Extended Concepts of Occipital Retinotopy

Christopher W. Tyler*, Lora T. Likova, Chien-Chung Chen, Leonid L. Kontsevich, Mark M. Schira and Alex R. Wade

Smith-Kettlewell Brain Imaging Center Eye Research Institute, 2318 Fillmore Street, San Francisco, CA 94115, USA

Abstract: Retinotopic mapping is a key property of organization of occipital cortex, predominantly on the medial surface but increasingly being identified in lateral and ventral regions. The retinotopic organization of early visual areas V1-3 is well established, although anatomical landmarks can help to resolve ambiguities in poorly-defined functional maps. New morphing techniques are now available to define the metric mappings quantitatively within each retinotopic area. In the dorsal occipital regions, there is fair agreement that area V3A should be split into separate V3A and V3B maps, and that beyond them lies a further area, V7. We specify the eccentricity mapping of both V3B and V7 for the first time, showing how the latter is roughly parallel to the meridional mapping and offering formal accounts of such paradoxical behavior. In ventral occipital cortex, we support the analysis of Zeki and Bartels [1] and Wade *et al.* [2] that V4 maps the full hemifield, and show the existence of two more areas, a ventromedial map of the lower quadrant, emphasizing the upper vertical meridian, and an adjacent area with a dominant foveal representation. In lateral cortex, the motion area defined by a motion localizer shows pronounced retinotopy, particularly in the eccentricity parameter. A dorsolateral map between the motion area and V3B, which represents the lower quadrant with an emphasis the foveal part of the lower vertical meridian, may be a counterpart to the ventromedial map.

INTRODUCTION

Now that the entire medial surface of occipital cortex is established as being devoted to the primary visual projection areas V1-3 [3-9], efforts are switching to the lateral occipital cortex, which is less strongly retinotopic. Numerous functional MRI studies have demonstrated extended retinotopic activation in the lateral occipital lobe, as in the example shown in Fig. **1**. The activation in this case is for a rotating wedge stimulus of a flickering checkerboard spanning a 45° sector of the visual field Fig. **2**. The activation phases relative to visual field position are indicated by the colors in the icon (right field).

In order to have the most comprehensive view of occipital retinotopy, it is important to have clear definitions for each retinotopic area. There is broad agreement on the definitions of retinotopic areas V1-3 as fanning out from the horizontal meridian of V1, lying along the fundus of the calcarine sulcus, through the dorsal and ventral quadrants of V2 and V3 projecting in mirror-symmetric fashion in the adjacent sulci [10]. The anatomical arrangement of the occipital lobe is presented in Fig. **3** in terms of flatmaps centered on the occipital pole [11]. This approach to cortical representation retains the full local connectivity of the occipital lobe by avoiding the cut along the horizontal meridian of V1 that is common in other flatmap representations.

For our study, the retinotopic areas were defined with the rotating wedge and scaled expanding ring stimuli depicted in Fig. **2**. One innovation is the use of a stable fixation grid of thin dark lines that was continually present during the varying stimulus cycle. These thin dark lines do not generate any fMRI signal in themselves, but provide an invariant pattern to help the observer stabilize the fixation of the eyes at the center of the pattern throughout the long period of the scan. Without this fixation grid, small movements of the eyes can seriously perturb the accuracy of the mapping in the region of the foveal representation.

To provide a complete representation of the occipital activation patterns with minimal distortion, we employ flatmaps centered near the occipital pole of each hemisphere (Fig. **3**). The gyral and sulcal landmarks are shown in terms of the local cortical curvature as light-gray and dark-gray shading, respectively. It may be noted that this kind of occipital-pole flatmap offers an alternative view of the organization of occipital function with several advantages. It is easy to orient the flatmaps relative to the anatomical brain structure because they show the cortex as though the brain were unfolded as viewed from the back of the head. Unlike 3D rendered views of the brain Fig. **1**, this view has the great advantage that it allows presentation of medial, ventral and lateral views of the occipital cortex all in a single image.

The retinotopic boundaries obtained by standard methods in the cited studies generate the area definitions shown as colored outlines in Fig. **3** (see Methods). It can be seen that the border of area V1 as defined by retinotopic stimulation forms an arrowhead-shaped region lying along the lips of the calcarine sulcus (bright gray shading). This anatomical marker can be helpful in identifying the borders of V1 where the functional activation is less robust. The retinotopic areas V2 (green outlines) and V3 (blue outlines) are split into dorsal and ventral segments representing the lower and upper hemifields, respectively. They fall in the ladder-like structures of the two sulci adjacent to the calcarine, but the functional borders are rarely as well-defined as the calcarine anatomy.

*Address correspondence to this author at the Smith-Kettlewell Brain Imaging Center, Eye Research Institute, 2318 Fillmore Street, San Francisco, CA 94115, USA; Tel: (415) 345 2105; Fax: (415) 345 8455; E-mail: cwt@ski.org
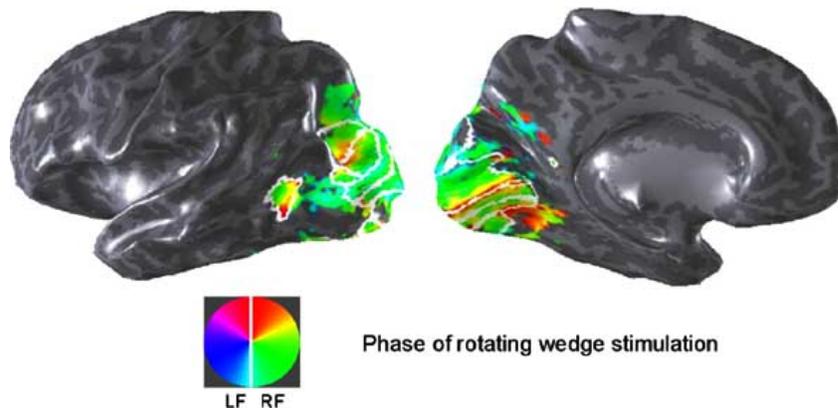
Fig. (1). Inflated reconstruction of segmented cortex of the left hemisphere of one observer, showing meridional activation by rotating wedges (inset) defining the retinotopic areas (white outlines) on the medial (right) and lateral (left) surfaces of the occipital lobe (see Methods). The most lateral site of activation is the motion area V5 (hMT+), here being activated retinotopically.
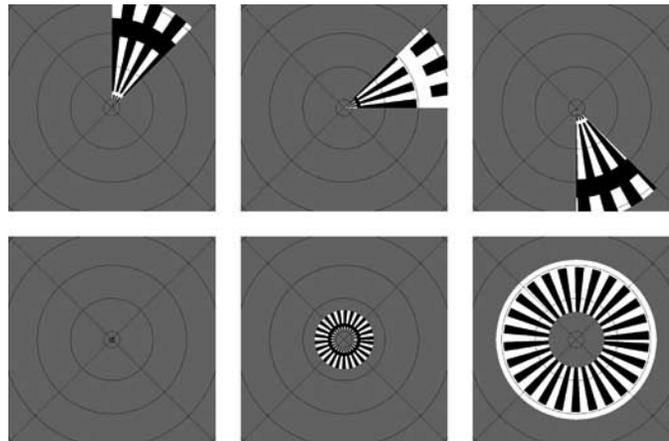

