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The two-dimensional mapping of the central and parafoveal visual field to human visual cortex.

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Running Title:

2D-mapping of visual field to cortex

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Abstract:

Primate visual cortex contains a set of maps of visual space. These maps are fundamental to early visual processing, yet their form is not fully-understood in humans. This is especially true for the central and most important part of the visual field - the fovea. We used functional Magnetic Resonance Imaging (fMRI) to measure the mapping geometry of human V1 and V2 down to 0.5° of eccentricity. By applying automated atlas fitting procedures to parametrize and average retinotopic measurements of 8 brains, we provide a reference standard for the 2-dimensional geometry of early human visual cortex of unprecedented precision and analyze this high quality mean dataset with respect to the 2-dimensional cortical magnification morphometry. The analysis indicates that 1) area V1 is meridional isotropic in areal projection: equal areas of visual space are mapped to equal areas of cortex at any given eccentricity. 2) V1 has a systematic pattern of local anisotropies: cortical magnification varies between iso-polar and iso-angle lines and 3) the shape of V1 deviates systematically from the complex-log model, whose fit is particularly poor close to the fovea. We therefore propose two modified models that result in a more accurate description of V1 shape. 4) V2 is elongated by a factor of 2 in eccentricity direction relative to V1 and has significantly more local anisotropy. We propose that V2 has systematic intrinsic curvature, but V1 is intrinsically flat.

Keywords: visual cortex, fovea, retinotopy, V1, striate cortex, magnification

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Introduction

Human primary visual cortex (V1) contains a map of visual space: to a good approximation, each two-dimensional location in the visual field is represented at a single physical location within V1 (Hubel and Wiesel, 1974). This mapping was first studied in human by Inouye (1909) and subsequent work (Holmes, 1917; Horton and Hoyt, 1991a,b) refined our understanding of the way that the visual world is represented in early visual cortex. Early behavioral studies (Wertheim, 1894) and anatomical examination of the retina (Østerberg, 1935; Curcio, 1990) showed that the fovea is a region of high spatial acuity. It is therefore not unexpected that the visual system allocated proportionally more gray matter to the representation of the fovea. This 'cortical magnification' was quantified in the monkey by Talbot and Marshall (1941) and in more detail by Daniel and Whitteridge (1961). Subsequent studies (Levi et al., 1984; Yap et al., 1987; Dow et al., 1981, 1985; Van Essen et al., 1984) have improved our estimates of this function, which describes the way that linear magnification changes with eccentricity. Magnification (in *mm* displacement on the cortex/*deg* in the visual field) is often described by the function:

$$M(E) = \frac{k}{E + a}, \quad (1)$$

In this notation, magnification M depends on eccentricity (E) but not angular ('polar') position (which we will denote as P) in the visual field. In fact linear magnification can also be measured parallel to isopolar lines (M_P) or parallel to isoeccentricity lines (M_E) and in general, M_E and M_P are not equal. The product of these two metrics is M_A or the 'areal magnification' (Myerson et al., 1977; Tusa et al., 1978): the area of cortical surface (in mm^2) per area of visual field (in deg^2). The distinctions between these metrics are important in this paper and we provide a detailed analysis in the Appendix.

In 1977, Schwartz proposed an analytical expression to describe the two-dimensional mapping between retinal and cortical coordinates. By using complex numbers to represent both retinal eccentricity and angular deviation from the horizontal

meridian simultaneously, he showed that the map of visual space in area V1 symbolized by $w(E, P)$, was approximated by a complex-log transform of the retinal image (Schwartz, 1977).

$$w(E, P) = k * \log(E * e^{i*P} + a), \quad (2)$$

where a defines the limit of the foveal singularity and k is a scaling constant.

This simple and convenient complex-log transform (or variants thereof – Schwartz 1983; Balasubramanian et al., 2002; Polemeni et al., 2006) captures several important features of the V1 map - most notably the roughly logarithmic scaling of cortical area with eccentricity. It has become the de facto standard for describing the shape of human V1. However, the complex-log representation makes some counterintuitive predictions about the way that space is represented in visual cortex (see Appendix). Specifically, it requires that the amount of cortex dedicated to a particular area of visual space varies with polar angle as well as eccentricity. There is no *a priori* reason for believing that this is the case and in fact behavioral studies show that psychophysical properties that might be expected to depend on local cortical area (for example Vernier acuity or contrast sensitivity) are essentially independent of angular position in the visual field (Rovamo and Virsu, 1984; Toet and Levi, 1992).

We term a change in cortical magnification with polar position but constant eccentricity *meridional anisotropy*, to distinguish it from local anisotropy (see Appendix), following previous work (Mitchell et al., 1967; Buchanan-Smith and Heeley, 1993; Westheimer, 2003). It has also been termed “radial bias” (Van Essen et al., 1984; Fiorani et al. 1989).

Since the mid 1990s, researchers have used functional magnetic resonance imaging (fMRI) to measure the mapping of the visual field in the cerebral cortex. Early studies (Engel, 1994; Sereno, 1995; DeYoe et al., 1996) demonstrated that it was possible to distinguish the 'first tier' retinotopic visual areas (V1, V2 and V3). More recent work has focused on measuring the linear (one-dimensional) cortical magnification function (Sereno, 1995; Duncan and Boynton, 2003) or the area of cortex associated with different

eccentricity ranges (Dougherty et al., 2003). However, none of these studies has quantified the 2-dimensional shape or the dependence on polar position.

Measuring the shape of V1 in the fovea is critical for several reasons. Firstly, the fovea is represented by a disproportionately-large amount of cortex. Although the visual field extends over almost 180° of visual angle, roughly 30% of V1 is devoted to the central 3° . Secondly, the fovea supports a large proportion of functional vision: it is the location where visual acuity and color discrimination are highest and many visual functions such as object and face identification, stereopsis and reading are essentially limited to the central visual field (Zegarra-Moran and Geiger, 1993; Battista et al., 2005). Finally, as we show in this study, different models of retino-cortical mapping can make similar predictions in the periphery, but very different predictions near the fovea depending on the strategy adopted to avoid the singularity at zero degrees eccentricity. If a simple analytical expression for the mapping between visual space and cortical location can be found, it is most strongly constrained (and most effectively tested) in the fovea. Conversely, incorrect models produce the most extreme errors in this region.

In the present study, we used high-resolution fMRI to measure the shape and morphometry of V1 and V2 to within 0.5° of the center of the visual field. This allowed us to model the way in which the amount of cortical area dedicated to a particular region of the visual field changes with both polar angle and eccentricity. We used an atlas fitting procedure to determine the retinotopic map in V1-V3 semi-automatically and made detailed local measurements of all the distances between arrays of points in the V1 and V2 maps. We then averaged the metric data from 8 observers to generate a 'mean' V1 morphometry that strongly constrained our subsequent modeling. Our results indicate that the standard complex-log transform does not adequately describe the way in which visual space is mapped to cortex. In particular, we find that this model overestimates the dependence of M_A on polar angle near the fovea. We show that a modified version of the complex-log transform provides a good fit to the measured data and we suggest an analytic mapping function as a useful way to describe the transformation between two-dimensional visual space and cortex. Our new model also provides a good approximation of human V2 and suggests detailed hypotheses about differences between V1 and V2.

Materials and Methods:

We analyzed retinotopic measurement data from 8 subjects, 5 male and 3 female, ranging in age from 25-60. Protocols were approved by the Institute Institutional Review Boards of both the Stanford and the Smith-Kettlewell Eye Research, and informed consent was obtained from all subjects. Their vision was normal or corrected to normal for the stimulus presentation in the scanner.

