Retinotopic Mapping of the Peripheral Visual Field to Human Visual Cortex by Functional Magnetic Resonance Imaging

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Abstract: Retinotopic mapping is a key property of organization in the human occipital cortex. The retinotopic organization of the central visual field of visual areas V1, V2, and V3 has been well established. We used fMRI to measure the retinotopic map of the peripheral visual field (eccentricity up to 60°). We estimated the sizes of the visual areas between 0° and 60° and obtained results consistent with anatomical studies. We also estimated the cortical distances and magnification factors for reconstruction of the retinotopic map using the peripheral wedge dipole model. By comparing the retinotopic map with the flattened surface, we analyzed the datasets used to reconstruct the map. We found that: (1) the percentage of the striate cortex devoted to peripheral vision in humans is significantly larger than that in the macaque, (2) the estimate of the scaling factor in linear magnification is larger than that found in previous studies focusing on central vision, and (3) the estimate of the peripheral factor in the dipolar model is too large to make the curve direction of the dipolar map in the periphery equivalent to that in the center. On the basis of our results, we revised the dipolar map to fit our conditions. The revised map in humans has a similar elliptical shape to that of macaques, and the central parts of the two species are the same. The different parts of the map are the peripheral regions, for which the peripheral wedge dipole model in humans is reversed compared to that of macaques. *Hum Brain Mapp* 27:1727–1740, 2012. © 2012 Wiley Periodicals, Inc.

Key words: retinotopic map; cortical magnification factor; cortical distance; peripheral visual field; fMRI; visual cortex

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INTRODUCTION

The human visual cortex includes the entire occipital lobe and extends significantly into the temporal and parietal lobes. Anatomy studies have shown that the primary visual cortex (V1) is located in the occipital lobe within and surrounding the calcarine sulcus. Between 1940 and 1990, the number of reported visual field maps grew enormously, and investigators began to hypothesize about the organization among the maps themselves. Data from human lesion and postmortem studies showed that neurons within the primary visual cortex and extrastriate visual areas are retinotopically organized, roughly following a polar coordinate system. As a stimulus moves from the fovea to the periphery, the locus of responding neurons varies from posterior to anterior portions of the calcarine sulcus, the site of the human primary visual cortex [Adams et al., 2007; Daniel and Whitteridge, 1961b].

The functional magnetic resonance imaging (fMRI) technique has rapidly become the standard for inferring neuronal activity in human subjects for its non-invasive, reliable response localization, and high spatial resolution properties [Kwong et al., 1992; Ogawa et al., 1992]. The fMRI is the preferred method for retinotopic mapping, which is the process of determining the correspondence between a visually selective neuron and its receptive field in visual space. Some early studies attempted to map the human primary visual cortex [Kwong et al., 1992; Schneider et al., 1993]. Engel et al. [1994] developed phase-encoded retinal stimulation. In their experiment, an annular contrast-reversing checkerboard pattern was presented at the center of gaze. This ring expanded in size until the beginning of the next cycle, when the stimulus returned to its original size and the period of expansion repeated. Expanding rings elicit a traveling wave of activity in the V1 and adjacent areas that is phase-locked with the period of the stimulus. As a result of phase encoding, Engel et al. could distinguish between the cortical representation of the fovea and that of the periphery. Many similar methods have been developed to define the borders of V1, V2, V3, V3a, and other visual areas on a computationally flattened representation of the cortical surface [Brewer et al., 2005; DeYoe et al., 1996; Dougherty et al., 2003; Engel et al., 1997; Fischl et al., 1999; Sereno et al., 1995].

Over the past century, neuroscientists have worked to compile an accurate retinotopic map of the visual cortex [Adams and Horton, 2003; Adams et al. 2007; Schira et al., 2007]. This effort has been motivated by a conviction that a more precise map would lead to a better understanding of how the brain converts the external world into an internal representation for visual perception. Compared to human visual research, the retinotopic map of the macaque monkey, which was constructed by Inouye [1909] and Holmes [1918], was relatively uncomplicated. Several groups have refined this retinotopic map to achieve greater accuracy [Adams and Horton, 2002; Blasdel and Campbell, 2001; Van Essen et al., 1984].

In contrast, it is more difficult to obtain accurate results for the human retinotopic map. Based on the work by Holmes, the map of the representation of the visual field in the human striate cortex was revised by lesion evidence [Horton and Hoyt, 1991] and postmortem data [Adams et al., 2007; Amunts et al., 2007]. Most recently, fMRI has become the dominant neuroimaging approach used to assess probe patterns of cellular organization in the human cerebral cortex [Qiu et al., 2006; Schira et al., 2007, 2009]. Since the means of stimuli delivery beyond $\sim 20^\circ$ off center were not readily available, however, most studies thus far have only concentrated on the center and/or peri-center of the visual field. Using a novel device that was specially built by our group, the primary aim of the current study was to map the retinotopic peripheral visual field extended to 60° of eccentricity, thereby expanding the map of the human primary visual cortex.

