V1 (ks=0.12, p=0.42), despite a similar overall pattern. Across visual field maps, the distributions of aspect ratio in dorsal divisions were shifted towards smaller aspect ratios (more circular), with ventral divisions showing broader distributions.

Next, we computed the median aspect ratio in each participant and visual field map separately. Across participants the mean aspect ratio was larger in

ventral than dorsal divisions of EVC **(Figure 5A)**. A three-way repeated-measures ANOVA with within-participant factors of Visual Field Map (V1, V2 & V3), Division (ventral, dorsal) and Hemisphere (left, right), revealed a significant main effect of VFM ($F_{(2, 22)}$=49.79, p=6.80^{-9}), reflecting on average larger aspect ratios in V1. The main effect of Division was also significant ($F_{(1, 11)}$=29.92, p=0.0002), reflecting on average larger aspect ratios in ventral over dorsal divisions within each region. These main effects however are qualified by a significant VFM by Division interaction ($F_{(2, 22)}$=16.59, p=0.0004). No other interactions were significant (p>0.05, in all cases).

To determine what is driving this interaction, we computed three separate two-way ANOVAs for each pair of regions with VFM and Division as within-participant factors. Given the lack of a significant main effect of Hemisphere ($F_{(1, 11)}$=0.12, p=0.74), aspect ratios were averaged across hemispheres. These analyses revealed that the ventral/dorsal difference in aspect ratio was significantly different between V1 and both V2 and V3, but not between V2 and V3 (V1-V2: VFM by Division ($F_{(1, 11)}$=19.96, p=0.001); V1-V3: VFM by Division ($F_{(1, 11)}$=28.47 p=0.0002); V2-V3: VFM by Division ($F_{(1, 11)}$=0.15, p=0.70). We then compared directly the mean aspect ratios within ventral and dorsal divisions of EVC using paired t-tests (one-tailed). Consistent with our predictions, ventral aspect ratios were significantly larger than dorsal aspect ratios in each VFM (V1v versus V1d ($t_{(11)}$=2.53, p=0.01); V2v versus V2d ($t_{(11)}$=5.19, p=0.0001); V3v versus V3d ($t_{(11)}$=5.61, p=0.00007)) **(Figure 5A)**, with a larger difference in the further anterior regions.

Ventral pRFs cover larger area of visual space than dorsal pRFs

Although we observe an increase in aspect ratio for ventral pRFs, it is important to consider the area of visual space covered by these elliptical pRFs. An increase in aspect ratio alone could reflect either elongation of the major axis but shrinking of the minor axis and thus an overall reduction in area or elongation of the major axis and an enlarging of overall area. In order to distinguish between these two possibilities, we calculated the median area in each participant and visual field map, respectively. On average pRF area was larger in ventral compared to dorsal divisions of EVC **(Figure 5B).** A three-way repeated-measures ANOVA (VFM, Division, and Hemisphere) revealed significant main effects of both VFM ($F_{(2, 22)}$ =37.47, p=8.21^{-8}) and Division ($F_{(1, 11)}$=13.19, p=0.004). However, these main effects are qualified by a significant VFM by Division interaction ($F_{(2, 22)}$=14.76, p=0.00008), which highlights that the magnitude of the difference between ventral/dorsal divisions varies across regions. No other interactions were significant (p>0.05, in all cases). Given the non-significant main effect of Hemisphere ($F_{(1, 11)}$ =2.38, p=0.15), pRF area values were averaged across hemispheres. Again, three separate two-way ANOVAs were computed to better interpret the above interaction. These analyses revealed a larger ventral/dorsal difference in V3 compared with both V1 and V2 (V1-V2: VFM by Division ($F_{(1, 11)}$=0.14, p=0.71); V1-V3: VFM by Division ($F_{(1, 11)}$=15.53 p=0.002); V2-V3: VFM by Division ($F_{(1, 11)}$=23.34, p=0.001). Next, we compared directly the pRF area within ventral and dorsal divisions of each visual field map using paired t-tests (one-tailed). Ventral pRFs covered a significantly larger area of the visual field than dorsal pRFs in V1 and V3 (V1v versus V1d ($t_{(11)}$=3.04, p=0.005); V3v

versus V3d ($t_{(11)}$=4.58, p=0.0005)), but not V2 (V2v versus V2d ($t_{(11)}$=1.59, p=0.07), although the numerical increase trended towards significance **(Figure 5B)**.