Functional measurements:

Functional magnetic resonance data were acquired on a GE 3T Signa LX scanner (GE Medical Systems, Milwaukee, WI) using a custom-built high-gain head coil. Functional acquisition was taken with a resolution of either $2 \times 2 \times 3$ or $2.5 \times 2.5 \times 3$ mm, using a spiral K-space sampling sequence of the T2* weighted (TE: 30 ms, 2 interleaves, 70 deg flip angle) activation (Noll et al., 1995) with 21 or 30 slices perpendicular to the calcarine sulcus, and a volume repetition time (TR) of 3 seconds. Subjects' heads were fixed throughout the measurement period by means of snug-fitting pads and tape across the chin and forehead.

Anatomical measurements:

Several high-resolution T1 datasets ($1 \times 1 \times 1$ mm) were acquired for each subject using a fast 3D SPGR sequence. These datasets were corrected for inhomogeneity, aligned and averaged using the FMRIB software library (<http://www.fmrib.ox.ac.uk/fsl>) and SPM (<http://www.fil.ion.ucl.ac.uk/spm/>) to generate low noise, spatially homogeneous datasets. Segmentation was performed using mrGray software package (<http://white.stanford.edu/~brian/mri/segmentUnfold.htm>) and each white-matter segmentation was carefully hand-edited to ensure an accurate segmentation and surface reconstruction.

Stimulus generation and presentation:

Rotating wedges and expanding rings containing 4 Hz contrast-reversing checkerboard stimuli were generated using custom software and routines from the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). To ensure good fixation, an extended fixation grid was present throughout the stimulus presentations. The fixation grid was one pixel wide, light gray on dark gray background and consisted of a diagonal cross extending from corner to corner and four concentric circles at 0.5, 5, 10 and 15° eccentricity. All subjects were experienced psychophysical observers and eyetracker measurements indicated that the standard deviation of fixation position during fMRI experiments was less than $\frac{1}{4}^\circ$. Subjects viewed stimuli displayed on a small translucent screen mounted on the head coil. The stimuli were projected using a LCD-projector placed in a shielded box at the foot of the scanner bed. This display system subtended $\pm 16^\circ$ vertically and $\pm 20^\circ$ horizontally. The display, calibrated by a PR-650 PhotoResearch Spectroradiometer, had a mean luminance of 30 cd/m^2 .

Data Analysis

The functional data was analyzed using the Stanford VISTA-Tools, and an improved version of the ATLAS-toolbox (Dougherty et al., 2003). The atlas tools estimate area boundaries by fitting a canonical scheme for V1-V3 simultaneously to retinotopic data for both the eccentricity and meridian sweeps. It is semi-automated since the operator has to generate a starting scheme and control the results of the fit, which may terminate in local minima of the optimization. Repeated fits were therefore made with different starting points to confirm stable convergence in the V1-V3 region identified by eye at the first pass. The algorithms of this optimization are described in Fischer and Modernitz (2004). This method estimates the boundaries between the visual areas and also the position of each isopolar or isoeccentricity line. This fit provided an objective method for identifying these key features, providing the basis for the analysis of this paper.

Distance Measurements

In order to specify the shape of cortical projection areas as accurately as possible, we estimated 3D distances along the cortical manifold using the Dijkstra algorithm in an

overcomplete mesh of the boundary between white and gray matter. Measuring distances along a grid (in either 2D or 3D) is subject to errors of the ‘city-block’ type. The mesh was over-complete in the sense of including all diagonals of the city-block connections, since this reduces the city-block error significantly. We estimated the extent of this using a spherical model of the cortex and a Monte Carlo simulation. Irrespective of the radius of the sphere the error distribution was approximately normally distributed with a SD of only $\pm 2.1\%$. The method also results in a mean overestimation of distances by 7.5%, but we corrected this overestimation by dividing the measures by a factor of 1.075, leaving only the residual error of $\pm 2.1\%$ (see Supplementary Materials). All distance measurements presented in this paper are measured using this method within the 3D manifold of the undistorted cortex.

Results and Analysis

Retinotopy

We performed retinotopic mapping on 8 subjects and analyzed areas V1 and V2 in the right hemispheres using a semi-automated atlas fitting procedure (Dougherty et al., 2003). Briefly this method fits a schematic model of the early visual areas (V1, V2 and V3) to the measured polar angle and eccentricity maps simultaneously (see Methods). Its purpose is to determine the borders between these early visual areas and to fit a smooth representation of both polar angle and eccentricity within these borders. We restricted our analysis to V1 and V2. For a reliable fit of V3 one would need a reliable specification of the organization of its neighboring visual areas (V3A, V3B, hV4), which are still under dispute. Figure 1 shows two examples of our atlas fits.

--- Figure 1 ---

Dependence of M_A on Eccentricity

The first parameter we measured was the classical eccentricity magnification function. Each subject's V1 was segmented into annular regions of $\pm 15\%$ eccentricity at several

eccentricities (*e.g.* $0.6\text{-}0.8^\circ$ for the 0.7° eccentricity and $6.8\text{-}9.2^\circ$ for the 8° eccentricity). We then measured the size of each of these subregions to estimate the areal magnification M_A (in mm^2 of cortex / deg^2 of visual field) for these eccentricity ranges, averaged across the range of polar positions (from $-\pi/2$ to $\pi/2$ in radians or -90° to $+90^\circ$ in). The square root of this number is a linear measurement (the geometric mean of the magnification in the eccentricity and polar angle directions) and can be fitted by eq. 1. It is these numbers ($M_{\sqrt{A}}$) that we show in for V1 and V2 in Figure 2.

--- Figure 2 ---

It is interesting to note that V1 and V2 have a similar values for a ($t = 2.6$, *d.f.*, 7, n.s.), but significantly different scaling parameters k ($t = 28.6$, *d.f.*, 7, $p < 0.01$). As reported by Dougherty et al. (2003) there is considerable variability in the linear magnification function across subjects – particularly at eccentricities less than three degrees. However, we find that these differences can be modeled as changes in the scaling parameter. After accounting for differences in the overall size of area V1 the form of the cortical magnification function is remarkably constant (Figure 2b, S1).

--- Figure 3 ---

The cortical magnification function has been described previously in several primate species and for macaque monkey by several authors using different procedures and frameworks. In Figure 3a we plot several of these to allow a comparison between different species. For illustration we multiplied the areal magnification functions M_A provided by these authors and multiplied them with the values depicted in Figure 3b. We then took the square root of these numbers to obtain linear magnification ($M_{\sqrt{A}}$).

Average Map

To obtain an average two-dimensional map of human V1, we identified the cortical locations for 10 meridians and 11 iso-eccentricity rings (110 locations) in each subject's V1. The locations are specified as the voxels lying most closely within the cortical gray matter, defined for the zone 2 *mm* above the gray/white matter segmentation boundary (in the direction normal to this boundary). We then measured the distance between each pair of these 110 positions (6050 distances per subject) along the 3D cortical manifold, resulting in a 'distance grid' for each subject's cortical map. We averaged these distance grids to obtain an average distance grid, uncontaminated by any flattening distortions. This array constitutes the raw data for the specification of the shape of V1. This dataset is too large for publication in paper form, but we provide the data online, since it represents an undistorted reference for the distances between the projections of these 110 visual field positions.

In order to fit our data to the available mapping models and present it in a digestible form for reference purposes, we projected the three-dimensional data to a two-dimensional surface. We reconstructed a two-dimensional average V1 using a Multi-Dimensional Scaling algorithm (metric MDS; Torgerson, 1952). We flattened only once for the mean dataset, rather than averaging several individually flattened cortices. This approach has several key advantages: i) the reconstruction is optimized to minimize the error within V1 only; ii) the optimization is performed on a mean dataset with less noise than individual data and iii) the MDS algorithm gives a direct measurement of the amount of error introduced by the flattening. For our fits, the 2D reconstruction accounts for 95% of the variance in our data. This atlas for human V1 (shown in Figure 4) provides a ready reference for the distance on the cortex between any two locations in the visual field.