Fig. (2). Upper row: Three positions of the log-scaled rotating wedge of flickering bar structure used for the meridional retinotopy scans. Lower row: Three sizes of the expanding ring of flickering bar structure used for the eccentricity retinotopy scans. A stable fixation grid of thin dark lines was continually present during the varying stimulus cycle.
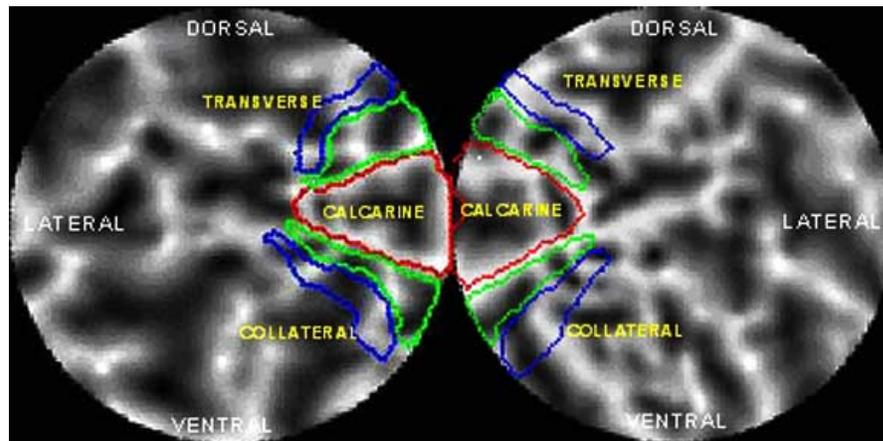

Fig. (3). Flatmaps centered near the occipital pole of the left (LH) and right (RH) hemispheres, showing the alignment of retinotopic areas V1-3 (orange, green and blue outlines) with anatomical landmarks and three named sulci (transverse, calcarine and collateral). The anatomy is depicted in terms of the convex (light grays) or concave (dark grays) local curvature of the cortex.

Examples of the definitions of the retinotopic areas are shown for three typical observers in Fig. **4**, on the same kind of flatmaps as in Fig. **3**. The two left columns depict the activation pattern of the rotating wedge stimulus that defines the projection of the retinal meridians. The two right columns depict the activation of the expanding rings defining the eccentricity mapping in the same format. For each retinotopic area, its approximately radial boundaries are
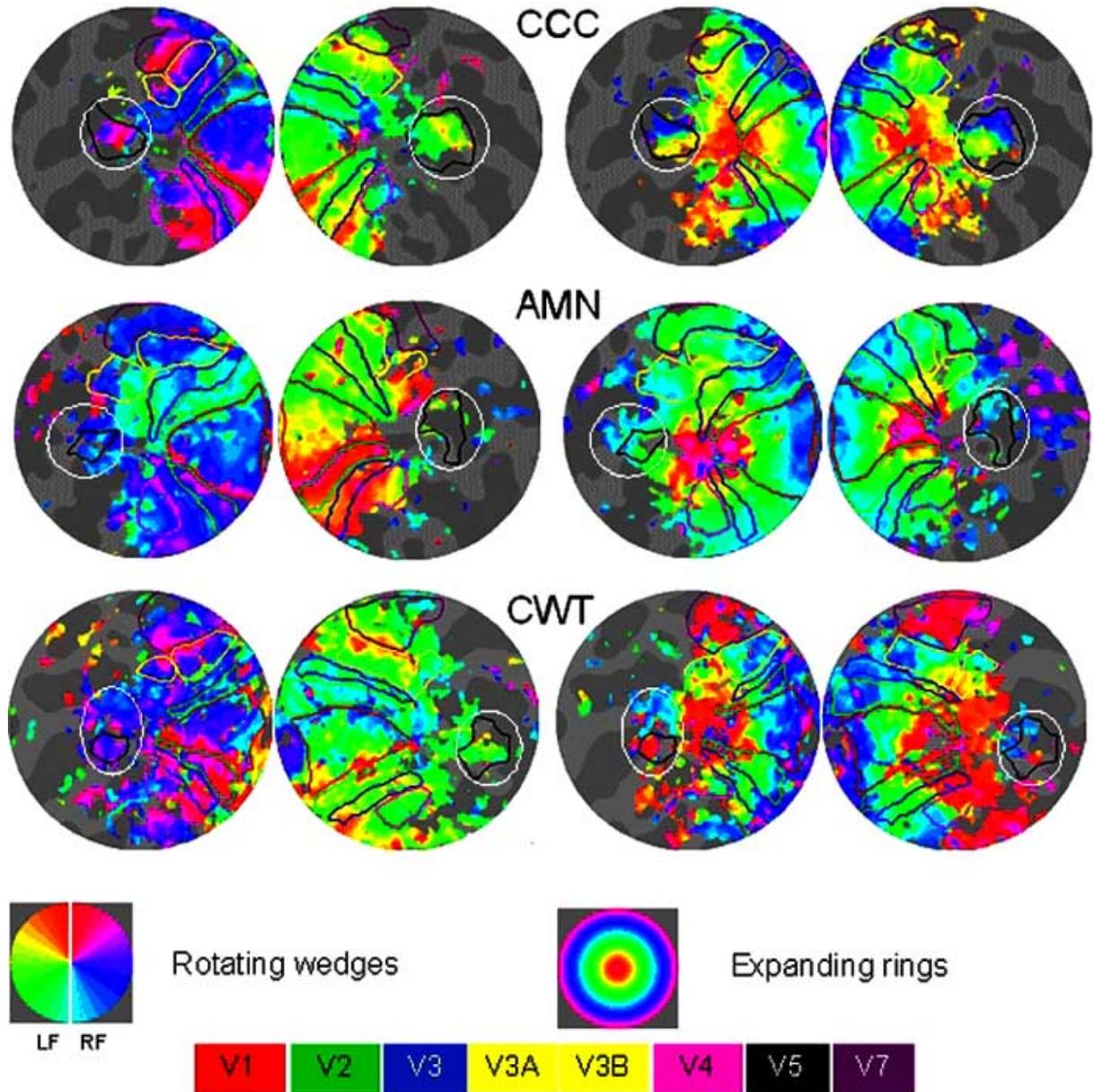
Fig. (4). Retinotopic activations for rotating-wedge stimuli (left columns; radial color map segregating left field, LF and right field, RF, stimulation) and expanding-ring stimuli (right columns; concentric color map) for three observers. Retinotopic area boundaries are defined by consideration of the response phase (inset) jointly for the meridional (rotating wedges) and eccentricity (expanding rings) maps and colored according to the color bar. Small differences among observers are expected in the phase maps due to both differential retino-cortical mapping parameters and different hemodynamic delays. Black outlines define the regions of the low-contrast motion/static response; white ellipses circumscribe the expanded zone of retinotopic response thereabouts.

defined by the rotating wedge phases (left columns; coded from cyan to red for a 180° map such as V1, V3A, V4 and V7). The center to peripheral extent is defined by the expanding ring phases (right columns; coded from deep red in the central fovea to blue in the periphery).