MATERIALS AND METHODS

Subjects and Stimuli

Eight healthy subjects without previous neurological or psychiatric disorders (age 19–31 years, mean age of 25 years; two women, six men) participated in the study. The subjects had normal or corrected-to-normal vision and were all right-handed. We obtained written informed consent from all subjects before the experiment. The study was approved by the Institutional Research Review Board of Kagawa University, Japan.

Visual stimuli were created on a display using a resolution of 800×600 pixels. The display stimulus was brought to the subject within the scanner by a wide-view optical-fiber presentation system. Monocular (right eye) presentations were performed with the optical-fiber screen (with a curved surface having a 30-mm curvature radius) placed in the center of the bore, 30 mm from the subject's eye. The visual field of the stimulus was 120° horizontal $\times$ 120° vertical. Because the screen was so close to the their eyes, subjects wore a contact lens (Menicon soft MA; Menicon, Japan) with +20, +22, or +25 magnification to retain their length of focus. The enlargement was taken into account when the sizes of the stimuli were calculated. Refraction of light in the +25, +22, and +20 diopter lenses increased the stimulus size by $\sim 8.9\%$ (+20) to 11.3% (+25) of the stimuli.

To identify the retinotopic areas of the visual cortex, fMRI scans were carried out while the subjects viewed phase-encoding stimuli [DeYoe et al., 1996; Engel et al., 1994; Sereno et al., 1995]. A high-contrast, black-and-white, radial checkerboard pattern (mean luminance 110 cd m^{-2} , contrast 97%) was used to reverse the contrast at a frequency of 8 Hz, with eccentricity ranging from 0 to 60° visual angles. For each hemi-field, two types of stimuli were used to locate visual area boundaries and to estimate the eccentricity. The stimulus for locating boundaries was a 22.5° wedge that rotated slowly counterclockwise around

Figure 1.

Dipolar map and isopolar angle maps of human visual areas. The top row shows a dipolar map coded by color [brown (fovea) -> orange -> blue -> cyan (periphery)] displayed on the original cortical surface (**A**), the unfolded cortical surface (**B**), and the

cut and flattened cortical surface (**C**). The bottom row shows the polar angle (blue (upper vertical meridian) -> green (horizontal meridian) -> red (lower vertical meridian)) plotted on the same three surfaces (**D-F**).

a red fixation spot at the center of the stimuli. The wedge rotated at steps of 22.5° , remaining at each position for 4 s before rotating to the next. The stimulus for estimating eccentricity was an expanding checkered annulus. The flickering radial checkerboard was moved from the center to the periphery in discrete steps (each step 7.5° , with a total of eight steps), remaining at each position for 8 s before automatically expanding to the next position. Each experimental run lasted 300 s. In each run, four complete rotations and expansions of the flickering checkerboard were presented. Six such runs were conducted, three using wedges and another three using rings. All experiments employed passive viewing, and subjects were required to maintain fixation throughout the period of scan acquisition. To minimize head motion, subjects' heads were stabilized with foam pads. All subjects wore a black mask to cover the left eye.

MR Data Acquisition and Analysis

The fMRI experiment was performed using a 1.5T Philips clinical scanner (Intera Achieva; Best, The Netherlands). All images were acquired using a standard radio-frequency head

coil. We acquired 23 slices that were approximately orthogonal to the calcarine sulcus to encompass most of the cortical visual areas. The T2*-weighted gradient echo-planar imaging sequence was used with the following parameters: TR/TE = 2,000/50 ms; FA = 90° ; matrix size = 64×64 ; and voxel size = $3 \times 3 \times 3 \text{ mm}^3$. Before acquiring the functional images, T2-weighted anatomical images were obtained in the same planes as the functional images using the spin echo sequence. A T1-weighted high-resolution image ($1 \times 1 \times 1 \text{ mm}^3$) was also acquired after each functional experiment. The functional and anatomical data were processed using the BrainVoyager software (Brain Innovation, Maastricht, The Netherlands; http://wiki.brainvoyager.com/BVQX_Matlab_tools) in Matlab (The MathWorks, Natick, MA).

Preprocessing of the Anatomical Data

The high-resolution T1-weighted three-dimensional (3D) MRI was used for cortical surface reconstruction of each subject. After the brain was segmented from surrounding head tissue, the gray and white matters were segmented via a region-growing method to reconstruct the gray matter cortical surface using the established procedures [Goebel

Figure 2.

Eccentricity maps of the left and right visual areas of subject LS and other subjects. The top row shows an eccentricity map coded by color [brown (fovea) → orange → blue → cyan (periphery)] displayed on the original cortical surface and the folded, inflated, and flattened cortical surface of the left hemisphere (LH) and the right

hemisphere (RH). In the bottom part of the figure, a detailed organization of the eccentricity representation is shown using close-up views of the inflated left and right hemispheres of six subjects. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

et al., 2006; Kriegeskorte and Goebel, 2001]. With a fast, fully automatic 3D morphing algorithm [Goebel, 2000], the resulting meshes were transformed into inflated cortex surface. The surface was then flattened with a cut along the calcarine from the occipital pole to slightly anterior to the parieto-occipital sulcus. With this standard procedure, the accumulated distortion bias due to segmentation, surface reconstruction, inflation, cut, and flattening was less than 13% [Goebel et al., 2006; Linden et al., 1999].