PRF area and aspect ratio increase with increasing eccentricity

Until now, our analyses have focused on isolated parameters (e.g. angle, aspect ratio or area), but it is also important to consider the relationship between parameters. It is commonly reported that the size of receptive fields (or pRFs) increases with increasing eccentricity, and that this increase is often linear (Hubel & Wiesel, 1974; Maunsell & Newsome, 1987; Dumoulin & Wandell, 2008; Winawer et al., 2010). Therefore, we investigated the relationship between eccentricity and both pRF area and aspect ratio, which we predicted to show a similar near linear relationship. For each participant and visual field map we calculated 1) the median area and 2) the median aspect ratio of pRFs in bins of 1° of eccentricity. Next, we computed the average pRF values within each bin collapsing across hemispheres **(Figure 6A, 6B)**.

The largely near linear trend between eccentricity and pRF size reported previously (Dumoulin & Wandell, 2008; Winawer et al., 2010) is evident in both the estimates of pRF area **(Figure 6A)** and aspect ratio **(Figure 6B)**. Indeed, the general tendency for larger pRFs within successive visual field maps at equal eccentricities is also present for area, with V3 area estimates being larger than those of V2 and V1, respectively **(Figure 6A)**. Notwithstanding differences in absolute aspect ratio **(Figure 6B)** all regions

exhibit a similar near linear relationship whereby aspect ratio increases as a function of eccentricity.

Differential sampling of space between ventral and dorsal EVC not due to differences in explained variance

Whilst we observe systematic differences between pRFs in ventral and dorsal divisions of EVC, it is important to rule out the possibility that these differences are due to systematic differences in explained variance of our model between these ventral and dorsal divisions. To test this, we calculated the median explained variance in each participant and visual field map, respectively. A three-way repeated measures ANOVA (VFM, Division, Hemisphere), revealed only a significant main effect of VFM ($F_{(2, 22)}$ =6.66, p=0.005), reflecting on average larger explained variance in V3 [mean (sd) V1=0.55 (±0.02); V2=0.58 (±0.03); V3=0.60 (±0.02)]. All other main effects and interactions were not significant (p>0.05, in all cases). Thus, the systematic differences reported here between ventral and dorsal EVC are not due to poorer model fits in one division over the other.

Summary comparison of circular and elliptical pRF models

Finally, to summarize and exemplify the additional information provided by the elliptical pRF model, we calculated the average pRF parameters (x, y, aspect ratio and angle) in V2d and V2v (in the left hemisphere) across participants using both circular and elliptical pRF models. A visualization of the resulting average pRFs **(Figure 7)** demonstrates the additional information of the elliptical model. In both models, the centers (x, y) of each pRF are largely

448 equivalent, indicating that the addition of parameters for aspect ratio and
449 angle made little difference to the center of the pRF. However, allowing the
450 shape of the pRF to vary, not only captures the greater elongation of ventral
451 pRFs, but also, demonstrates that this elongation is accompanied by an
452 increase in the area of covered visual field. The orientation of both pRFs
453 towards the fovea is also evident and cannot be captured by a strictly circular
454 model.
455
456 **Discussion**
457 Using a pRF implementation that models elliptical and oriented pRFs, we
458 demonstrate that ventral and dorsal EVC differentially sample visual space.
459 First, we demonstrate that pRFs in ventral and dorsal V2 and V3, in particular,
460 are oriented towards the fovea. Second, we highlight that pRFs in ventral
461 divisions of EVC in general exhibit larger aspect ratios and cover a larger area
462 of the visual field than their dorsal counterparts. Third, we show a positive
463 relationship between pRF eccentricity and both area of covered visual field
464 and aspect ratio throughout EVC.
465
466 The differential sampling of visual space between ventral and dorsal EVC has
467 implications for visual processing within downstream regions of both the
468 ventral and dorsal pathways, which receive biased inputs from these ventral
469 and dorsal antecedent areas (Kravitz et al., 2013). It is possible that functional
470 differences observed within the ventral and dorsal pathways, such as those
471 for object selectivity ventrally (Kravitz et al., 2013) and attentional allocation
472 dorsally (Danckert & Goodale, 2001) are related to the differences in the

sampling of visual space between ventral and dorsal EVC. It remains an open question whether these differences constrain the functions of downstream areas, are created or strengthened by feedback from those areas, or most likely, both.