MORPHING THE CANONICAL RETINOTOPIC MAP

Because the intrinsic curvature of the cortex is roughly ellipsoidal, any flatmap is subject to some degree of distortion. In the occipital-pole flatmaps, the distortion is in the form of an expanded area representation with distance away from the occipital pole. Nevertheless, the roughly

triangular shape of the retinotopic areas seen in Fig. **3** is not an artifact of this distortion. For example, our measurements show that the true intracortical width of V1 increases by about a factor of 3 from the foveal to the mid-peripheral representation spanned by our stimuli (in contrast to the approximately rectangular shape that might be assumed on the basis of flatmaps with a cut along the horizontal meridian showing the almost parallel sequence of dorsal and ventral retinotopic strips of V1/2/3, as exemplified in [12], directly accessible at http://www. jneurosci.org/content/vol17/issue18/images/large/ns1871400 002.jpeg. Specification of the distortion in these flatmaps is
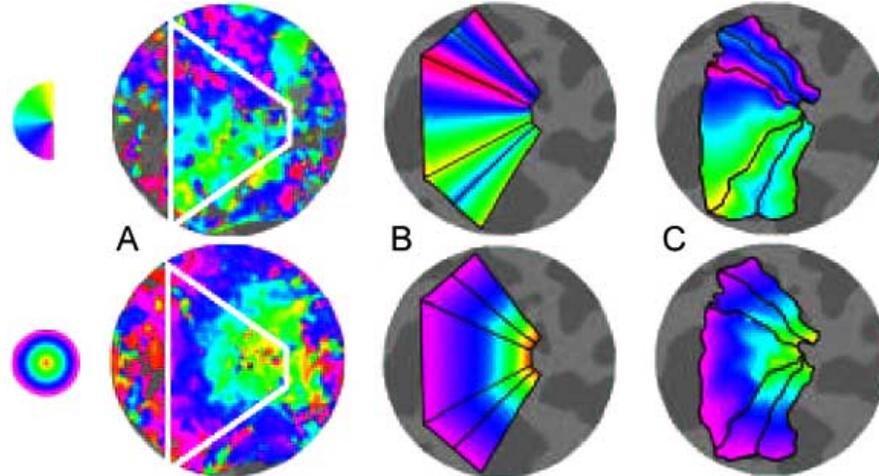
Fig. (5). Morphing of the retinotopic projection to fit to the empirical map. A. Sample retinotopic data are shown for meridional (upper row) and eccentricity (lower row) variations, together with a fiducial trapezoid for reference. (Note that the color coding has been expanded relative to that in Fig. **3**). B. Ideal retinotopic mappings for the left-hemifield meridional and eccentricity parameters for areas V3d, V2d (quadrants), V1 (hemifield), and V2v, V3v (quadrants). C. Map morphed for best fit to the data of a typical hemifield. Observer TF.

not provided, but the error is estimated as averaging ±15%.) The veridical width increase may be characterized as forming a rough arrowhead shape, increasing out to an eccentricity of about 8° then asymptoting and perhaps decreasing in width beyond this point. It should be noted that the log scaling of our eccentricity mapping means that the outer band, from 8-16° eccentricity, occupies a strip only about 1 cm in width along the 'base' of the arrowhead. Such issues are important in estimating the true cortical magnification function in human cortex.

A recent advance in retinotopic mapping is the ability to morph a canonical pair of orthogonal retinotopic maps (the meridional and eccentricity maps) onto the cortical flatmap representation [13]. A sample data set is shown in Fig. **5A**. The canonical maps are shown in Fig. **5B** for areas V1-3, for the right hemisphere. This is the signature phase structure that is being sought in the flatmap representation. The morphed V1-3 retinotopy is shown in Fig. **5C**, illustrating how the canonical map is distorted for best fit to the functional data concurrently in the two orthogonal mappings. The goal of the morphing technique is to be able to derive a one-to-one metric for the retinal mapping of every point on the cortical surface, allowing quantification of all the size and shape parameters of each cortical map. Such quantification is not possible for the source data because a one-to-one mapping is not guaranteed, and is often violated in practice.

RETINOTOPIC AREAS V3A AND V3B

We may now progress beyond the primary retinotopic areas to regions where there has been a substantial level of disagreement among the various investigative groups. In specifying the retinotopic landmarks in the region of V3A, for example, all agree that there is a 180° representation of the contralateral field, but it has more recently been split into two areas, V3A and V3B [1,9]. To clarify this behavior, the data for one observer are replotted in expanded format for the dorsal retinotopic zone in (Fig. **6**). (To maximize the range of response specification, the coherence threshold for

these plots is lowered to 0.15.) V3 is designated by blue outlines and V3A/B by yellow outlines, with V3A being the larger and more dorsal of the two yellow regions. The key feature requiring this V3A/B split is that the (dorsal) foveal representation within the traditional V3A area (Fig. **6 C,D**) lies well away from the foveal confluence of areas V1-3, implying that V3A is substantially shorter than its neighbor, V3 (dorsal). However, the retinotopic stimuli of rotating wedges reveal strong retinotopic activation in the regions lateral to this dorsal foveal response, implying that there is a second retinotopic region that shares the same foveal confluence, termed V3B [1, 9].

On the other hand, both Smith *et al.* [9] and Zeki, Perry & Bartels [14] identified V3B as being the same area as the kinetic occipital area KO, on grounds of the similarity of its Talairach localization and responsiveness. Neither group performed mapping studies to clearly specify V3B on retinotopic criteria, however. The other studies that specify retinotopic areas in this region of cortex are from the Harvard group [4, 6, 8, 12, 15-18] but they did not recognize a separate V3B area. Instead they designate all the cortex lateral to area V3A as being incorporated into the "V4d topolog", which is defined topologically rather than functionally as the region of cortex connecting the boundaries of V3A, V7 and V5 (hMT+) (cf. Fig. **6**). Thus, their V4d topology would incorporate both V3B and KO, regardless of whether they are separate or coextensive areas.