Retinotopic Mapping

The retinotopy of the polar angle and eccentricity were revealed via linear correlation maps analysis. After the selection of a 22.5° reference wedge of the visual field, the blood oxygen level-dependent (BOLD) time course of the fMRI was correlated with an ideal response function that assumed a value of 1 for the 4 s that the checkerboard covered only the reference section and 0 for the remaining 64 s of each cycle. Stimulation and fixation blocks were modeled by boxcar functions convolved with a canonical he-

modynamic response function [Friston et al., 1995; Qiu et al., 2006].

The color-coded cortical regions were classified based on a P -value < 0.01 . To aid in visualization, retinotopic maps were projected onto computationally flattened representations of the cortical surface [Dale and Sereno 1993; Dale et al., 1999].

Surface Area Measurements

All surface area measurements were made on the 3D cortical manifold. To measure the surface area, a functionally defined region of interest (ROI) was identified on a two-dimensional (2D) flat map. Just as in the 3D volume analysis, active voxels in the 3D surface analysis can be saved as ROIs. After identification on the flattened map, the surface area of the ROI was calculated in Matlab using the BrainVoyager software, which used the 3D cortical manifold coordinates of the ROIs.

TABLE I. Surface area measurements

Subject	Hemi.	Ventral			Dorsal			Total		
		V1	V2	V3	V1	V2	V3	V1	V2	V3
BY	left	1,207	1,115	897	895	1,013	878	2,102	2,012	1,775
BY	right	1,019	965	756	1,209	998	762	2,228	1,721	1,518
DB	left	986	578	576	1,388	729	674	2,374	1,154	1,250
DB	right	883	921	839	1,033	927	631	1,916	1,760	1,470
FZ	left	1,187	776	774	1,033	884	799	2,220	1,550	1,573
FZ	right	1,013	924	730	1,147	950	760	2,160	1,654	1,490
HO	left	1,179	1,131	1,025	1,231	1,182	870	2,410	2,156	1,895
HO	right	1,147	1,639	1,115	1,071	987	870	2,218	2,754	1,985
KS	left	746	957	886	1,076	790	610	1,822	1,843	1,496
KS	right	1,060	1,126	886	1,104	908	809	2,164	2,012	1,695
LS	left	951	980	699	950	810	681	1,901	1,679	1,380
LS	right	1,044	1,212	792	984	1,017	799	2,028	2,004	1,591
NK	left	1,425	805	477	1,170	529	599	2,595	1,282	1,076
NK	right	1,047	908	664	1,220	990	781	2,267	1,572	1,445
WH	left	895	872	891	1,472	805	589	2,367	1,763	1,480
WH	right	1,155	1,088	919	1,319	844	863	2,474	2,007	1,782
	left mean	1,072	901	778	1,151	842	712	2,223	1,679	1,490
	right mean	1,046	1,097	837	1,135	952	784	2,181	1,935	1,622
	total mean	1,059	999	807	1,143	897	748	2,202	1,807	1,556
	stdev	159	232	160	158	149	103	215	370	232

Distance Measurements

The area corresponding to each eccentricity angle (between 7.5 and 60°) was the intersection of V1 region with the one activated by the corresponding expanding ring. We identified the cortical locations for eight isoeccentricity rings (eight locations/hemisphere) in each subject's V1. To measure the distance between each eccentricity area along the original cortex, we defined the middle line of each eccentricity area in V1 dorsal and V1 ventral. Three voxel points were localized as the midpoint on each of three lines, the first for the boundary of V1/V2, the second along the middle line of the V1d or V1v and the third along fundus of the calcarine. Line segments were formed by connecting each possible pairing of the three points for each eccentricity area on the inflated cortex surface. These segments were then transformed back to the original cortical folded surface. An in-house developed matlab program was applied to calculate the length of each line segment. The length is the distance between the two points on the original cortical surface. The average distance for each object was over the six line segments (three in dorsal and three in ventral). All distance measurements presented in this paper were acquired using this method within the 3D original cortex of the undistorted cortex.

RESULTS

Eccentricity Maps

Figure 1 shows a 3D rendering of the left hemisphere of one of the eight subjects (LS). The surface represents the

boundary between the white and gray matter, which was identified using the segmentation algorithm (see Methods and Materials).

Figure 1A shows a color map of the response to an expanding ring on a medial view of the cortical surface, with the color indicating the eccentricity (distance from the fovea) that caused the activation. The hue of the color at each cortical surface point indicates the response phase, which was proportional to the eccentricity of the local visual field representation. The cortical surface was then unfolded (Fig. 1B), a process performed by the inflation algorithm. The surface region that contained the activated area, including the occipital lobe, posterior parts of the parietal lobe, and temporal lobe, was then removed, and the resulting approximately conical surface was cut again along the fundus of the calcarine sulcus to allow it to be flattened completely (Fig. 1C).