Why do we observe elliptical and oriented pRFs?

Through a cross-validated approach we demonstrate that our elliptical model captures significantly more of the variance in the time-series than the circular model, which has been used widely in the past (Dumoulin & Wandell, 2008; Harvey et al., 2013; Silson et al., 2015; 2016a; 2016b, and many more). Our finding of elliptical pRFs oriented toward the fovea is consistent with prior fMRI findings (Greene et al, 2013) as well as human intracranial recordings (Yoshor et al, 2007).

To understand why we observe elliptical and oriented pRFs, it is important to bear in mind that the pRF for a given voxel will reflect the properties of the individual neurons contributing to that voxel (e.g. receptive field size, orientation) as well as the spatial distribution of those neuronal receptive fields (scatter) and the aggregation function between their activity and the BOLD signal.

First, we consider pRF size. A difference in pRF size between voxels could reflect a difference in the size of the receptive fields of individual neurons or a difference in the spatial scatter of those receptive fields. The amount of scatter will be reflected by the cortical magnification factor, which describes

the amount of cortex representing a given unit of visual space. The higher the cortical magnification the less the scatter within a given voxel and the smaller the pRF. It has previously been reported that there are larger cortical activations for stimuli at the lower than upper vertical meridian, consistent with a difference in cortical magnification (Liu et al, 2006). Further, a recent study (Silva et al., 2017) reported larger cortical magnification factors (smaller pRFs) in representations of the lower visual field (V1d-V3d) than upper visual field (V1v-V3v). Such findings are consistent with some prior studies in non-human primates (van Essen et al, 1984; Tootell et al, 1988; but see Adams and Horton, 2003) and suggest that the pRF size differences we find between ventral and dorsal EVC could reflect differences in cortical magnification.

Second, for aspect ratio, any difference between voxels could reflect: 1) anisotropic spatial scatter, 2) a difference in the aspect ratio of the underlying neuronal receptive fields, or 3) differences in the distribution of oriented neuronal receptive fields within voxels. We discuss each of these possibilities in turn.

Anisotropic spatial scatter could result from anisotropy in the sampling of the cortex (i.e. voxel orientation relative to the cortical surface), although systematic differences between ventral and dorsal EVC seems unlikely. Alternatively, anisotropic spatial scatter could result from anisotropy in cortical magnification. Given we find that pRFs tend to be oriented toward the fovea, any anisotropy in cortical magnificantion would have to reflect reduced cortical magnification in the iso-polar compared to the iso-eccentric dimension,

523 although the prior literature tends to support the opposite (van Essen et al,
524 1984, Adams and Horton, 2003; Larsson and Heeger, 2006).
525 Instead, it is important to note that a consistent finding in the
526 neurophysiological literature is that neuronal receptive fields tend to be
527 oriented in space (Hubel and Wiesel, 1962). Thus, differences in the aspect
528 ratio of the underlying neuronal receptive fields could potentially explain our
529 pRF results. However, a diference in pRF aspect ratio between voxels could
530 also arise from equivalent aspect ratios of the neuronal receptive fields, but a
531 difference in the angular distribution of those receptive fields across voxels.
532 With our current data it is hard to tease apart these two possibilities.
533
534 ***Differences between ventral and dorsal EVC***
535 Our finding of differential sampling of visual space between ventral over
536 dorsal divisions of EVC, is consistent with previous evidence demonstrating
537 differences between the processing of information from the upper and lower
538 visual fields. For example, studies of retinal ganglion cell density (Packer et
539 al., 1989; Curcio et al., 1990; Curcio & Allen, 1990) and GABA receptor
540 concentrations in cortex (Eickoff et al., 2008) demonstrate that these
541 differences are present at even the earliest stages of visual processing.
542
543 The larger aspect ratio of pRFs in ventral compared with dorsal EVC could
544 reflect a bias for isotropic representations of space dorsally for spatial
545 processing, but a bias toward an over-representation of the fovea ventrally for
546 object and face recognition. For example, as noted earlier, in non-human
547 primate inferior temporal cortex neuronal receptive fields tend to overlap the