--- Figure 4 ---

Cortical Area does not Depend on Polar Position

Schwartz's complex-log models predict that the area representing the vertical meridian is greater than the area representing the horizontal meridian (see Figure 5 a,b). This

meridional anisotropy reaches the theoretical maximum of a factor of 2 at $a = 0.77^\circ$ eccentricity. We therefore made detailed measurements of this area in our dataset. Specifically, we measured the area of cortex in V1 representing the central 0.5° to 1.5° of eccentricity at 9 different polar angles (Figure 5c). To avoid distortion we performed all measurements in the 3D surface reconstruction of the cortical manifold (see Methods). The average cortical area of the areal bins is 52 mm^2 . There was no significant effect of polar position on M_A .

--- Figure 5 ---

The Concept of Equal-Area:

To clarify the amount of meridional anisotropy inherent in the Schwartz model, we estimated the ratio of the area representing a small square at the horizontal and the vertical meridians (see Figure 6a red digits, see also Figure 5). The meridional anisotropy is 1 (or none) at the fovea, increasing up to a factor of 2 (in area) at 0.77° (at $E = a$), then decreasing again towards the periphery. In peripheral regions the predicted anisotropy increases again (as E approaches b). In short the Schwartz model predicts that there is up to twice as much visual cortex associated with the vertical meridian than the horizontal meridian, and does so and does so in a critical part of the visual field: the fovea.

We did not observe the meridional anisotropy near a as predicted by the complex-log model in our fMRI data (Fig. 5c). Squirrel monkey data from Adams and Horton (2003) are consistent with our observations. We therefore suggest a new model that would preserve meridional isotropy of the area (M_A) at the expense of a small degree of local anisotropy (linear, ratio of M_E/M_P).

In principle, there are several ways to achieve equal-area meridional mapping. A mathematically simple approach is to ensure that the imaginary part (azimuth or polar position) of the complex-log transform stays small. In practice, our suggestion is to first divide the polar position value by a large number (the larger the better, in practice 5 is

sufficient) and subsequently multiply the real part of $w(P, E)$ by the same value (Divisory Model).

$$w(E, P) = k * \left\{ \text{real} \left[\log(E * e^{i*P/\eta} + a) \right] + \text{imag} \left[\log(E * e^{i*P/\eta} + a) \right] \right\} * \eta \quad (3)$$

in the limits as $\eta \rightarrow \infty$. For $\eta = \infty$ the derivative of this function is equation 1. Although eq. 3 solves the meridional anisotropy, it does so at the expense of a strong compression of the local angles in the central fovea (Fig.4b). To avoid this compression, we therefore introduce a second method that takes an iterative approach to solving the problem of meridional anisotropy by a parametric shear of the polar angle magnification (Parametric-2D-Shear Model). This model calculates the projected area for a given eccentricity and various polar angle ranges starting from the horizontal meridian. The increase of projected area further away from the horizontal meridian is then corrected iteratively by the application of successive local rotational shears in the polar direction. This operation results in the 2D shear map presented in Figure 6c resulting in an equal-area model (Figure 6d), note that the amount of shear varies with eccentricity and polar position. This model has near-zero meridional anisotropy ($< 0.1\%$ after 10 minutes of iteration) at the cost of introducing a local anisotropy (indicated by the coloration in Figure 6d).

Since this iteration process is time consuming, we approximated the numerical fit with a two-dimensional shear function that provides the same map within 0.3% of the iterative result. Accordingly we suggest the mapping function:

$$w(E, P) = k * \log(E * f_a(E, P) + a), \quad (4)$$

where $f_a(E, P)$ is a shear function that can be either determined iteratively or using the simple closed form approximation

$$f_a(E, P) = \exp \left(i * P * \text{sech}(P)^{\text{sech} \{ \log(E/a) * 0.76 \} * 0.1821} \right) \quad (5).$$

This Double-Sech approximation provides a near optimal fit over a wide range of a or b . The 2-dimensional shear function was chosen by inspecting the iteratively determined shear function. The fact that the functions that combine to describe the shear are both hyperbolic secants may be coincidence. However, the $\text{sech}(P) - \text{sech}(\log(E))$ combination of eq. 5 gave a particularly accurate approximation to the iterative determined shear. A third parameter g/Sh can be used to apply a global shear, analogous to the rotational shear α_1 suggested by Balasubramanian et al. (2002), but may not be necessary. We fitted these three models to our V1 data and found that both the Divisory and the Parametric-2D-Shear models describe our data better than the models proposed by Schwartz and its variations proposed by Balasubramanian et al. (2002). (We provide additional descriptions, fits and errors, including Matlab code demonstrating the models, in Supplementary Materials).

--- Figure 6 ---

In 2002 the Schwartz group proposed an intriguing extension of their model, the Wedge-Dipole Model (Balasubramanian et al., 2002). This model presents a simple way to integrate V1, V2 and V3 into one single mapping function, potentially providing the possibility of predicting the detailed properties of these visual areas, by introducing a single polar shear/scaling parameter $\alpha_1, \alpha_2, \alpha_3$ for each retinotopic area. Unfortunately, the Wedge-Dipole Model suffers even more from the meridional anisotropy flaw of the original Schwartz model (Fig. 7a). Our equal-area models fix this problem not only for V1, but also for V2 and V3, making the approach suggested by Balasubramanian et al. (2003) feasible. The correction is shown for the Divisory Model and the Parametric-2D-Shear Model in Figures 7b,c.

--- Figure 7 ---

Widths of V1 and V2

The widths of area V1 and its neighboring maps (V2, V3) are important properties of the visual cortex mapping. However, these widths have never been measured systematically. All current models of V1 assume that, at the representation of the center of the visual field, the width of V1 is zero. The width of V1 then increases with eccentricity until it reaches a maximum at around 12 - 16°. It then decreases again at the peripheral end of the representation (see V1 diagram from Horton and Hoyt, 1991a, their Fig. 3). Imaging data for human visual areas are usually presented as flatmaps, computationally unfolded and flattened approximations of the cortical surface (Serenio et al., 1995; Tootell, 1996; DeYoe et al., 1996; Van Essen et al., 2001; Press et al., 2001). These illustrations are useful for visualization purposes but the computational flattening distorts the true shape of V1. We therefore measured the widths of V1 and V2 along isoeccentricity lines through the 3D cortical manifold. Our measurements show that the widths of both areas increases steadily from 0.5° to 8° eccentricity, a key property of human V1 and V2 that has not been previously quantified. The sketch of human V1 provided by Horton and Hoyt (1991a), for example, suggests that human V1 reaches its maximum width as early as 2.5° eccentricity (Fig. 8).

--- Figure 8 ---

The Lengths of the Meridians

All the retino-cortical projection functions described so far share one effect of polar position: the representation of the vertical meridian is longer than that of the horizontal meridian. If the cortical manifold can be flattened without distortion it follows that the true lengths for the meridians, as measured on the three-dimensional cortical sheet, must differ as well. To test if this particular effect of polar position is present in our data, we measured the lengths of lines of constant polar angle within cortex. For each line, we plotted eccentricity in visual space against cortical distance. Crucially, these measurements were made in the undistorted 3D cortical manifold and they provide a critical test of whether V1 can be described with 2D models.

--- Figure 9 ---

We found that in V1 the average vertical meridian representation ($n = 8$) is longer than the average horizontal meridian representation by a factor of $1.26 (\pm 0.06)$ over the range 0.5 to 12° eccentricity (Figure 9). The lengths of these isopolar meridians increase gradually with polar angle and there was no difference between the upper and lower visual fields (see Supplementary Material). These results match the predictions from our models (see Supplementary Materials). This match between the measured lengths and the planar model with no intrinsic curvature suggests that there is little intrinsic curvature in V1. The consequence of the difference in length between the two meridian lines is that M_P depends on polar position: it is larger for the vertical meridian than for the horizontal meridian. Since M_A is independent of P (Figure 5), M_E must vary with P as well. And since $M_A = M_E * M_P$ the local anisotropy (M_E/M_P) must vary with polar position as well.