A systematic increase in eccentricity (red → orange → yellow → green → blue → cyan → dark cyan → purple) moving anteriorly along the medial wall of the occipital cortex was present. As the expanding ring stimulus moved from the fovea to the periphery of the retina, the location of the responding areas varied from the posterior to anterior portions of the calcarine sulcus in what is referred to as the eccentricity dimension of the retinotopic map. The larger peripheral representation crossed to the fundus of the parieto-occipital sulcus.

A parallel treatment of data from the rotating hemi-field stimulus is shown in Figure 1D and 1E. The color also indicates the phase of the periodic response, which was proportional to the polar angle of the local visual field representation. The locations of several visual areas were

Figure 3.

Average areas of V1/V2/V3 for different eccentricity degrees, which were measured in 7.5° increment from 0° to 60° spans. A significant decrease was observed in the response area in V1 (diamond; $y = -123.98 \ln(x) + 553.99$, $R^2 = 0.9822$), V2 (square; $y = -82.69 \ln(x) + 372.58$, $R^2 = 0.9898$), and V3 (triangle; $y = -75.329 \ln(x) + 313.91$, $R^2 = 0.9876$). The smooth curve is the logarithmic exponential function that best fit these data. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

identified by measuring the angular visual field representations [DeYoe et al., 1996; Engel et al., 1997; Sereno et al., 1995]. Figure 1D–F shows the angular visual field representations on the folded (Fig. 1D) and unfolded (Fig. 1E,F) surface spanning most of the occipital lobe and posterior parts of the parietal and temporal lobes. The color at each location represents the angle of the rotating wedge that elicited an fMRI response.

In Figure 2, the top row shows the eccentricity map for subject LS in right hemisphere. The eccentricity map coded by color [red (center) → orange → blue → cyan → purple (periphery)] displayed on the original cortical surface and on the folded, inflated, and flattened cortical surface of the left hemisphere (LH) and the right hemisphere (RH). In the bottom part of the figure, a detailed organization of the eccentricity representation is shown using close-up views of the inflated LH and RH of six of the subjects.

The Sizes of V1/V2/V3

Table I shows the measurements obtained for the surface area of the visual field representations from 0° to 60°, except the area of the foveal center. Right and left hemispheres (left and right visual field) and dorsal and ventral aspects (lower and upper visual field) are listed separately for each subject.

The surface areas of the corresponding visual areas were correlated across subjects. We found a significant correlation between V2 and V3 ($r = 0.761$, $P < 0.001$, $df = 32$), but not between V1 and V2 ($r = 0.072$, $P = 0.696$, $df = 32$) or between V1 and V3 ($r = 0.231$, $P = 0.204$, $df = 32$).

The V2 surface area in the wide-field 60° representation was roughly 82% that of V1, and the size difference was statistically significant (pairwise t test = 3.249, $P < 0.01$, $df = 31$). The surface area of V3 was $\sim 1,556 \text{ mm}^2$, which was 71% of the size of V1. The size difference between V3 and V1 was significantly different (pairwise t test = 7.790, $P < 0.001$, $df = 31$). In Dougherty et al.'s [2003] data, the surface area of V2 was $\sim 75\%$ and V3 was $\sim 55\%$ of the size of V1. In our results, the areas of V2 and V3 were significantly larger than those in 0°–12°.

We also conducted a statistical evaluation of treatment before performing all statistics using SPSS, and plotted our results with a logarithmic function. We measured the average areas of V1, V2, and V3 at different degrees as a function of eccentricity (see Fig. 3). There was a significant decrease in the response area in V1 ($y = -123.98 \ln(x) + 553.99$, $R^2 = 0.9822$), V2 ($y = -82.69 \ln(x) + 372.58$, $R^2 = 0.9898$), and V3 ($y = -75.329 \ln(x) + 313.91$, $R^2 = 0.9876$). A trend toward a decreasing response area in V2 and V3 was observed, and this trend was slower than those observed for V1 and the areas of V1, V2, and V3 at 50°. This decreasing trend slowed down at 40–50° in V2 and V3, and differed from that of V1.

Figure 4.

Visual field eccentricity as a function of distance from the 10° point in V1 for the each of the two hemispheres of eight subjects. Symbols represent data from different subjects, and the triangle for the data of left hemisphere, the round for right hemisphere. The smooth curve is the exponential function expression ($E = e^{0.047(d+48.8)}$) that best fit the data ($R^2 = 0.9997$), where d is the cortical distance (mm). [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Figure 5.

Comparison of the cortical distance estimates between the present and previous studies. The blue dotted line represents the data from the function described in Horton and Hoyt's human lesion study [1991]. The green dashed line represents the data from the function described in Engel et al. study [1997]. The yellow dotted and dashed line represents the data from the function described in Adams et al. [2007]. The purple line represents the cortical distance of the present study. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

In line with the previously reported physiological finding, we also measured the V1 surface area of the peripheral 15°–60° and the area of the central 0°–15°. A criterion eccentricity of 15° equated the central and peripheral areal representation within 1% error [Adams et al., 2007]. And a mean of 49.6% of the striate cortex was estimated to be the representation of the peripheral vision at 15°–60°. This was similar with the postmortem finding that the peripheral cortex was ~46.9% of the striate cortex. However, the percentage was numerically larger than the 39.1% of the striate cortex devoted to peripheral vision in the macaque.