548 fovea regardless of eccentricity (Op de Beeck and Vogels, 2000) and our
549 results may reflect a similar effect in EVC.
550
551 The differences in the orientation we found between dorsal and ventral EVC
552 could reflect an underlying radial bias (Sasaki et al, 2006; Freeman et al,
553 2011), although the strength of this radial bias remains disputed (Pratte et al,
554 2016). Specifically, our analyses demonstrate that the distributions within V2
555 and V3 peak close to the oblique angle in each quadrant (V2v=45°, V2d=-36°,
556 V3v=36°, V3d=-32°).
557
558 We did not observe significantly different angle distributions in V1. One
559 potential reason for this is that unlike ventral and dorsal V2 and V3, which are
560 largely anatomically segregated, apart from the difficult-to-map shared central
561 representations of these areas (Schira et al., 2009), our delineation of ventral
562 and dorsal V1 was based on the polar angle of each pRF. It is therefore
563 feasible that the spatial separation between these divisions in V1 is not
564 sufficient enough to detect significant differences in pRF angle. Differences
565 between ventral and dorsal V1 could be further complicated by the
566 vasculature, which likely results in BOLD signals that are pooled from both
567 upper and lower banks of the calcarine sulcus. Future work should
568 systematically compare the orientation selectivity of individual voxels with its
569 pRF orientation and angular position.
570
571 ***Implications for visual processing and future work***

572 The differential sampling of visual space between ventral and dorsal EVC
573 likely impacts visual processing in high-level regions comprising both ventral
574 and dorsal pathways. For instance, anterior regions of the dorsal pathway,
575 such as the superior parieto-occipital cortex, which is crucial for guiding hand
576 movements, shows a lower visual field bias (Rossit et al., 2013) that is likely
577 inherited from connections with dorsal EVC (Kravitz et al., 2013). Our data
578 suggest that dorsal divisions of EVC exhibit less elongation, evidenced by
579 smaller aspect ratios, resulting in a more isotripic representation of space
580 (Gattass et al., 2005), which may help explain behavioral advantages for
581 actions such as visually-guided pointing in the lower visual field (Danckert &
582 Goodale, 2001). A more isotropic sampling of space in dorsal EVC and the
583 broader dorsal visual pathway likely facilitates the guidance of eye-
584 movements and attentional allocation that are thought to reflect dorsal
585 pathway functioning (Goodale et al., 1991; Kravitz et al., 2011), as regions
586 that evenly sample most of visual space are suited ideally to identify items in
587 the visual field that need to be brought into the focus of attention. Whether
588 pRFs in these regions also exhibit similar shapes and orientations as dorsal
589 EVC is a potential avenue for future work.
590
591 Although intuitive to think that ventral and dorsal EVC project principally to the
592 ventral and dorsal visual pathways, the neuroanatomy is not as
593 straightforward (Kravitz et al., 2013). Indeed, in human, category-selective
594 regions considered to comprise the ventral pathway are found in matched
595 pairs on both the lateral and ventral surfaces of occipitotemporal cortex
596 (Kravitz et al., 2010; Silson et al., 2015; 2016a), and exhibit differential

retinotopic biases that mirror those in ventral and dorsal EVC, respectively. Although our previous work (Silson et al., 2015; 2016a) has focused on the different visual field biases in these areas (e.g. occipital place area – lower visual field, parahippocampal place area – upper visual field) our current data suggest that more focus should be placed upon understanding how these regions sample space within the visual field. Future work could assess the distributions of pRF shape and orientation within these matched category-selective regions, which may inform the specific computations each region performs.