In the definition of retinotopic areas, the main criterion is that the map for each parameter (meridian or eccentricity) should be continuous and singular. A reverse in the meridian-map phase or a discontinuous jump in the eccentricity map is therefore a sign of an area boundary. In defining novel area properties, it is typically important to see symmetrical structure in the two hemispheres and similar properties across observers. It is rare to find identical properties in every observer tested, however, so the properties described should be regarded as statistical, with high probability in the population but not necessarily identifiable in every brain.
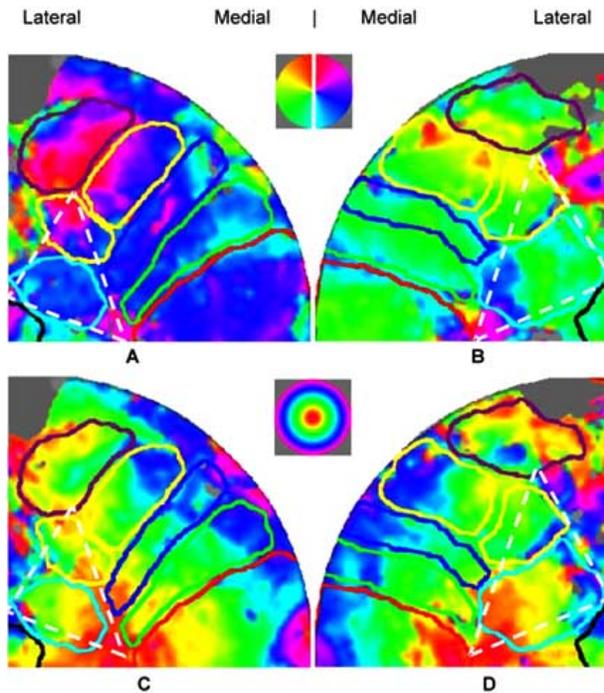
Fig. (6). Definition of retinotopic areas dorsal to V3d (blue outlines) at a coherence level of 0.15. A,B. Meridional maps. Areas V3A and V3B (yellow outlines) map a full hemifield (cyan to orange, through purple on the left, through green on the right). C,D. Eccentricity for V3A and V3B diverges from a distinct fovea confluence (orange through green to blue). V7 (violet outlines) has parallel maps for meridional and eccentricity sweeps. Dashed triangles: V4d topolog. Other color codings as in Fig. **3**. Observer CCC.

With this preamble, we may consider the retinotopic organization of area V3B. Dorsal to V3d is a region with a full hemifield meridional map, as seen in Fig. **6A,B**. Rather than having the foveal representation (red/yellow activation phase; Fig. **6C,D**) adjacent to that of V3d, however, it is displaced dorsally and can be seen to have a double peak in some cases (e.g., Fig. **6D**). (Note that this double foveal peak cannot be due to partial voluming effects across a sulcus because the tranverse sulcus in which it sits runs perpendicular to their dividing line, with no fold at the V3A/B border). The eccentricity map for the region lateral to this fovea extends dorsally at an oblique angle rather than being exactly opposed to that of V3A along the V3d border. The V3B area defined according to these criteria is usually smaller than V3A (as in Fig. **6A,C**, although its eccentricity map is not very convincing in the left hemisphere in this example). However, as is evident in Fig. **3**, an oblique eccentricity map extending dorsolaterally from the foveal confluence can usually be found that, together with the hemifield map, defines a complete retinotopic map lateral to V3A. This recipe constitutes the retinotopic definition for area V3B.

RETINOTOPIC AREA V7

For reasons of exposition, it is convenient to treat the definition of area V7 adjacent to areas V3A/B before dealing
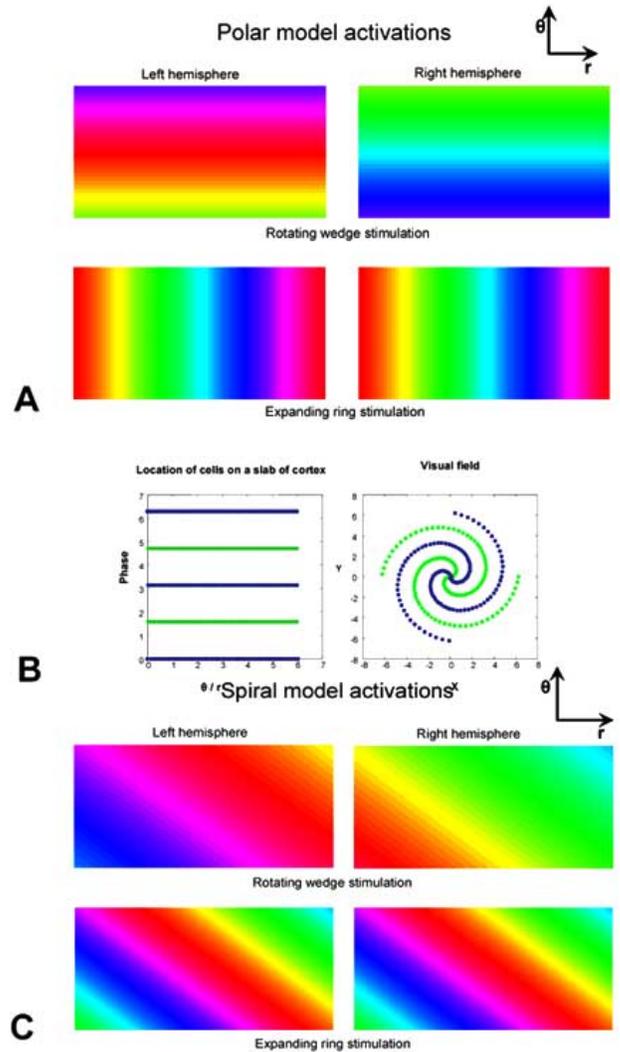

Fig. (7). A. Color-coded phase maps for usual polar mapping scheme. B. Logic of a novel spiral mapping scheme. C. Color-coded phase maps for the spiral mapping. Note that the mapping is oblique but has parallel mappings for the meridional (wedge) and eccentricity.

with the V4 complex. Tootell *et al.* [17] defined retinotopic area V7 as lying adjacent and dorsal to V3A and including at least a lower-field quadrant. Press *et al.* [19] expanded this definition to include a full hemifield projection. However, the eccentricity dependence of this area remained undefined, since there is no obvious eccentricity map running orthogonal to the meridian map. We find that area V7 (violet outlines in Figs. **4** and **6**) is a special case in which the meridional and eccentricity phases appear to run parallel to each other. We note that each observer in Fig. **4** shows consistent retinotopic activation dorsal to V3A at the chosen coherence level of 0.3, providing assurance that area V7 is a definable entity. Moreover, it is clear that the activity extends through the full range of wedge phases. There is extensive retinotopic activation for both retinotopic stimulus types, matching the color gamut of V1 in each hemisphere, although it is becoming weaker in the more dorsal regions. In all hemispheres examined, the meridional map runs in the

opposite direction to that in V3A/B (inferior > superior = upper > lower meridians), with the eccentricity map running out to a separate (dorsal) foveal representation away from the V3A/B foveal confluence.