Cortical Distance

Cortical distance was measured as a way to describe the increase in eccentricity. We measured the cortical distance linking response points to a line along the fundus of the calcarine sulcus, which is the axial line of V1. Figure 4 shows the results of this analysis for the eight subjects in each hemisphere. The line that was used to measure cortical distance fell at positions that represented slightly different eccentricities in the different hemispheres. To evaluate the data across hemispheres, we calculated the eight distances from the mid points in each isoeccentricity rings area to the point representing 10° of eccentricity (approximate to midpoint of the activation area eccentricity

0°–15°). We also calculated the best fit ($R^2 = 0.9977$) at every eccentricity with the distance data of the eight subjects. The smooth curve in Figure 4 was derived using the exponential function:

$$E = e^{0.047(d+48.8)}$$

where E is the eccentricity in degrees, and d is the cortical distance in mm.

Several groups reported the cortical distance in non-wide-field vision using fMRI [Duncan and Boynton, 2003b; Qiu et al., 2006; Sereno et al., 1995]. Sereno et al. compared the human's cortical distance with non-human primates, such as the macaque monkey and the owl monkey. Retinal eccentricity as a function of cortical distance relative to the 10° point was provided by Engel et al. [1997], who developed a simple formula that related position within area V1 (millimeters from the point representing 10°) to a position within the visual field:

$$\ln E = 0.063(d + 36.54)$$

where E is eccentricity measured in degrees from fixation, and d is the cortical distance (in millimeters) from the cortical position representing 10° of eccentricity. Cortical locations anterior to that point were assigned positive values and cortical locations posterior to that point were assigned negative values. This representation agrees with estimates obtained using completely different means in monkeys and humans [DeYoe et al., 1996; Duncan and Boynton, 2003b; Engel et al., 1997; Horton and Hoyt, 1991; Qiu et al., 2006].

Figure 5 shows that the cortical distances at 0°–60° were consistent with the estimate obtained in the study of Engel et al. [1997], who estimated the relationship for the data from 0° to 12°. The result also agrees with Horton and Hoyt's [1991] lesion study and Adams et al.'s [2007] post-mortem study. Because the widths of the visual cortex vary along with the increase of cortical distance, and because the borders of the response area in different eccentricities are irregular, the response areas in different eccentricities demonstrated great variability.

Cortical Magnification

The magnification factor (M) of the retina is the linear extent of the visual striate cortex to which each degree of the retina projects. It has been suggested that the magnification factor is directly proportional to visual acuity. The magnification factor measured in monkeys, however, was compared with visual acuity in humans. In Figure 6A–C, we first described the calculation of the magnification factor in humans by wide-field stimulus, and then compared it to human visual acuity based on the previous data. To calculate the area magnification factor, we measured (in mm^2) the cortical surface area of each compartment in each of the eight retinotopic maps. Next, we calculated the area (i.e., the

Figure 6.

Surface area cortical magnification for eight subjects and cortical areal magnification M_a as a function of eccentricity. Surface area cortical magnification of V1 (Panel a), V2 (Panel b), and V3 (Panel c) for each of the eight subjects. Curve on panel d is all subjects with error bars. Red curve represents the V1, $Ma =$

solid angle in degrees squared) of each corresponding compartment in the visual field. Dividing the two values yielded the area magnification in $\text{mm}^2/\text{degree}^2$.

The resulting magnification curves for V1, V2, and V3 are illustrated in Figure 6D. The cortical surface area per degree of visual field decreased systematically with the eccentricity. The curves for all three areas were similar in shape, with the downward offsets for V1 ($Ma = 405.3/(E + 1.717)^2$, $R^2 = 0.9998$), V2 ($Ma = 242.2/(E + 1.11)^2$, $R^2 = 0.9996$), and V3 ($Ma = 157.2/(E + 0.486)^2$, $R^2 = 0.9995$) reflecting their smaller total surface area relative to V1. Because the cortical magnification factor was small for large eccentricities, the logarithmic map reflected the factor's change in large eccentricities. We found that M_a declined in an approximately exponential manner (see Fig. 7).

405.3/($E + 1.717$)²; blue curve V2, $Ma = 242.2/(E + 1.11)^2$; and yellow for V3 $Ma = 157.2/(E + 0.486)^2$. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Using retinotopic data from different sources, various authors have attempted to mathematically model how M varies as a function of eccentricity [Daniel and Whitteridge, 1961a; Fischer, 1973; Hubel and Freeman, 1977; Johnston, 1989; LeVay et al., 1985; Schein and de Monasterio, 1987; Schwartz, 1977; Stensaas et al., 1974; Van Essen et al., 1984]. The general formula for the magnification factor [Van Essen et al., 1984] is:

$$M = \frac{k}{(E + a)^n}$$

where E is eccentricity and k , a , and n are constants. The constant k is a scaling factor. The constant a was introduced by Schwartz [1977], which prevents M from

Figure 7.