Conclusion

Taken together, our data suggest systematic differences in the sampling of space between ventral and dorsal divisions of EVC. The differential sampling of space is consistent with previous differences between the upper and lower representations of the visual field at both retinal and cortical levels, and likely contribute to and/or stem from the functional differentiation of visual processing observed in higher level regions of the ventral and dorsal cortical visual pathways.

Author Contributions

E.H.S jointly designed the study, acquired and analyzed the neuroimaging data and wrote the manuscript. R.C.R designed the elliptical and circular pRF models in AFNI and analyzed the neuroimaging data. D.J.K jointly designed the study, analyzed the neuroimaging data and wrote the manuscript. C.I.B jointly designed the study and wrote the manuscript.

Acknowledgments

We thank Iris Groen, Martin Hebert, Eli Merriam, Alexis Kidder and members of the Section on Learning and Plasticity for helpful comments on earlier versions of the manuscript.

References

Adams, D. L., & Horton, J. C. (2003). A precise retinotopic map of primate striate cortex generated from the representation of angioscotomas. *Journal of Neuroscience*, *23*(9), 3771-3789.

Arcaro, M. J., McMains, S. A., Singer, B. D., & Kastner, S. (2009). Retinotopic organization of human ventral visual cortex. *Journal of neuroscience*, *29*(34), 10638-10652.

Curcio CA, Allen KA. 1990. Topography of ganglion cells in human retina. J Comp Neurol. 300:5--25.

Curcio CA, Sloan KR, Kalina RE, Hendrickson AE. 1990. Human photoreceptor topography. J Comp Neurol. 292:497--523.

Danckert J, Goodale MA. 2001. Superior performance for visually guided pointing in the lower visual field. Exp Brain Res. 137:303-308.

DeYoe, E. A., Bandettini, P., Neitz, J., Miller, D., & Winans, P. (1994). Functional magnetic resonance imaging (FMRI) of the human brain. *Journal of neuroscience methods*, *54*(2), 171-187.

Dumoulin, S. O., & Wandell, B. A. (2008). Population receptive field estimates in human visual cortex. *Neuroimage*, *39*(2), 647-660.

Eickhoff, S. B., Rottschy, C., Kujovic, M., Palomero-Gallagher, N., & Zilles, K. (2008). Organizational principles of human visual cortex revealed by receptor mapping. *Cerebral Cortex*, *18*(11), 2637-2645.

Engel, S. A., Glover, G. H., & Wandell, B. A. (1997). Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cerebral cortex (New York, NY: 1991)*, *7*(2), 181-192.

Freeman, J., Brouwer, G. J., Heeger, D. J., & Merriam, E. P. (2011). Orientation decoding depends on maps, not columns. *Journal of Neuroscience*, *31*(13), 4792-4804.

Fortenbaugh, F. C., Silver, M. A., & Robertson, L. C. (2015). Individual differences in visual field shape modulate the effects of attention on the lower visual field advantage in crowding. *Journal of vision*, *15*(2), 19-19.

Gattass, R., Nascimento-Silva, S., Soares, J. G., Lima, B., Jansen, A. K., Diogo, A. C. M., & Azzi, J. (2005). Cortical visual areas in monkeys: location, topography, connections, columns, plasticity and cortical dynamics. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *360*(1456), 709-731.

Genzano VR, Di NF, Ferlazzo F. 2001. Upper/lower visual field asymmetry on a spatial relocation memory task. Neuroreport. 12:1227--1230.

Goodale, M. A., & Milner, A. D. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, *349*(6305), 154.

Greene, C. A., Dumoulin, S. O., Harvey, B. M., & Ress, D. (2014). Measurement of population receptive fields in human early visual cortex using back-projection tomography. *Journal of vision*, *14*(1), 17-17.

Harvey, B. M., Klein, B. P., Petridou, N., & Dumoulin, S. O. (2013). Topographic representation of numerosity in the human parietal cortex. *Science*, *341*(6150), 1123-1126.

He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature*, *383*(6598), 334.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *The Journal of physiology*, *160*(1), 106-154.

Hubel, D. H., & Wiesel, T. N. (1974). Uniformity of monkey striate cortex: a parallel relationship between field size, scatter, and magnification factor. *Journal of Comparative Neurology*, *158*(3), 295-305.