We now consider the length of the next horizontal meridian representation, the V2/V3 border. It is interesting that the V2/V3 border length is very similar to that of the V1/V2 border as well as the intermediate, *i.e.*, oblique, isopolar meridian in V2 (not shown). This means that M_P at the V2/V3 horizontal meridian is roughly the same as on the V1/V2 border, but is significantly different from M_P at the horizontal meridian in V1, despite the fact that they represent the same part of the visual field. Since M_P is larger in V2 than in V1, while V2 has a smaller areal magnification than V1, it follows that M_E in V2 has to be much smaller than in V1. In other words, there is large local anisotropy in V2, with M_P being about twice the value of M_E on average.

Discussion:

We have presented a new dataset that allows us to test different models of the way that visual space is mapped to visual cortex. As is well known, the dominant principle in these mappings is a compression of the visual field representation with eccentricity. This compression is approximately logarithmic, with a small offset to avoid an infinite

magnification in the center of the visual field (Fig. 2c). Areas V1 and V2 both contain complete maps of visual space and because they share borders; their shapes are highly constrained, especially in and around the foveal confluence.

These constraints set up competing requirements between global isotropy, local isotropy and local conformality of the V1 map and of the two segments of the V2 map lying adjacent to it. In principle, these requirements could all be satisfied if the maps had appropriate intrinsic curvature, but violations of one or other of these principles are necessary if the maps are intrinsically flat or if the curvature is constrained by other factors. Our detailed measurements assess both the intrinsic curvature of the mappings and the particular solution that has evolved in the human brain among the competing mapping principles.

We first consider the foveal measurements in the present study and how they constrain the layout of the foveal confluence. We then discuss the assumptions and implications of the three-dimensional shape of visual cortex, and why we think that flat models for V1 are useful. Finally, we discuss inter-subject variability and show that it consists of predominantly a scaling factor and with little variation in the other mapping parameters.

Measuring the Fovea

One of the most important contributions of this paper is to provide detailed data down to 0.5° of eccentricity. Retinotopic mapping in the fovea is technically challenging and consequently data from this region is not usually analyzed in studies of human cortical magnification. One of confounding factors for foveal measurements is the occurrence of spontaneous eye movements. Assuming that subjects fixated most of the time and that eye movements are random, sufficient averaging should reveal the mapping up to the centermost part of the visual field, with gradually increasing noise towards the center of the fovea. Although all subjects are instructed to maintain fixation at the center of the fixation cross, some eye movements are inevitable. However, the use of an invariant fixation grid while viewing the cycling retinotopic stimulus provided substantial improvement in the fixation accuracy during the scans and repeated averaging reduces

the effects of momentary eye movements. In separate experiments, we made high precision measurements of our subjects' ability to fixate by presenting the retinotopy stimuli whilst simultaneously imaging the fovea using a Rodenstock scanning laser ophthalmoscope. On average, our subjects fixated with a standard deviation of only 11 arc min. Our measurements of subject fixation in the MR scanner are consistent with this value although our MR eyetracker can only measure with a precision of 20 minutes of arc.

Another problem with measuring at the foveal representation is the limited spatial resolution of fMRI. Based on the analysis of this paper, the average human foveal projection (0 to 0.5° of eccentricity) of V1 covers an area of 142 mm^2 (~ 14 voxels), and is roughly 17 mm (~ 5 voxels) wide at 0.5° while being only 9 mm (~ 3 voxels) wide at 0.25° eccentricity. This calculation illustrates how difficult it would be to measure the widths of V1 and V2 at 0.25° eccentricity, where each half of V2 would be only about 4 mm wide (i.e., the V2/V3 border is little more than a voxel away from the V1/V2 border). To image the last 0.5° of the fovea one would therefore need higher resolution scans. We estimate that using 1.5^3 mm voxels would allow substantially better detail, allowing one to map down to 0.2° eccentricity.

Layout of the Foveal Confluence

The maps of the early visual areas V1, V2 (dorsal and ventral) and V3 (dorsal and ventral) converge toward a 'foveal confluence' near the occipital pole in human brains (Sereno et al., 1995; Tootell et al., 1996; Press et al., 2001; Dougherty et al., 2003; Brewer et al., 2005). Unfortunately, the layout of early visual areas at the very center of the fovea remains unclear. All current theoretical models based on the Balasubramanian wedge-dipole layout propose that V1, the two halves of V2 and even the two halves of V3 come down to a single point. Current anatomical reviews in monkeys, however (Rosa and Tweedale, 2005 for marmoset; Gattass et al., 2005 for cebus and macaque), suggest that V2 does not come down to a point but rather forms a strip with significant width. Our measurements indicate that if V2 forms a strip at the fovea, at least in humans this strip is not more than 7 mm wide at 0.5° (see Figure 8b). Gattass et al. (2005), on the other hand

suggests a rather wide strip of V2 from 0 up to 2° eccentricity, even proposing a larger representation of foveal V2 than foveal V1. This is in clear disagreement with the width data we present here (see Figure 8; V2 is narrower than V1 at every eccentricity). The results of Rosa and Tweeddale (2002) on the other hand indicate that this strip narrows down below 1 mm in the tiny brain of the marmoset monkey.

The Flatness of Human V1 or the ‘Rugby Ball’ Concept.

All published models of the properties of human V1 would be invalid if human V1 contained significant intrinsic curvature. One could imagine that human V1 was intrinsically ellipsoidal, having the 3D shape of the surface a rugby ball (or a part of it), where the poles represent the fovea and the far periphery. Each seam on the rugby ball would represent a different polar angle and each one could thus have precisely the same geometry, allowing a log-polar projection function with ideal properties: local and global isotropy as well as conformality of the angular mappings. Any 2D projection of this ideal mapping would, however, introduce systematic distortion ruining these perfect properties. A similar argument was presented by Rovamo and Virsu (1984), arguing that macaque operculum is not flat. Although we know that human V1 is a convoluted manifold in 3D space, it appears that the V1 geometry is intrinsically flat and only folded within the calcarine sulcus (see following paragraphs). Human V1 may be more folded, but appears to be flatter than for example squirrel monkey V1, which incorporates substantial intrinsic curvature (Adams, D.L., personal communication). Kaplow and Schwartz (1986) investigated the flatness of macaque V1 and came to the conclusion that the error due to flattening is small (5%) and therefore intrinsic curvature is negligible. However, the fact that the average distortion is small means neither that it is not systematic nor that is small in every location.

The strongest argument for human V1 being intrinsically flat is the increasing length of the isopolar lines with polar angle from the horizontal meridian (see Figure 9, and Supplementary Materials). While a rugby-ball-shaped V1 would imply that the lines should have equal length, any flat V1 model consistent with our data would predict that these lengths increase with polar angle. Tootell et al. (1988) reported such a result in

macaque. However, these measurements were made in a flattened macaque cortex, and the difference might possibly have been due to some flattening distortion. Here, we measure the same effect directly in the folded and unflattened cortex, providing strong evidence that human V1 is at least not a perfectly symmetric rugby ball. Further, the strength and layout of the anisotropy matches the predictions from our flat model (Supplementary Figure 3), suggesting that V1 is indeed intrinsically flat.