Nevertheless, as depicted in the detail of Fig. **6**, the meridional and eccentricity maps in area V7 do not appear to be orthogonal, as in the adjacent V3A area, but run close to parallel. Although it is difficult to interpret this behavior, the parallel structure of the meridional and eccentricity maps seems to be a consistent feature and should be taken as the signature characteristic of area V7. It is obviously impossible for a two-dimensional map to have parallel structure of orthogonal retinal coordinates while providing a point-to-point mapping of the visual field. We can, however, conceptualize two forms of mapping that could produce the empirical result observed:

a)   Oblique squeeze. The V7 map could be distorted such that the mapping directions for the meridional and eccentricity axes, though independent, are rotated to lie close to each other in the anterior-posterior direction, simulating a parallelism although there is still a finite angle between them. Under this scheme, the orthogonal map would be rotated by 45° relative to the adjacent V3A/B maps, and then squeezed in the dorso-ventral direction. The angle between the meridional and eccentricity mappings may be too small to be readily resolved by the present level of accuracy of the retinotopic maps. On this scheme, the two mapping parameters could be functionally orthogonal even though they are mapped close to each other in the cortical space.

b)   Spiral mapping. The V7 map could be rotated in polar coordinates such that the orthogonal variables are not (r,) in retinal coordinates but (r+ , r-), i.e., not rings and wedges but clockwise and counterclockwise spirals. In this case, both the wedge and ring scans would generate a progression from center to periphery along the spiral map, and provide parallel mapping.

A simulation of the spiral mapping hypothesis is implemented in Fig. **7**. Fig. **7A** sets up the conventions for the usual polar mapping. Fig. **7B** defines the spiral mapping structure and Fig **7C** shows the parallel output of the spiral map for the orthogonal ring and wedge stimuli. This scheme provides a formal basis for a mapping that would generate the observed behavior in V7. The test for the spiral mapping hypothesis is to change the stimulus structure so as to stimulate with a spiral progression of the retinotopic stimuli. In this case, a retinotopic area with spiral mapping should generate orthogonal rather than parallel maps for the clockwise and counterclockwise spirals. This prediction remains untested, however.

RETINOTOPIC AREA V4

In ventral occipital cortex adjacent to V3v lies a further region of retinotopic activation that is given the designation of V4 [1, 2, 20]. Tootell & Hadjikhani [21] evaluated whether area V4 in human is split, as in monkey, into ventral and dorsal components V4v (adjacent to area V3v or VP) and V4d (in lateral occipital cortex between areas V1-V3A

and V5/hMT+). The implication of this homology is that these components of V4 should represent the upper and lower quadrants of the visual field, respectively, although Tootell & Hadjikhani [21] make it clear that the dorsal region that they define topologically lacks many features that would qualify it as the dorsal quadrant of V4. Moreover, it is now generally agreed [1, 2, 20, 21] (and as corroborated in Figs. **4** and **8**), the ventral cortical region representing the fourth retinotopic map always continues for a full hemifield representation. In Fig. **8A,B**, this hemifield map appears as coloration from red to cyan within the magenta outline, running through blue for the left hemisphere and through green for the right. The two hemispheres together thus constitute a full field map, for which the appropriate designation is V4, without the ventral or dorsal modifier [2].

What is also suggested by the Wade *et al.* study [2] is that the eccentricity extent of V4 is substantially truncated relative to its neighboring V3v. There is a full eccentricity cycle extending for about half the length of V3v, and then a second cycle completing the map to the end of V3v (Fig. **8 C,D**). This dual cycle structure makes it clear that, like the dual structure of V3A/B next to V3d, there are two retinotopic areas adjacent to V3v. The posterior one that we are designating V4 is well-behaved in retinotopic terms, with meridional and eccentricity maps orthogonal to each other and parallel to the adjacent V3v, and is widely recognized.

The anterior portion of the region adjacent to V3v, however, has an anomaly in its meridional map. In many brains, this region (cyan outline) seems to have a hypertrophic mapping of the upper vertical meridian, as illustrated in Fig. **4** and in the local maps of Fig. **8A,B**. A large swatch of cortex extending over the entire width of V4 is colored close to zero phase (red). An adjacent strip can be found that completes the quadrant coloring to blue (left hemisphere) or green (right hemisphere) before rotating back again to red beyond the cyan outline. This phase reversal is particularly clear in Fig. **8A,B**, necessitating the separation of this area adjacent to V3v from the more ventrolateral portion discussed below. When this region is marked (ventral cyan outline), it can be seen to show a full range of eccentricity phases (orange through green to blue). We propose to term this region the ventromedial occipital (VMO) retinotopic area. It must be emphasized that it represents only the upper field (predominantly the upper vertical meridian) so one may expect to find a matching dorsal area to complete the representation of the lower vertical meridian. Note that the second cycle of eccentricity phases is evident in four of the six hemispheres mapped in Fig. **4**, but is not obvious in the other two, although all six show the hypertrophic meridian mapping. Our interpretation is that blurring of the activity map obscures the small foveal activation in the other two maps (since it is not possible to generate such a feature by blurring, but it is possible to lose it by blurring if it exists).