Kay, K. N., Winawer, J., Mezer, A., & Wandell, B. A. (2013). Compressive spatial summation in human visual cortex. *Journal of neurophysiology*, *110*(2), 481-494.

Kravitz, D. J., Kriegeskorte, N., & Baker, C. I. (2010). High-level visual object representations are constrained by position. *Cerebral Cortex*, *20*(12), 2916-2925.

Kravitz, D. J., Saleem, K. S., Baker, C. I., Ungerleider, L. G., & Mishkin, M. (2013). The ventral visual pathway: an expanded neural framework for the processing of object quality. *Trends in cognitive sciences*, *17*(1), 26-49.

Levine MW, McAnany JJ. 2005. The relative capabilities of the upper and lower visual hemifields. Vision Res. 45:2820-2830.

Liu, T., Heeger, D. J., & Carrasco, M. (2006). Neural correlates of the visual vertical meridian asymmetry. *Journal of Vision*, *6*(11), 12-12.

Maunsell, J. H., & Newsome, W. T. (1987). Visual processing in monkey extrastriate cortex. *Annual review of neuroscience*, *10*(1), 363-401.

Op De Beeck, H., & Vogels, R. (2000). Spatial sensitivity of macaque inferior temporal neurons. *Journal of Comparative Neurology*, *426*(4), 505-518.

Packer O, Hendrickson AE, Curcio CA. 1989. Photoreceptor topography of the retina in the adult pigtail macaque (Macaca nemestrina). JComp Neurol. 288:165--183.

Rossit, S., McAdam, T., Mclean, D. A., Goodale, M. A., & Culham, J. C. (2013). fMRI reveals a lower visual field preference for hand actions in human superior parieto-occipital cortex (SPOC) and precuneus. *Cortex*, *49*(9), 2525-2541.

Rutkowski JS, Crewther DP, Crewther SG. 2002. Normal readers have an upper visual field advantage in change detection. Clin Exp Ophthalmol. 30:227--330.

Sasaki, Y., Rajimehr, R., Kim, B. W., Ekstrom, L. B., Vanduffel, W., & Tootell, R. B. (2006). The radial bias: a different slant on visual orientation sensitivity in human and nonhuman primates. *Neuron*, *51*(5), 661-670.

Schall, J. D., Perry, V. H., & Leventhal, A. G. (1986). Retinal ganglion cell dendritic fields in old-world monkeys are oriented radially. *Brain research*, *368*(1), 18-23.

Schira, M. M., Tyler, C. W., Breakspear, M., & Spehar, B. (2009). The foveal confluence in human visual cortex. *Journal of Neuroscience*, *29*(28), 9050-9058.

Sereno M, Dale AM, Reppas JB, Kwong KK, Belliveau JW, Brady TJ, Rosen BR, Tootell RBH (1995) Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. Science 268:899–893.

Sheth, B. R., & Young, R. (2016). Two visual pathways in primates based on sampling of space: exploitation and exploration of visual information. *Frontiers in integrative neuroscience*, *10*.

Silson, E. H., Chan, A. W. Y., Reynolds, R. C., Kravitz, D. J., & Baker, C. I. (2015). A retinotopic basis for the division of high-level scene processing between lateral and ventral human occipitotemporal cortex. *Journal of Neuroscience*, *35*(34), 11921-11935.

Silson, E. H., Groen, I. I., Kravitz, D. J., & Baker, C. I. (2016b). Evaluating the correspondence between face-, scene-, and object-selectivity and retinotopic