Cortical areal magnification M_a as a function of eccentricity. The dotted line represents the best fit to the equation $M_a = K^2/(E + a)^2$. The blue dotted and dashed line represents the data in Horton and Hoyt's human lesion study [1991], the black double-dotted and dashed line the data in Sereno's human study [1995], the red dotted line the data in Schira's human central visual field study [2007], the yellow dashed line and green dashed line separately the data in Van Essen [1984] and Adams and Horton [2003] Macaque studies, and the purple line data from presented study. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

climbing to infinity as E approaches 0° , thus correcting the error in Inouye's map. If the visual field map in the striate cortex conformed to the complex logarithmic mapping function of Schwartz [1983], the constant n would equal -1 for linear magnification and -2 for areal magnification.

We estimated the function of the areal magnification by

$$M_A = \frac{k}{(E + a)^2}$$

Figure 7 shows the areal magnification factor (M_a), estimated from the present study and reported in previous ones [Adms, 2003; Horton and Hoyt, 1991b; Schira et al., 2007; Sereno et al., 1995; Van Essen, 1984]. The purple solid line was obtained by non-linear curve fitting of our data in the current study with sum of the differences squared as the object function. With the parameters estimated, the fitted function is ($Ma = 405.3/(E + 1.717)^2$). We compared our fitted curve with the ones obtained in previous studies: $Ma = 386.9/((E + 2.5)(E + 0.9))$ (blue curve) by Sereno et al. [1995], $Ma = 300/(E + 0.75)^2$ (green curve) by Horton and Hoyt [1991], and $Ma = (19.2/(E + 0.77))^2$ by Schira et al. [2007] (red curve). Orange and green dotted curves are separately the areal magnification factor Ma

$= 144/(E + 0.75)^2$ by Van Essen et al. [1984] and $Ma = 105/(E + 1.33)^2$ by Adams et al. [2003] for the macaque striate cortex studies.

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

$$M = \frac{k(b - a)}{(E + a)(E + b)}$$

We also estimated the best fit of the constants k , a , and b for V1, V2, and V3 ($k = 20.13$, $a = 1.717$, $b = 7.50E+05$ for V1; $k = 15.6$, $a = 1.97$, $b = 27.889$ for V2; and $k = 12.5$, $a = 0.486$ and $b = 2.53E+08$ for V3).

The Map of V1/V2/V3

A point can be denoted in the visual hemi-field (Fig. 8a) with the eccentricity (E) and polar angle (P). The complex representation is therefore an obvious candidate to model the two dimensional structure of the mapping. As the magnitude of its derivative is inverse-linear [Inouye, 1909], Schwartz's complex-log model (Fig. 8b) [Balasubramanian et al., 2002; Polimeni et al., 2006; Schwartz, 1977; Schwartz et al., 1985] described was introduced to describe the singularity at the foveal portion. Schwartz [1983] extended the complex-log transform to a dipole model (Fig. 8c). However, the full dipole model should only be used if there is precise measurements in the fovea to estimate the parameter a , and peripheral-field data available to constrain the value of the b parameter. The wedge-dipole map is presented to provide a unified model of V1, V2, and V3. [Balasubramanian et al., 2002; Polimeni et al., 2006]. The wedge map warps three area of the visual hemi-field and places them into the shape shown in Figure 8d, and fitted with the anatomic mapping of the macaque. Each area has been compressed by an amount in the azimuthal direction, resulting in a rotational shear in each of the wedges. Schira et al. [2007] provided the divisory and the parametric 2D-shear models from the retinotopic map for central and parafoveal, which corrected the meridional map anisotropy flaw of the wedge-dipole.

The present wide-field retinotopic map data was tried to define the peripherally parameters for the dipole model, but not was adequate to reveal out the meridional map anisotropy raised by Schira et al. [2007]. The cortical distances and magnification factors were used to reconstruct the retinotopic map of the visual cortex using a dipole model. The map was compiled by averaging maps for the fMRI data from our eight subjects (see Fig. 8). Eccentricity is denoted by the vertical lines representing 5.3° , 11.8° , 19.1° , 26.5° , 33.9° , 41.2° , 48.8° , and 56.4° . The shape of the map contrasted with that predicted. In Schwartz's map, it

Figure 8.

The evolution of the complex log model. (a) Right visual hemi-field, (b) the monopolar model, (c) the dipolar model, and (d) the wedge-dipolar model.

appeared that the isopolar rays converged peripherally, and the dipolar map rings became curved and shortened. In our map, however, the isopolar rays did not appear to converge peripherally.

We followed the procedure described in [Polimeni et al., 2006] to compute the peripheral wedge dipole mapping of the visual field coordinates to the cortical coordinates. We used the code listing for Matlab (The MathWorks, Natick, MA), as described below. To be more detailed, the mapping itself requires three global parameters, k , a , and b (in our result, the best fits were $k = 405.2$, $a = 1.717$ for V1, $k = 242.193$, $a = 1.197$ for V2, and $k = 157.2476$, $a = 0.487$ for V3), and three shear parameters, α_1 , α_2 , and α_3 , as discussed in the previous reference [Polimeni et al., 2006]. Finally, the mapping also requires three addi-

tional discretization parameters, ecc , $Necc$, and $Npol$. The output is an array containing the visual field coordinates, z , three arrays containing the wedge representations, $zV1$, $zV2$, and $zV3$, and three arrays containing the cortical representations, $wV1$, $wV2$, and $wV3$ (Fig. 9).