The same logic of the presence of consistent retinotopic activation prompts analysis of the subsequent cortical region adjacent to the ventral V4 and VMO regions just defined:. This adjacent region has strong activation to the foveal phases of the eccentricity scan (orange coloration within the white outlines in Fig. **8C,D**) that also shows meridional
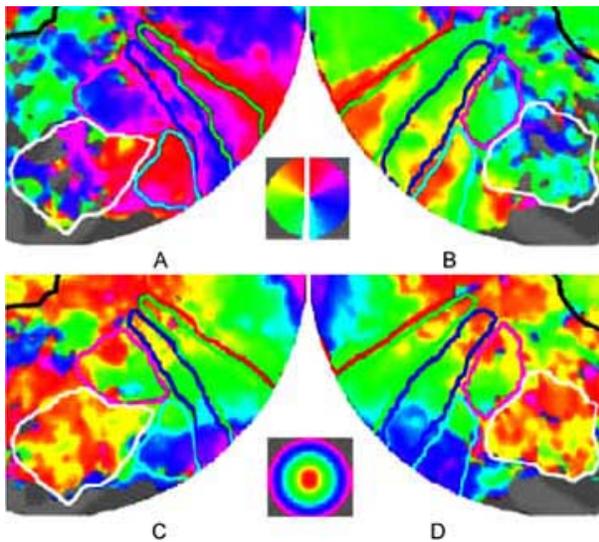
Fig. (8). Ventral flatmaps at a coherence level of 0.15 showing retinotopic activation ventromedial to area V3v (blue outline). Area V4 (magenta outline) represents a full hemifield (A,B) and an abbreviated eccentricity map (C,D). A medial area (VMO; cyan outline) lies adjacent to V3v with hypertrophy of the upper vertical meridian (orange coding in A,B) and a second eccentricity map (C,D). A third region (VOF; white outline) has a weak hemifield representation (A,B) but a dominant foveal activation (orange coding in C,D). Other color codings as in previous figures. Observer CCC.
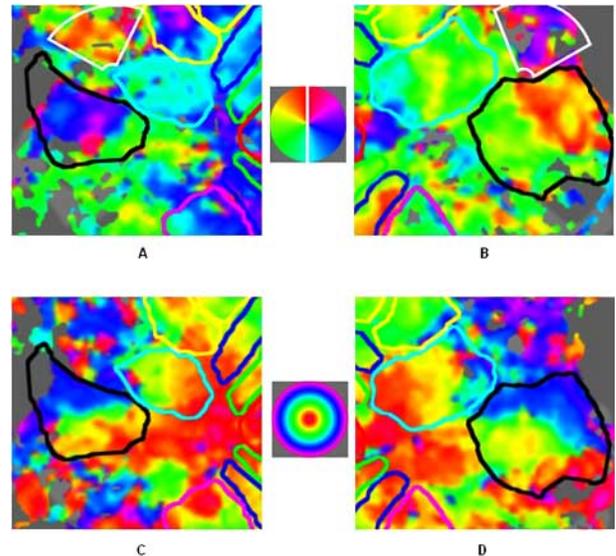

Fig. (9). Retinotopic activation in lateral occipital cortex at a coherence level of 0.15. V5/hMT+ (full blue contour) shows weak meridional mapping (A,B) but strong eccentricity mapping (C,D). An adjacent DLO region (cyan contour) has strong mapping of the lower vertical meridian (cyan coding in A,B) and predominantly foveal eccentricities (orange in C,D). Retinotopy in the adjacent ventral neighborhood is patchy and disorganized. Dorsal to V5/hMT+ is a region specific to ipsilateral activation (white fan-shapes). Observer CCC.

activation, a region described by Zeki and Bartels [1] as V4 . Like VMO, this area seems to emphasize the upper vertical meridian. In view of its strong foveal representation in most brains, we will term it the ventral occipital foveal representation (VOF). (Wandell [22] and Wade *et al.* [2], referred to this region simply the ventral occipital (VO) cortex, but we now propose a parcellation into at least two retinotopic areas, VMO and VOF).

RETINOTOPY OF THE HUMAN MOTION AREA

The human motion area (V5/hMT+) may be defined by a motion localizer consisting of low-contrast dots forming alternately expanding and contracting flow fields, against a null stimulus of otherwise equivalent static dots. Such motion stimuli activate the retinotopic areas to some extent but identify a motion selective region in lateral occipital cortex that is located as though area V1 were an arrowhead pointing to its location, as seen in the examples of Fig. **4**. The eccentricity flatmaps in Fig. **4** and the expanded example of Fig. **9** illustrate how the V5/hMT+ region (black outlines) exhibits pronounced retinotopic activation to the relative motion signals incorporated into the retinotopic wedge and ring stimuli. The upper panels of Fig. **9** show substantial activation in the same region with some tendency to meridional specificity although a full hemifield map is difficult to discern. However, the eccentricity maps show convincing rainbows of ventral/foveal to dorsal/peripheral activation in all hemispheres. The lower panels of Fig. **9** provide a particularly compelling example of the retinotopy that has been identified previously in V5/hMT+ [23]. Note

that the other examples in Fig. **4** show extended retinotopy within the regions defined by the white ellipses, beyond the specific region of the motion localizer (black outlines).

RETINOTOPY OF LATERAL OCCIPITAL CORTEX

One known property of the dorsolateral occipital cortex is that it has retinotopic specificity adjacent to area V5/hMT+ when stimulated by a retinotopic localizer stimulus (see Figs. **4** and **9**). Tootell & Hadjikhani [21] showed pronounced eccentricity mapping in this region, which they consider to be part of their "V4d topolog" region, defined as extending from the lateral borders of V1-V3A to area V5/hMT+ (see dashed triangles in Fig. **6**). They observed that the retinotopy of their V4d has a discrete character, subdividing into central- and peripheral-responsive areas that they designated "LOC" (lateral occipital central) and "LOP" (lateral occipital peripheral), respectively. However, we note that several of the regions just discussed, such as V4, VMO and V7, often appear to have a sharp boundary between foveal and peripheral representations. It seems somewhat excessive to give each such subdivision its own designation, so we prefer to avoid this nomenclature. Because "LO" and "LOC" have been used with many different connotations, we will adopt the term dorsolateral occipital area (DLO) for the dorsal cortical region lying between V1-V3A/B and V5/hMT+ that can be identified as retinotopically unitary (cyan outlines in Fig. **9**). This region shows an exaggerated response to the *lower* vertical meridian (cyan coloration), matching the exaggerated response to the *upper* vertical meridian in the VMO region (Fig. **8**). This strong lower meridian

representation with very little upper meridian representation in the region between V3d and V5/hMT+ is evident in most hemispheres examined.

In many respects, DLO matches the properties identified by Tootell & Hadjikhani [21] for their putative V4d topolog. However, we have considered it important to identify the retinotopy in this region rather than relying on a topographic definition. The concept of the hypertrophic vertical meridian representation helps to make sense of an otherwise uninterpretable meridional map. In our observation, the DLO region represents exclusively the lower-field quadrants. Tootell & Hadjikhani [21] reported that the retinotopy of their V4d topolog was "seemingly random", but we attribute that analysis to the fact that they were deriving the retinotopy for a large region of dorsal occipital cortex extending out to V7 and V5/hMT+, whereas we are focusing on the region adjacent to V3d and V3B, which has more consistent properties. It is for this retinotopically defined region that we propose the restricted term DLO.