For V2 the situation is different, however. Although the models we propose in Figure 7 assume that both V2 and V1 lie within a homogeneous flat plane, this may not be the case. To our knowledge the flatness of V2 has not been investigated so far. The equal-area maps of Figure 7b,c illustrate that an equal-area planar map of V2 must violate conformality. Maintaining conformality in a flat V2 would require a huge degree of meridional anisotropy (see Figure 7a, and Figure 8b, red lines). Both problems could be solved if the V2 mapping were intrinsically ellipsoidal (the rugby-ball model). In this context it is interesting to note that – in contrast to V1 – all measured V2-meridian representations from horizontal through vertical, have the same length within the precision of our measurement. This suggests that V2 is probably best described with the rugby-ball model, rather than the intrinsically flat and only folded variants of the Balasubramanian model. We do not have sufficient material to test this hypothesis further, but we present and illustrate it in Supplementary Materials.

Reconstructed average map of Human V1

Since we did not find systematic curvature in V1 we reconstructed a 2-dimensional reconstruction of human V1 in Figure 4a. This map allows a ready reference for the average distance between the representations of visual field locations on human primary visual cortex. An interesting feature of this reconstruction is that the isoeccentricity lines beyond 8 degree appear convex with their representation around the horizontal meridian closer to the fovea than the ends of the isoeccentricity representations. This is an interesting feature that is strongly present in the data from Tootell et al. (1988), where it is clearly evident as early as 3 deg. of eccentricity. While the dipole model proposed by Schwartz (1983) predicts such convex isoeccentricity lines, the strength and the onset at

small eccentricities, would suggest a very small value for b . A very small b , however would put several other constraints on the model (see Supplementary Materials).

The map of local deviation of the reconstruction with the originally measured grid shows that there is more local error in the perifoveal part of the reconstruction and more error in the ventral half than in the dorsal half. We did not find any other significant difference between the ventral and the dorsal half of V1. The higher error in the foveal part of the reconstruction could be explained by the fact that smaller distances are more difficult to measure (see Supplementary Materials).

Intersubject Variability

Dougherty et al. (2003) investigated the representation of the visual field in V1 to V3 of 6 human subjects using a similar methodology. The Dougherty et al. study illustrated the high degree of intersubject variability in V1 area (up 2.4 times; see also Stensaas et al., 1974). We confirm these results: the largest V1 in our sample has 2.3 times the area of the smallest. However, as we illustrate, these extreme cases basically differ in overall size and have no significant difference in the shape of their V1s (see Supplementary Materials). This invariance is in agreement with the finding by Tootell et al. (1988) that magnification correlates with the size of striate cortex.

It could be argued that, due to the substantial variation between different subjects' V1s, there is little point in making a detailed average. If one is not in a position to measure the V1 morphometry for individual subjects, however, a good average is certainly the best estimate of its parameters. This is also true if we wish to relate cortical magnification to psychophysical data averaged across subjects. Besides, it is worth noting that a maximum variation of 2.3 in area reflects a factor of only 1.5 in linear size, and that the standard deviation of our k parameter is only $\pm 15\%$.

Is Visual Cortex Conformal?

One of the central questions to distinguish the different variants of models proposed here is the degree to which they exhibit conformality of the angular mapping. The original

Schwartz model is perfectly conformal for V1, such that right angles in the visual field project to right angles on cortex, for example. However, subsequent refinements to this model introduce a shear in the polar angle direction (Balasubramanian et al., 2002) and, as the authors note, this eliminates conformality. Unfortunately there are no good estimates as to how conformal the organization of visual cortex is, and even the benefits of a conformal visual cortex are unclear. This issue is even less clear when considering V2 and V3. In the fovea there is theoretically space only for a conformal V1 and V2 (leaving no room for V3), but this conformality can be achieved only at the cost of a strong meridional anisotropy between the horizontal and vertical meridian representations. That is, conformality would produce a small horizontal meridian and large vertical meridian representations in V1, with the opposite arrangement in V2). However, this does not match our data (Figures 7 and S3).

The Different Forms of Magnification and anisotropy

Our results agree with current estimates of cortical magnification in humans, (Levi et al. 1984, Slotnick et al 2001, Dougherty et al 2003), but cortical magnification must be considered as a two-dimensional property of visual cortex, depending on both eccentricity and polar position. When investigating cortical magnification, for example using psychophysical methods, it is essential to be clear about what kind of magnification one is investigating (linear or areal), and it is also important to map it in both dimensions of the visual field. The models that we have developed (Figures 6, 7) enforce equal-area magnification within each eccentricity range. This uniformity comes at the cost of a systematic pattern of *local* anisotropy. In particular, we predict large differences in local anisotropy on the horizontal and the vertical meridian representations around 0.77° eccentricity.

Most psychophysical studies relating performance to (presumed) cortical area have used relatively eccentric stimuli. We suggest that investigation of such properties at the critical eccentricities below 1° would allow a test of the predictions we make here, possibly improving the fit of the parameters a , b , and k . Such studies could also evaluate

the intersubject variability of the parafoveal mapping in the manner used by Duncan and Boynton (2003) for analyzing mapping functions beyond 1.5° eccentricity

Ocular Dominance Columns and anisotropy:

One of the most prominent anatomical features of human and macaque V1 are the ocular dominance columns (LeVay et al. 1975; Horton and Hedley-Whyte, 1984). These and other substructures of visual maps are not part of any current retino-cortical projection model. There is strong evidence that each of these substructures contains a continuous representation of most parts of the visual fields, and that these maps are interdigitated (Blasdel and Fitzpatrick, 1984; Tootell et al., 1988; Shipp and Zeki, 2002) into the overall map of a given area. However, in V1 these interdigitated maps are shown in the monocular input layers (Blasdel and Fitzpatrick, 1984; Tootell et al., 1988) and may not extend throughout the binocular layers.

In V2 Shipp and Zeki (2002) have termed the organization of these submaps a “ratchet model” and demonstrated that the mean of each of the roughly 1mm wide stripes follows the continuous macro map, a model that could easily be integrated into the current models. With the current resolution of fMRI being 3 mm, however, these micro deviations are invisible. Tootell et al. (1988) found local anisotropy in macaque V1, but no overrepresentation (in area, as estimated by width) of the vertical versus the horizontal meridian. They suggest that the pattern of local anisotropy is associated with the pattern of ocular dominance columns. To be precise, they suggest a higher magnification perpendicular to the ocular dominance columns than along them. We would like to point out that this is precisely the same pattern suggested by our Parametric-2D-Shear Model. Based on this model, we would suggest a magnification of roughly 1.4:1 (perpendicular/parallel) across pairs of ocular dominance columns (or in layer 2/3 and 6 or in the macro map), implying a ratio of 0.7:1 within one ocular dominance column (or within the micro map).

The pattern of local anisotropy suggested by our model matches the pattern observed in several monkey species (Gatass et al., 1987, for cebus monkey; Tootell et al., 1988, for macaque monkey; Fritsches and Rosa 1996 for marmoset monkey, Adams and

Horton 2003 for squirrel monkey). In short: sectors along the horizontal meridian are compressed along eccentricity axis, whereas sectors along the vertical meridians are elongated (see Figure 6d).

For V2 we suggest (and measure) an overall anisotropy of 2:1, that is V2 is elongated in the eccentricity direction or parallel to the stripe structure. Assuming that the complete eccentricity range is represented in each of the three stripe types, this would result in anisotropy of roughly 0.66:1 within a stripe.

Conclusions:

Cortical magnification is a two-dimensional property of visual cortex, depending on both eccentricity and polar position. It can be described in terms of either linear magnification (in various directions), or areal magnification. When investigating cortical magnification it is important to express the magnification function for both axes of the maps, in terms of both the local and global anisotropies of the mapping. We provide high-density mapping data from many subjects over an extended range of eccentricities and derive an accurate mapping formalism (eq. 5) that accounts for the cortical morphometry of the first-tier retinotopic areas within a geometric error of 0.3%.