763 organization within lateral occipitotemporal cortex. *Journal of vision*, *16*(6), 14-
764 14.
765
766 Silson, E. H., Groen, I. I., Kravitz, D. J., & Baker, C. I. (2016a). Evaluating the
767 correspondence between face-, scene-, and object-selectivity and retinotopic
768 organization within lateral occipitotemporal cortex. *Journal of vision*, *16*(6), 14-
769 14.
770
771 Silva, M. F., Brascamp, J. W., Ferreira, S., Castelo-Branco, M., Dumoulin, S.
772 O., & Harvey, B. M. (2017). Radial asymmetries in population receptive field
773 size and cortical magnification factor in early visual cortex. *NeuroImage*.
774
775 Tootell, R. B., Switkes, E., Silverman, M. S., & Hamilton, S. L. (1988).
776 Functional anatomy of macaque striate cortex. II. Retinotopic
777 organization. *Journal of neuroscience*, *8*(5), 1531-1568.
778
779 Van Essen, D. C., Newsome, W. T., & Maunsell, J. H. (1984). The visual field
780 representation in striate cortex of the macaque monkey: asymmetries,
781 anisotropies, and individual variability. *Vision research*, *24*(5), 429-448.
782
783 Wandell, B. A., Dumoulin, S. O., & Brewer, A. A. (2007). Visual field maps in
784 human cortex. *Neuron*, *56*(2), 366-383.
785
786 Winawer, J., Horiguchi, H., Sayres, R. A., Amano, K., & Wandell, B. A. (2010).
787 Mapping hV4 and ventral occipital cortex: the venous eclipse. *Journal of*
788 *vision*, *10*(5), 1-1.
789
790 Yoshor, D., Bosking, W. H., Ghose, G. M., & Maunsell, J. H. (2006).
791 Receptive fields in human visual cortex mapped with surface
792 electrodes. *Cerebral cortex*, *17*(10), 2293-2302.
793
794 Zuiderbaan, W., Harvey, B. M., & Dumoulin, S. O. (2012). Modeling center–
795 surround configurations in population receptive fields using fMRI. *Journal of*
796 *vision*, *12*(3), 10-10.
797

Figures and Figure legends

Figure 1: Distribution of pRF parameters across the cortical surface. **(A)** A medial view of the surface reconstruction of the right hemisphere of a single participant is shown (gyri are light gray, sulci are dark gray). The group average (n=12) polar angle is overlaid in false-color ($R^2 > 0.2$). Red and blue represent the upper vertical meridian (UVM) and lower vertical meridian (LVM), respectively, with the horizontal meridian (HM) represented by green. The borders defining EVC (V1, V2d, V2v, V3d & V3v) are overlaid in white, with the horizontal meridian borders represented by the dashed-line. The polar angle representations follow predicted patterns with lower visual field representations dorsally and upper visual field representations ventrally **(B)** Eccentricity is overlaid in false-color. Blue represents central positions in the visual field with red representing the periphery. The progression of eccentricity follows a well established and predicted pattern, progressing gradually from central representations at the occipital pole, to peripheral representations more anteriorly. **(C)** Estimates of pRF angle are overlaid in false-color. Negative (lower visual field) angles are shown in green/blue colors with positive (upper visual field) angles shown in red. Although the organization of pRF angle is not as smooth as polar angle, there is a general tendancy for negative angles more dorsally (lower visual field representaitons in **A**), and positive angles more ventrally (upper visual field representations in **B**) **(D)** Estimates of pRF aspect ratio are overlaid in false-color. Circular pRFs (aspect ratio = 1) are shown in blue, with very elliptical pRFs (aspect ratio of 5:1) shown in red. Although the organization of pRF aspect ratio across the

cortical surface is not as smooth as eccentricity, there is a general tendancy for more circular (lower aspect ratios) pRFs to be located more posteriorly (central representatios in **B**), with very elliptical pRFs (higher aspect ratios) more anteriorly (peripheral representations in **B**). **(E)** Schematic of pRF mapping stimulus. Example frames during pRF mapping runs. Scene images (one every 400ms) were presented through a bar aperture that moved gradually through the visual field in eight sweeps (2 orientations, 4 directions). A single sweep took 36 s and consisted of 18 equal time (2 s) and width instances of the aperture. Over an entire sweep, 90 scene images (5 x 18 aperture postions) were presented at random without replacement, guaranteeing that no scene was presented twice during a sweep. Participants fixated centrally, identifying via buttom press eveytime the fixation dot changed from white to red (~ twice per sweep).