The region of lateral occipital cortex ventral to DLO also exhibits a degree of retinotopic specificity. The main property is a pronounced foveal preference in the eccentricity map (Fig. **9C,D**), forming continuity with that of the DLO. In our observation, however, this eccentricity map is not accompanied by a consistent meridional map that would justify regarding it as the upper-field completion of the DLO. It is more typically lacking in significant activation for the meridional stimuli. In this respect the ventrolateral region adjacent to DLO conforms to the description of Malach *et al.* [15] and Levy *et al.* [24] that it has only an eccentricity map. Tootell & Hadjikhani [21] also underwrite this difference by not associating the ventral and dorsal zones of lateral occipital cortex to form a single area. This behavior suggests that the retinotopy stimuli may not be the optimal stimulus type for this region of lateral cortex. It may well be specialized for some other stimulus property, and may show more consistent retinotopic organization once its optimal stimulus type is found.

Since V4 represents a complete hemifield, we are in accord with Zeki and Bartels [1], Tootell & Hadjikhani [21] and Wade *et al.* [2] that V4 would not be the appropriate ventral counterpart to the DLO area, which itself is therefore in need of an upper-field counterpart to complete the hemifield representation in each hemisphere. A better pairing for DLO seems to be with the VMO region adjacent to V4, which represents only the upper-field quadrant. In an extended similarity, the DLO and VMO regions both have predominant vertical meridian representation, for the lower and upper vertical meridians, respectively. This pairing is coded by the cyan outlines in Figs. **8** and **9**. Although it is difficult to divine why cortical maps should incorporate such an emphasis on the vertical meridian, these two quadrant representations appear to share this property, and therefore to form a paired representation of the whole visual field in this fashion. One possibility is that it is the dorso-ventral split between DLO and VMO that led to the identification of separate V4d and V4v representations in homologous locations in the monkey. The monkey data need to be re-evaluated in light of the pairing of DLO and VMO, to determine whether the occipital organization in monkey is susceptible to the same analysis.

THE NATURE OF THE FOVEAL CONFLUENCE

The other issue that arises from the detailed consideration of the lateral occipital cortex, in relation to the occipital-pole flatmaps favored here, is the nature of the foveal confluence. It is very clear that the eccentricity maps show a strong foveal activation centered at the occipital pole (Fig. **4**, right panels). This feature has often been interpreted to imply that the foveal representations of areas V1-3 all converge on the same region in a pie-shaped fashion, generating a singularity at the center of the 'pie'. However, two observations emerge from the occipital-pole flatmap representation. One is that the foveal representation is roughly circular, with eccentricity increasing in all directions from the occipital pole. This complete convergence leads one to expect a set of lateral retinotopic maps diametric to the medial maps of V1-3. However, as laid out in the previous section, no such regular organization emerges. Only the dorsal quadrant of the DLO area is identifiable with any consistency. The adjacent regions of lateral foveal activation do not yield any identifiable meridional mapping, in our observation. It is possible that such an organization may emerge with finer resolution scans, but such structure as we see at present varies dramatically from brain to brain, so we do not expect such improvements to provide the solution.

The second observation is that the mapping in the area lateral to the V1-3 foveae is clearly *inconsistent* with the idea of a foveal confluence for area V3 and perhaps also for V2.. It is not simply that the map becomes indeterminate so that one cannot be sure where the area boundaries lie. Instead, there seems to be strong activation with phases that block the extension of the V2 and V3 boundaries across the foveal confluence. The connection of V2, for example, would be represented by the continuity of its outer boundary (the horizontal meridian representation), forming a continuous line of blue for the left hemisphere and yellow for the right hemisphere passing dorsoventrally through the foveal confluence (see Figs. **4** and **9**). Instead, the mapping colors seem to switch back and forth within the foveal confluence, as if to imply that there is more retinotopic structure there than the direct convergence of the second-tier areas. It is noteworthy that Drury & Van Essen [25], summarizing the evidence for the visual cortical mapping structure in human, mark the connection between the dorsal and ventral representations of both V2 and V3 with question-marks. We therefore prefer to curtail the designation of V1-3 at the fringe of the foveal confluence and look for other kinds of stimuli that may provide a more robust mapping in this region. It is well known, for example, that there is strong activation by face stimuli in this region [15,26]. It would be interesting to take a detailed look at the retinotopy of the face activation within the lateral portion of the foveal confluence (with null stimuli that equate the activation of the medial retinotopic areas V1-3).

THE ECCENTRICITY-BIAS HYPOTHESIS

The Malach group [15, 24, 27] has proposed that lateral occipital cortex is laid out according to an abstract spatial-resolution principle that they characterize as "a center-

periphery organization based on resolution needs, in which objects engaging in recognition processes requiring central vision (e.g., face-related) are associated with center-biased representations, while objects requiring large-scale feature integration (e.g., buildings) are associated with periphery-biased representations." They test this *eccentricity-bias hypothesis* by varying the size of objects from the two classes, faces and buildings, and showing that their cortical representation is relatively invariant under this manipulation. However, detailed consideration reveals that this whole conceptualization is subject to the following criticisms:

1. It is not clear how the two stimulus classes have a foveal/peripheral differentiation. Faces are experienced at a wide range of distances, from indefinitely far to only few inches away (for our intimates). The same can be said of houses, especially when the houses are viewed as a whole from outside, as in typical stimulus sets. It may be the case that houses are *known to be* larger than faces, but both types of stimuli have a similarly enormous range of retinal projection sizes in the typical visual experience, so neither can be reliably associated with particular retinal eccentricities, foveal or peripheral. If the foveal stimulus class had been something like pins, which are always seen with a small visual angle, and the peripheral class something like clouds, which are usually seen at a large visual angle, the logic of the analysis would have been more tenable.

2. The hypothesis draws a distinction between (presumptively-simple) central vision and large-scale feature integration in peripheral vision. This distinction could be valid even if there were no differences in the projected visual angle of the objects. Thus, there would be a valid complexity distinction between, say, lampshades (simple) and houses (complex). However, the choice of faces for the comparison vitiates the distinction, because faces are renowned for their long-range configural properties [28-31]. Thus, it is untenable to propose that the distinction between these stimulus types is related to differences in "large-scale integration".

3. The size-invariance property that was measured for these two stimulus classes, far from establishing the foveal/periphery distinction, tends to contradict it. The size-invariance shows that the mapping to the respective face and house areas is essentially *independent* of projective size, violating the inference that the differential mapping is concerned with the projective size of the objects onto the retina.

4. The only remaining size-difference between the two object classes is in their physical size as objects in the world. What the authors seem to be proposing is a metaphorical distinction between the cortical mapping of objects of different physical size, regardless of visual angle. That is to say, objects that are *known* to be small map near the foveal retinotopic representations and objects that are *known* to be large map near the peripheral retinotopic representations This is a different hypothesis from the one that they express, and could easily be tested by using a class of objects that are smaller than faces, such as common household items like playing cards and golf-balls. Such objects should be represented even more "foveally" than faces, according to the hypothesis.