Appendix

Cortical Magnification in Two Dimensions

The concept of cortical magnification was introduced by Talbot and Marshall (1941) and described as a function by Daniel and Whitteridge (1961), who defined it as the displacement of two cells in *mm* on the cortex divided by the displacement of their receptive field centers in *deg* (in units of *mm/deg*). This is a one-dimensional measurement and accordingly magnification is often specified as:

$$M(E) = \frac{k}{E + a}, \quad (\text{A1})$$

where E is the eccentricity of the receptive field (in *deg*) and k (in *mm*) and a (in *deg*) are free parameters. Note that, in this formulation, the magnification is assumed to be independent of azimuthal position in the map (which we will call ‘polar angle’, P). If this assumption is relaxed, then M becomes a function of both E and P , requiring the definition of two magnification directions, M_E and M_P that combine into a full two-dimensional function. The assumption that the angular position has no effect on the magnification is based on two observations (Daniel and Whitteridge, 1961):

i) The cortical magnification is the same in both the angular and radial directions ($M_P = M_E$). For clarity we will call this **local isotropy** (or **anisotropy**, where violated). However, it is important to note that later studies indicate that V1 may show only approximate local isotropy. For example, Adams and Horton (2003) find a pattern of systematic local anisotropy in V1 of the squirrel monkey.

ii) The cortical magnification for a given eccentricity is the same at different angular positions. This means that the cortical magnification changes with E , but not with P , and is therefore identical along the horizontal and the vertical meridians for a given eccentricity. We will call this property meridional isotropy (but see Van Essen et al., 1984 for a report of meridional anisotropy in macaque monkey).

It is important not to confuse these two properties of the magnification parameters. The degree of local (an)isotropy says little about any meridional difference between the horizontal and the vertical meridians (or intermediate meridians), and the degree of meridional (an)isotropy says nothing about the local ratio between M_P and M_E at a given point of the visual field. In this paper, we show that V1 exhibits local anisotropy, but a reasonable degree of meridional isotropy is found for the areal magnification M_A .

Areal magnification (Myerson et al., 1977; Tusa et al., 1978) is a two-dimensional metric: the **area** of cortex per **area** of visual field ($M_A(E,P)$ [in mm^2/deg^2]), where (P,E) are the coordinates of the visual field. Areal and linear magnifications are closely related. Specifically,

$$M_A = M_E * M_P . \quad (\text{A2})$$

If M_E and M_P are the same (isotropy), they are also the equal to $\sqrt{M_A}$.

In short, areal magnification, as well as the linear magnifications in any direction, are two-dimensional functions of both visual field dimensions. The analysis of any of these functions in terms of one of its dimensions has to be parameterized by the other, orthogonal, dimension. In particular, any magnification as a function of eccentricity may be specified separately for the horizontal meridian by $M(E,0)$ and at the vertical meridian by $M(E,\pi/2)$, respectively (see Figure 6).

Schwartz (1994) pointed out that the linear magnification is a partial derivative of the overall retino-cortical projection function $w(E,P)$. To be precise, there are three interesting derivatives of this function: We can consider the partial derivative with respect to eccentricity which yields the conventional linear eccentricity magnification function, along lines of constant angular position:

$$M_P = \frac{\partial w}{\partial E} \quad (\text{A3})$$

We could also consider the partial derivative with respect to polar angle giving the polar magnification function along lines of constant eccentricity:

$$M_E = \frac{\partial w}{\partial P} \quad (\text{A4})$$

Finally, we can compute an areal magnification function that takes account of both of these quantities:

$$M_A = \frac{\partial w}{\partial E} * \frac{\partial w}{\partial P} \quad (\text{A5})$$

Different forms of magnification (M_P , M_E , M_A) as well as the retino-cortical mapping function are frequently estimated in both physiological and psychophysical experiments and to interpret them clearly it is important not to confuse the definitions.

The Retino-Cortical Mapping Function

It is clear that the various forms of the cortical magnification function depend on the form of the retino-cortical mapping function $w(E,P)$. Schwartz (1977) proposed that this function can be approximated by:

$$w(E,P) = k * \log(E * e^{i*P} + a), \quad (\text{A6})$$

and noted that the derivative of this function is “in the order of”

$$w' = \frac{k}{E + a}. \quad (\text{see eq. A1}) \quad (\text{A7})$$

In fact, we point out that the exact derivative of the Schwartz function (eq.A6) is:

$$M_P = \frac{\partial w}{\partial E} = k * \frac{e^{i*P}}{E * e^{i*P} + a} \quad (\text{A8a})$$

This derivative is a function of P , and consequently is not independent of P . When $P = 0$ (at the horizontal meridian) or when E is much greater or much less than the free parameter a , the expression reduces to equation A7, but for eccentricities close to a , the effect of P is significant. At the eccentricity $E = a$ it becomes

$$\frac{\partial w}{\partial E}(P) = k * \frac{e^{i*P}}{a * (e^{i*P} + 1)} \quad (\text{A8b})$$

The eccentricity magnification function is thus strongly dependant on P and changes by a factor of $\sqrt{2}$ between the horizontal and vertical meridians. In short, the Schwartz complex-log projection entails a strong dependence on polar position P in the neighborhood of the eccentricity of parameter a .

Estimates of the magnification function based on mapping theory (Schwartz et al., 1977, 1994), on anatomical measurements (Horton and Hoyt, 1991a) or on psychophysical estimates (Levi et al., 1984; Yap et al., 1987) suggest a value of roughly 0.75° for a . (Dow et al., 1981, 1985, give a lower value, but their data were reinterpreted by Levi et al., 1984 to be compatible with the 0.75° value). The Schwartz model therefore predicts the strongest global anisotropy around the perifoveal eccentricity of 0.75° .

The original Schwartz model only describes the singularity at the foveal portion of the projection function. In a figure caption, Schwartz (1983) extended the complex-log transform to a dipole model to account for the peripheral mapping behavior. This model (Figure 6a) introduces a third parameter b , creating a second singularity in the periphery.

$$w(E, P) = k * \log\{(E * e^{i*P} + a)/(E * e^{i*P} + b)\}, \quad (\text{A9})$$

or, if simplified to consider only the horizontal meridian by setting $P = 0$:

$$w(E) = k * \log\{(E + a)/(E + b)\}. \quad (\text{A10})$$

Under this assumption, the dipole model generates a more complicated expression for the magnification function:

$$w'(E) = k \frac{b - a}{(E + a)/(E + b)} \quad (\text{A11})$$

It is important to note that this expression for the V1 map introduces curvature into the magnification function that corresponds to the third-order term introduced by Rovamo and Virsu (1979) into their power series expression for their magnification function. The dipole model thus provides a simpler approach to the same concept. However, just as estimating the parameter a requires precise measurements in the fovea, estimating the parameter b requires good peripheral data. This dipole model has received considerably less attention, than the original model and there are no good estimates of b . Magnification data including peripheral data is therefore usually fit to a power function (van Essen et al., 1984; Adams and Horton, 2003), rather than to equation A11. Those studies that have attempted to estimate it give a value for b between 90 and 180° (Balasubramanian et al. 2002).

In conclusion, there has been no previous publication of the exact form of the 2D magnification function implied by the complex-log transform, which is widely regarded as an adequate characterization of the cortical mapping function. Our analysis reveals that the exact form of this is meridionally anisotropic, and that no mapping onto a planar metric can simultaneously preserve the meridional isotropy, local isotropy and conformality of the resultant map.

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Figure 1: a,b. Atlas fits in two subjects shown on flattened representations of visual cortex. The upper row shows measurements of angular position (semi-circular wedge icons); the bottom row shows measurements of visual field eccentricity (eccentricity bar). In each pair of maps, the original fMRI data are on the left and the resulting atlas fits are on the right. Visual areas V1, V2 and V3 are indicated by red, black and blue borders respectively. It is important to emphasize that, although these data are displayed most conveniently on flattened cortical sheets, all our measurements were made on the original, folded cortical manifold to avoid distortion.