Figure 2: Reliability of the elliptical and oriented pRF model. **(A)** Correlation values derived between independent sets of data for each of the parameters of interest. We observe significant positive correlations for all parameters of interest. The dashed vertical line separates our angle estimate from the other parameters, as this parameters reliability was calculated using a circular correlation method (***p<0.001, relative to zero). **(B)** Reliability of theta estimates as a function of aspect ratio. We tested the prediction that our theta estimates would become increasingly reliable and aspect ratio increased, as a pRF with an aspect ratio of 1 will result in an unstable theta estimate. As predicted, a one-way repeated-measures ANOVA confirmed that the reliability of our theta estimates increased with increasing aspect ratio (**, p<0.01 for

the main effect of aspect ratio). **(C)** Distributions of the absolute differences between odd/even runs for each parameter. For each distribution, the FWHM is shown by the black-line with the value given to the right.

Figure 3: PRF orientation biases in dorsal and ventral divisions of EVC. **(A)** Distributions of pRF orientation in V1d (blue-line) and V1v (red-line) collapsed across participants and hemispheres. Both distributions appear to be centered largely around zero (horizontal), with little difference in overall bias. The angle histograms of both distributions are plotted to the right. **(B)** Distributions of pRF orientation in V2d (blue-line) and V2v (red-line) collapsed across participants and hemispheres. V2d exhibits a distribution shifted towards negative orientations whereas V2v exhibits the opposite bias. These distributions were significantly different from one another (two-sample KS test). The angle histograms of both distributions are plotted to the right and better depicts the differential pRF angles in both regions. **(C)** Distributions of pRF orientation in V3d (blue-line) and V3v (red-line) collapsed across participants and hemispheres. V3d exhibits a distribution shifted towards negative orientations whereas V3v exhibits the opposite bias. These distributions were significantly different from one another (two-sample KS test). The angle histograms of both distributions are plotted to the right and better depicts the differential pRF angles in both regions. ***p<0.001.

Figure 4: PRF aspect ratio distributions in ventral and dorsal divisions of EVC. Plots depict the average distributions of aspect ratio in each visual field map and division, respectively (blue line = dorsal, red line = ventral). In each

873 case, dorsal distributions are shifted towards smaller aspect ratios, with
874 ventral distributions showing a more even distribution of aspect ratio.
875 Distributions within each visual field map were compared using two-sample
876 KS tests. In the each of V2 and V3, ventral and dorsal distributions were
877 significantly different from one another (*p<0.05).
878
879 **Figure 5:** Dorsal *versus* ventral comparisons. **(A)** Bars represent the mean of
880 the median aspect ratio in each visual field map division collapsed across
881 participants and hemispheres. PRF aspect ratio was significantly larger within
882 the ventral division of each visual field map (paired *t*-test between dorsal and
883 ventral divisions). **(B)** Bars depict the mean of the median pRF area in each
884 visual field map division collapsed across participants and hemispheres. PRF
885 area was nominally larger in ventral over dorsal V2, and significantly larger in
886 ventral over dorsal V1 and V3 (paired *t*-test between dorsal and ventral
887 divisions). *p<0.05, ***p<0.001.
888
889 **Figure 6:** PRF area and aspect ratio increase with eccentricity. In all visual
890 field maps pRF area **(A)** and pRF aspect ratio **(B)** increase with eccentricity.
891 The increase in area by hierarchical position (V1, V2, V3) at equal
892 eccentricities is present in **(A)** and is consistent with previous findings that
893 considered pRF size (diameter of circular pRF). Aspect ratio also increases
894 largely linearly with eccentricity **(B)** despite differences in the absolute aspect
895 ratio between visual field maps. In each participant and visual field map, the
896 median surface area and aspect ratio were calculated across nodes in bins of

1 deg of eccentricity (range 1-9 deg). Error bars at each eccentricity show the standard error of the mean across participants.

Figure 7: Representation of the information gained from the elliptical pRF model. **(Left)** The average pRF of all voxels in left V2d and left V2v across participants, derived from the circular pRF model are plotted on a schematic of the visual field. **(Right)** The average pRF of all voxels in left V2d and left V2v across participants, derived from the ellipitcal pRF model are plotted on a schematic of the visual field. Unlike the circular case, the elliptical model captures differences in shape (aspect ratio) and orientation between dorsal and ventral pRFs, which would be unavailable if pRFs were estimated as circles in space.