DISCUSSION

V1/V2/V3 Size

In several previously reported studies, the stimulation scheme employed caused linear increase eccentricity in central visual mapping nicely. However, it is not case in peripheral visual mapping. In order to make our results compatible with these previous studies, we adopted a

Figure 9.

Map of the peripheral wedge dipolar model with our data.

linear stimulation. Our findings are consistent with the model of previous researches, especially with those that used the non-wide-field visual field [Engel et al., 1994, 1997; Qiu et al., 2006; Sereno et al., 1995; Tootell et al., 1995]. Nevertheless, additional studies are needed to adequately quantify the non-linearity in the peripheral visual field. We intend to continue our line of research in this area and to collaborate with theoretical modelers to develop new experimental designs and collect data accordingly.

For stimuli ranging between 0° and 60°, which are larger than those obtained in previous studies, the area for the V1 surface found herein was larger than that reported in previous fMRI studies [Conner et al., 2004; de Wit et al., 2006; DeYoe et al., 1996; Dougherty et al., 2003; Engel et al., 1997; Schira et al., 2007; Sereno et al., 1995]. In fact, our data for 0°–60° were nearly twice that obtained for 0°–12°. In addition, these results agree with the anatomical data [Adams et al., 2007; Amunts et al., 2007; Andrews et al., 1997; Coop et al., 2008; Horton, 2006; Horton and Hoyt, 1991].

The numerical values reported for the mean surface area of the human striate cortex varied from 2,070 to 3,450 mm² [Adams et al., 2007; Amunts et al., 2007; Brodmann, 1918; Filimonoff, 1932; Popoff, 1927; Young et al., 2006; Zhao et al., 2006]. Although this wide range partially reflects different methods used to process and measure the cortex, there is ample evidence to suggest that the variability in area V1 is real [Stensaas et al., 1974]. We examined the brains of eight subjects and found a range of 1,822–2,595 mm² for the range of 0°–60°, with a mean of 2,202 mm². Although we did not calculate the monocular area, Adams et al. showed that this area covers ~6% of V1 [Adams et al., 2007].

In humans, the surface area of V2 is smaller than that of V1 when measured by fMRI [DeYoe et al., 1996; Dough-

erty et al., 2003; Engel et al., 1997; Sereno et al., 1995]. The area of V2 is about 70–80% of V1 [Dougherty et al., 2003]. Similar findings were also found in the macaque [Adams and Horton, 2003; Blasdel and Campbell, 2001; Brewer et al., 2005]. Results from postmortem studies [Adams et al., 2007; Amunts et al., 2007], however, showed different results compared to fMRI studies, indicating that V2 is ~10% larger than V1. Moreover, V2 receives significant input from both V1 and from the pulvinar [for a review, see Sincich and Horton, 2002]. In a study performed by Dougherty et al., the reduced size of V2 suggests that it may only receive a portion of V1 output or that it possesses a more efficient representation of this output [Dougherty et al., 2003]. Nonetheless, there is no significant evidence indicating that the surface area of the human V2 is larger than that of V1.

A previous study performed by Andrews et al. [1997] found a correlation between the surface area of V1 and the size of the retinal and geniculate input streams. Dougherty et al. observed that the surface areas were highly correlated between V1 and V2 and between V2 and V3, but not between V1 and V3.

We found that the correlation in size between V2 and V3 was significant, but the correlation between V1 and V2 and between V1 and V3 was not significant. Using diffusion tensor imaging (DTI), Kim et al. [2006] found bi-directional connections between V1/V2 and PPA and between V3 and FFA. Thus, connections between V1, V2, and V3 may be complex because of the influence of additional factors, such as the insertion of a significant pulvinar input at the level of V2/V3 and the increasing significance of feedback and other projections.

Distance and the Linear Magnification Factor

The cortical magnification M and the cortical distance d were used to characterize the internal structure of a visual cortical map. The cortical distance is related to the linear cortical magnification factor. To illustrate the correlation between the distance and linear magnification factor, Engel et al. plotted the eccentricity E that corresponded to the peak of each ridge as a function of the cortical distance d and fit the curve using the exponential function $E = e^{c(d+d_0)}$ (Engel et al. 1997). d_0 denotes the translation distance, which depends on the ridge selected as the reference line. We were only interested in parameter c , as it is a scaling factor that is inversely proportional to the linear cortical magnification factor. The distance function of the constant c is the inverse of the constant k , which is present in the linear magnification factor function:

$$M(E) = d'(E) = \frac{1}{c} E^{-1}$$

Expressing the change in cortical distance produced by a unit degree of the visual field at any given eccentricity.

Figure 10.