Figure 2: Mean $M_{\sqrt{A}}$ versus eccentricity across all subjects fitted by eq. 1. a) Measurements across areas and studies. V1 data are plotted in red (fit: $a = 0.77 \pm 0.03$; $k = 19.2 \pm 0.25$) and V2 data are plotted in blue (fit: $a = 0.73 \pm 0.03$; $k = 15.9 \pm 0.21$). The gray line shows the cortical magnification function (V1) from Horton and Hoyt (1991a) ($a = 0.75$; $k = 17.6$) and the red ‘*’ symbols are points from Dougherty et al. (2003). Error bars are one standard error of the means. Since our measurements did not extend beyond 12° of eccentricity, the data are well described by the monopole model or the corresponding linear magnification function (equation 1). b) Across subjects from this study. Colored graphs show the results on individual subjects, the dotted gray line the fit for V1. c) Mean inverse magnification of V1 with the best-fitting straight line, for ready comparison with studies such as Rovamo and Virsu (1979), Levi et al. (1984), McKee and Nakayama (1984), Stensaas et al. (2001), Tyler (2001) and Duncan and Boynton (2003).

Figure 3. a) Comparison of linear CMF in V1 across primate species. The black line displays the V1 fit from this study, compared to results from van Essen et al. 1984, Dow et al., 1985; Le Vay et al., 1985, Tootell et al., 1988; Adams and Horton, 2003; Rosa and Tweedale, 2000. b) For comparison we scaled the results from the different monkey species so that they roughly match the human data in area. For macaque we used the data by Van Essen et al., 1984.

Figure 4: a) Two-dimensional reconstruction of human V1, derived from our measurements. The colored numbers depict the isoeccentricity points, LVM = lower vertical meridian, HM = horizontal meridian, UVM = upper vertical meridian. b) map of local distortion of the reconstruction from the measured distances. The mean distortion is 9%, the highest distortion is 14%. This map depicts local error only, while the MDS optimizes the map for minimal error across all distances in the grid.

Figure 5: Dependence of M_A on the polar position. **a)** The central part of the visual field. **b)** The conventional Schwartz complex-log model with $a = 0.77^\circ$. The gray quadrilaterals depict the

projection from 0.7 to 1.1° eccentricity and 25° of polar angle, either at the horizontal or the vertical meridian. Note the significant difference in area with polar angle. **c)** Measured area of the visual representation from 0.5 to 1.5° eccentricity at 9 different polar angles: the error bars represent s.e.m. across subjects. The curve depicts the area predicted by the Schwartz model.

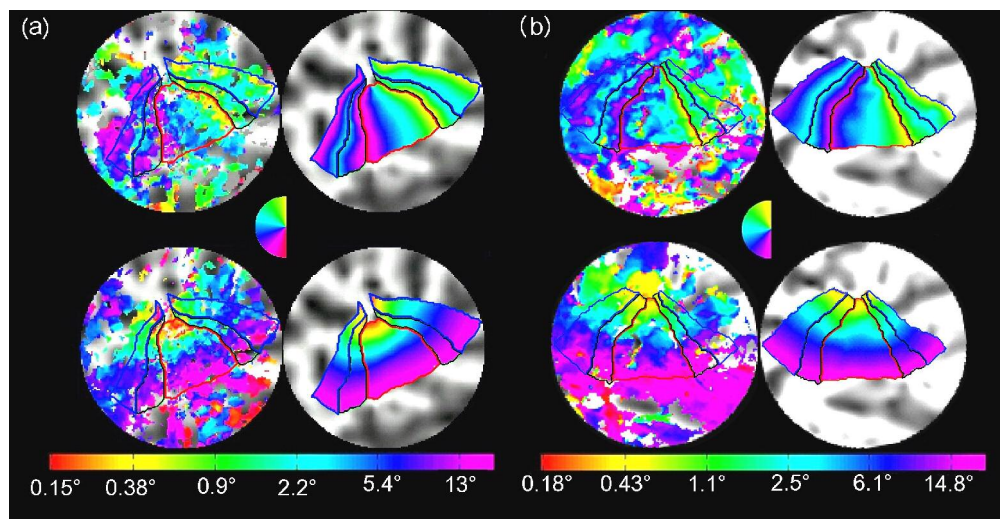
Figure 6: The new models and the predicted local anisotropies. All models: $a = 0.77$, $b = 150$, $k = 19.2$, and no further parameters. **a)** The Schwartz model predicts a complete local isotropy (that is $M_P = M_E$) over the whole visual field, although at the cost of a severe meridional anisotropy. The red digits at the top signify the degree of anisotropy (in area ratio) between the horizontal and the vertical meridians, the coloration signifies *local* anisotropy. **b)** The Divisory Model we suggest fixes the problem of meridional anisotropy, although at the cost of a small local anisotropy at the four corners of the projection. **c)** Map of azimuthal shear for the Parametric-2D-Shear Model. This figure shows only one quarter field, 0° being the horizontal meridian, 90° the vertical meridian. Note, that this figure has a completely different colormap than (a, b and d). **d)** The Parametric-2D-Shear Model depicted here has a balanced ratio where the average $M_P/M_E = 1$. This model predicts a complex pattern of local anisotropy, with $M_P > M_E$ (bluish) at the horizontal meridian, while $M_E > M_P$ (reddish) at the vertical meridian, as quantified in the color bar.

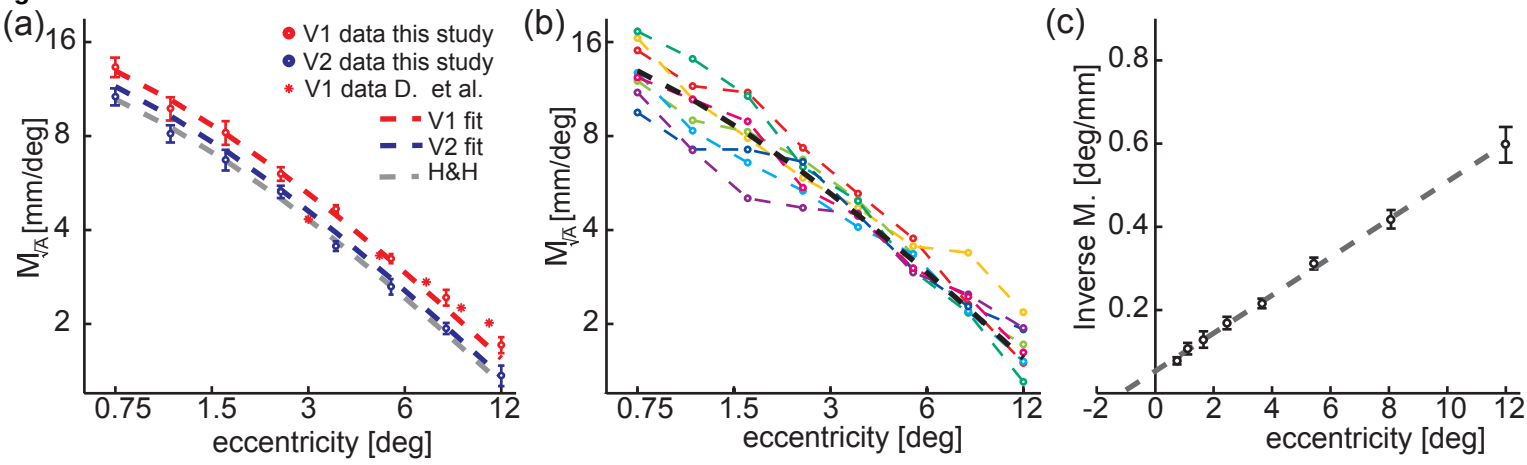
Figure 7: Modification of the Wedge-Dipole Model. **a)** The model as proposed by Balasubramanian et al. (2002), with $a = 0.9$ and $b = 170$, $\alpha_1 = 0.95$ $\alpha_2 = 0.5$. The gray areas represent the same part of the visual field in V1 and V2 at the eccentricity where $E = a$. The model predicts a dramatically larger representation of the central part of the visual field in V2 than in V1 (270%). **b)** The same parameters but using the Divisory Model, and **c)** using the Parametric-2D-Shear Model. The latter two models predict not a larger but a smaller representation in V2 than in V1 (55%, when using the same parameters as in Balasubramanian et al. (2002); we suggest a larger value for α_2 resulting 80% of the area), however all three models suggest that the representation in V2 is strongly elongated with respect to V1.