The different retinotopic maps of humans from our study compared to the maps of macaques. In the human map, the curve direction of the rings in the dipolar map contour differs from that in macaques.

In this study, the value of $k' = 1/c$ was estimated to be 21.27 from the cortical distance. This estimated value was similar to the $k = 20.13$ based on the cortical magnification factor, and is consistent with what human lesion and post-mortem studies reported [Adams et al., 2007; Horton and Hoyt, 1991]. In previous fMRI studies that focused on non-wide-field vision [Duncan and Boynton, 2003a; Engel et al., 1997; Schira et al., 2007; Sereno et al., 1995], the magnification scaling factor (k) varied from 13.48 to 20.05. Moreover, according to Sereno et al. [1995] and Schira et al. [2007], $M(E)$ is smaller near the fovea than one further away as we obtained in the present study (see Fig. 7). On the other hand, we can not exclude the possibilities that the different estimates might be due to potential stimulus wrap-around with the expanding stimuli used by Sereno et al. [1995] and Schira et al. [2007]. Sereno's estimate of $M(E)$ might be low in the periphery for the same reason.

For the different parameters of the cortical magnification factor functions in humans and macaques, the 15° eccentricity contours that pass through the blind spot of both species were extrapolated by their respectively cortical magnification factors in a study by Adams et al. [2007]. This group also reported that a significant difference in the layout of the eccentricity contours in humans and macaques is unlikely, as V1 has a similar elliptical shape in the two species.

When we compared our magnification estimate in humans with that found for macaques (see Fig. 7), the curves for the two species were similar in shape. The mag-

nification estimates in macaques are systematically smaller than that of humans at corresponding eccentricities.

The Revised Map of Human Primary Visual Cortex Based on a Dipole Map

In Schwartz's dipolar model, the second parameter b approximates the shape of the V1 boundary exhibited at the peripheral representation, as well as the super-linearity of the inverse cortical magnification factor in the peripheral field [Schwartz, 1977; Schwartz et al., 1985]. This function corresponds to the third-order term introduced by Virsu and Rovamo [1979] when expanding the expression into a power series. The dipole model thus provides a simpler approach to the same concept. This dipole model has received considerably less attention than the original model, and it fails to provide a good estimate of b . Magnification data that includes peripheral data are therefore usually fit to a power function [Adams and Horton, 2003; Van Essen et al., 1984] rather than to a dipole model. Moreover, studies that have attempted to estimate it have obtained a value for b of between 90° and 180° [Balasubramanian et al., 2002].

Dipole mapping provides a three-parameter conformal map model of the full-field topography of the primary visual cortex. The dipole map can fit well to the condition of macaque vision and human non-wide-field vision [Polimeni et al., 2006; Schwartz et al., 1985; Tootell et al., 1988]. In our study, which focused on human peripheral vision, the estimate of the constant b was too large. The result made the convex peripheral maps in the periphery the same as that in the center of the dipolar map. This effect is consistent with human lesion and postmortem studies. The large constant b , however, made the isopolar rays appear not to converge peripherally. In reality, the isopolar rays converged peripherally and the dipolar map rings became shortened.

On the basis of these observations, we revised the dipolar map to fit our conditions (see Fig. 10). As shown here, the dipolar map of the macaque is compared to the revised human map, which has a similar elliptical shape to that of macaques. Moreover, the central parts of the maps from the two species are the same. The peripheral parts, however, differ in that the convex peripheral map of humans is reversed compared to the macaque. The revised map can also explain why the proportion of the area of the peripheral cortex is larger than that of macaques.

However, Schira et al. [2007] proposed alternatives to improve Schwartz models. It is important to note that the divisory and the parametric 2D-shear models expression for the retinotopic map proposed by Schira et al. [2007] introduced meridional anisotropy into the magnification function. Unfortunately, the presented study was not designed to investigate the model introduced by Schira et al. Additional studies are needed to investigate meridional anisotropy of the visual map, especially the peripheral field.

The Different Retinotopic Maps of Humans and Macaques

Overall, our findings indicate striking parallels between visual cortex representations of the retinotopic in the human and macaque occipital cortex, providing evidence that there are genuine homologies between these two species. As shown in previous studies [Hinds et al., 2008], V1 has a similar elliptical shape in the two species. In addition, the cortical magnification factor is also similar in humans and macaques (as Fig. 7).

However, the difference over peripheral cortices is significant between humans and macaques with several lines of evidence as detailed below. The proportion of the area of peripheral cortex in humans is significantly larger [Adams and Horton, 2003; Adams et al., 2007; Van Essen et al., 2001], and the layout of the eccentricity contours in peripheral cortex between humans and macaques is also different as in sharp contrast to the similarity in the central cortices. The difference between these two species appears to be that the function of the peripheral cortex has been strengthened in humans, most likely because the observation of the surroundings and objects is more complicated in humans compared to macaques. In addition to size differences of the peripheral representations, the difference in the relative representation of the vertical meridian relative to the horizontal meridian might well reflect the differences in useful information content of these two dimensions for arboreal primates vs. bipedal ground-dwellers.

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