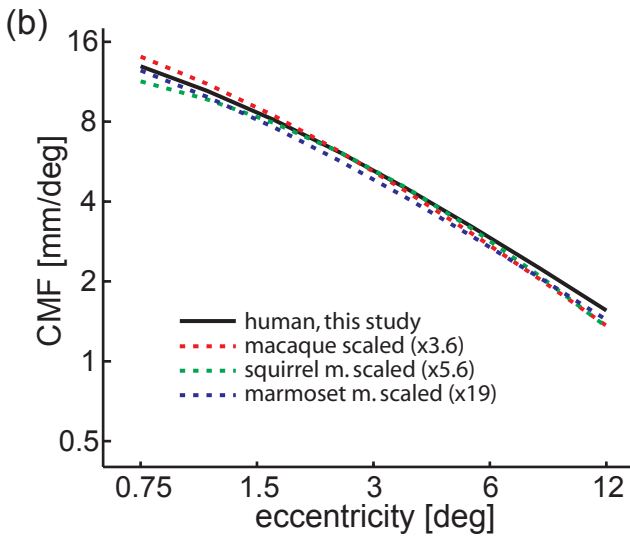
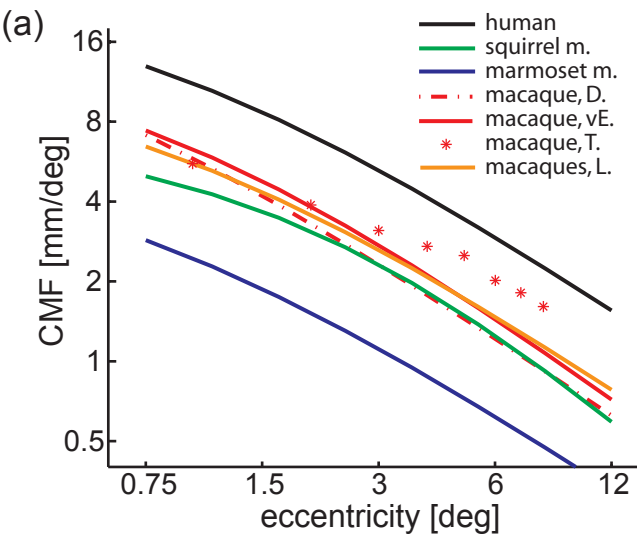
Figure 8: a) The width of V1 versus eccentricity. The blue curve shows the data averaged across 8 right hemispheres error bars indicate the standard error. The gray curve depicts widths measured from the sketch of Horton and Hoyt (1991a, Fig. 8), which is clearly narrower than our data. The red curve is the prediction of the Schwartz model, based solely on the parameters a (0.77) and k (19.2) from our fit of $M_{\sqrt{A}}$. The Schwartz model is an impressive approximation of the observed retino-cortical mapping widths. However, the prediction is too wide between 0.5° and 3° eccentricity, a symptom of the meridional anisotropy that we report in Figure 5. We plot the

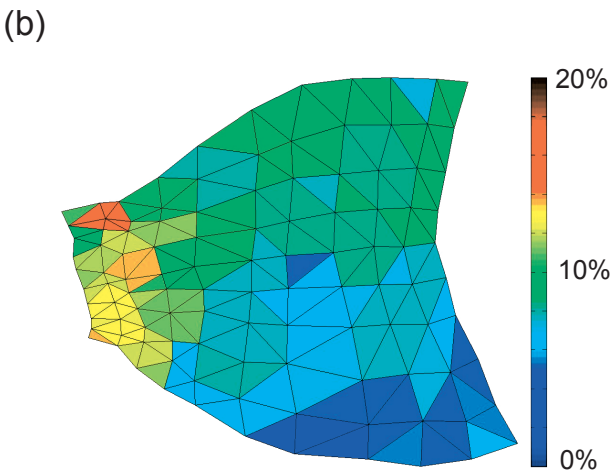
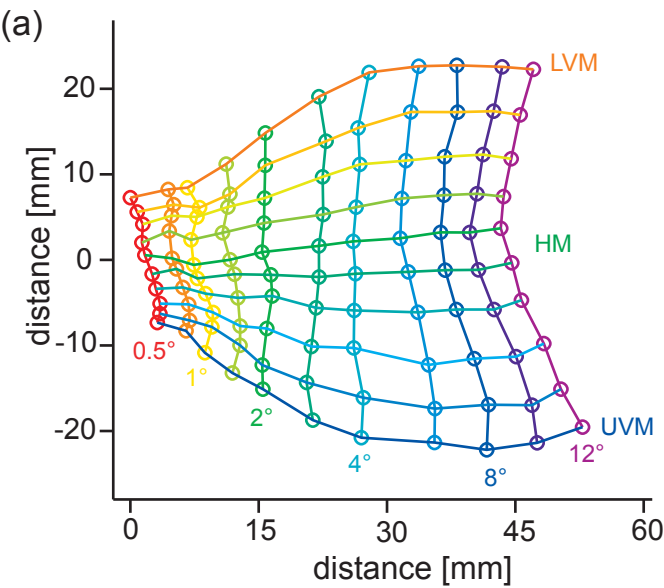
prediction from the Parametric-2D-Shear Model as the dashed green line. **b)** The width of V2 versus eccentricity. The blue curve shows our V2 data, averaged across 8 subjects. The red curves show the prediction from the Schwartz & Balasubramanian model (2002), the dashed green curve shows the prediction from the Parametric-2D-Shear Model (dashed lines - V2, dotted line - V3, although we did not measure V3 data). The prediction of the Schwartz model significantly overestimates the width at small eccentricities, while our model corrects for this. Note that we used the parameters suggested by Balasubramanian et al. (2002) throughout.

Figure 9. The length of isopolar lines. The solid black line shows the cumulative length for the horizontal meridian in V1, averaged across 8 subjects; error bars depict the standard error. The dashed black line shows the vertical meridian of V1 (*i.e.* the V1/V2 border). The dotted black line is for the horizontal meridian at the V2/V3 border. The dash-dotted gray curve shows the length difference for the horizontal vs. vertical meridians in V1.

**Figure 1**







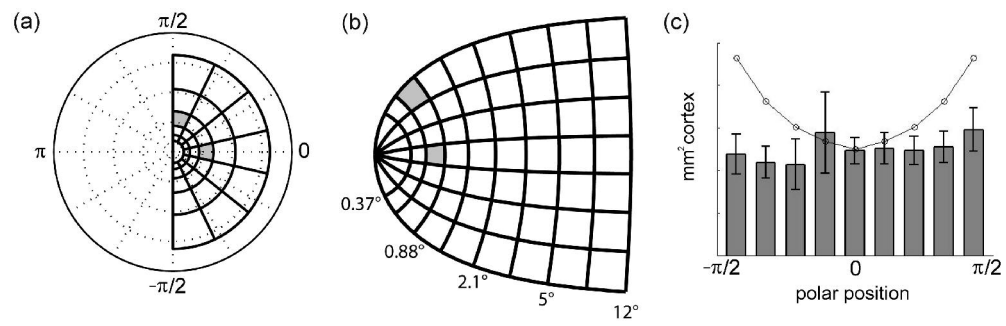


Figure 5