5. Finally, the eccentricity-bias hypothesis should predict that faces are mapped in the posterior foveal confluence close to the V1 fovea. In fact, the predominant face area is well known to lie in the fusiform gyrus on the ventral surface of the brain many centimeters away from this site. It is not clear how the eccentricity-bias hypothesis can account for this shift in the representation site. It is also inconsistent with the fact that face responses are seen medial to area V4 (coinciding with what we are terming the VMO area), as reported by Grill-Spector & Malach [26]. This area is adjacent to the *peripheral* representation in V3v, so should be responsive to house-like stimuli according to the eccentricity-bias hypothesis. Thus, even if the logical contradictions within the hypothesis are overlooked, its specific predictions do not seem to be borne out.

In summary, the eccentricity-bias hypothesis is poorly formulated and fails to offer a coherent embodiment of the core concept the authors wish to propose. This conclusion is not intended to impugn the size-invariance results, which clearly demonstrate that the coding is eccentricity invariant. This invariance, in turn, carries the implication that some other aspect of the face/house contrast accounts for the difference in cortical location. Possible aspects that were not explored include rectilinearity, convexity, segmentability and cognitive content, each of which varies between faces and houses, and any of which could be the controlling variable in the differential cortical processing.

CONCLUSION

The difficulty with extending retinotopic representation beyond areas V1-3 is that the mapping principles do not propagate with the same logic as these first tier areas. It is clear, however, that there is retinotopic activation of some kind over much of the lateral occipital cortex. This review proposes a series of extensions to the regular progression of retinotopic mapping to provide a scheme that accounts for much of the observed retinotopic activation pattern. These extensions include an oblique axis of eccentricity representation in V3B, a curtailed extent of area V4, a parallel mapping of the meridional and eccentricity axes in V7, a hypertrophic representation of the vertical meridian in two new areas, VMO and DLO, and predominantly foveal representations in areas lying lateral to the V1-3 foveal maps and in the VOF area ventral to V4. The basic layout of this conceptualization is exemplified for the meridional mapping (Fig. **10A**) and schematized in Fig. **10B** in a dual-flatmap representation centered on the two occipital poles. In many respects, these proposals coordinate concepts from previous work into an integrated scheme for the third-tier retinotopic representation in lateral occipital cortex, but one that offers novel interpretations in many details.

METHODS

Scanning Procedure

The fMRI responses for this study were collected with 2D spiral acquisition from a custom occipital surface coil in a GE Signa 3T scanner. There were 23 coronal slices at 3 *s*
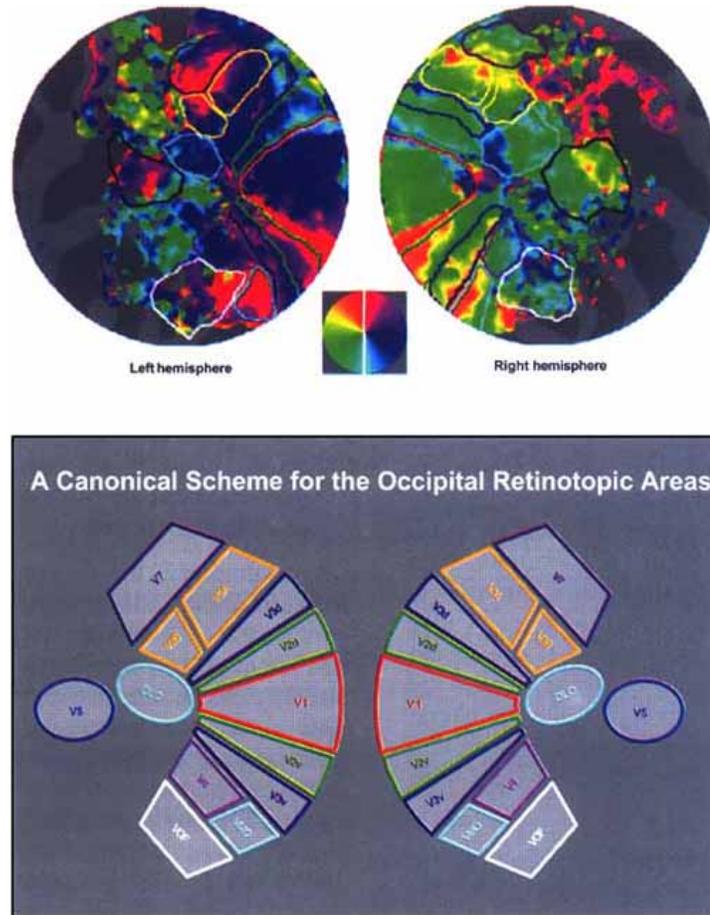
Fig. (10) A. Summary plot of the meridional mapping data for observer CCC. B. Canonical mapping summarizing the retinotopic layout proposed in this review, presented on dual flatmaps centered on the occipital poles. Areas V1, V3A, V3B, V4, V5, V7 and VOF have hemifield representation; all the others are quadrant representations. The applicable eccentricity range is up to about 16°.

TR, with TE of 30 *ms* and flip angle 70°, providing 2.5 x 2.5 x 3 *mm* voxels through the occipital cortex. Test and null stimuli alternated for 9 *s* each in 18 blocks per scan. The stimuli were rear-projected onto a translucent screen inside the bore of the scanner by means of an LCD projector controlled by a Macintosh computer. They had a maximum radius of 16° (total width of 32°). The observer's head was stabilized by chin and forehead tape, with the eyes looking into a 45° mirror to view the front of the projection screen. The observer's task was to maintain fixation on a red fixation point at the center of the stimulus and to concentrate on the stimulus pattern. No motor task was imposed, in order to limit the differential brain response to sensory processing signals and avoid confounding the perceptual responses with motor or decision processing.

Data Analysis and Visualization

A high-resolution anatomical (T1-weighted) 3D MRI volume scan of the entire brain was also obtained for each observer (voxel size = 0.94 x 0.94 x 1.2 *mm*). Gray (cortex) and white (nerve fiber) matter were segmented for each observer using publicly available software [32]. The voxel size is small enough to ensure full segmentation across adjacent cortical surfaces in the sulci, and any 'bridges' are removed to ensure an unconnected manifold before the flattening is implemented. The functional voxels are, however, substantially larger and subject to partial-voluming effects across the sulci, so there is a possibility of activation being spuriously transferred across from one side of a sulcus to the other. Inspection of the anatomical flatmap structure (Fig. **3**) can be used to determine whether such a transfer of the functional activation is likely to have occurred.

The differential fMRI activity profile was then mapped directly onto the cortical manifold, to allow visualization of the response properties over complete cortical areas. The boundaries of the retinotopic projection areas V1, V2d, V2v, V3d, and V3v were established as described in Engel *et al.* [7]. The boundaries between the areas are defined by lines of phase reversal across the flatmap corresponding to a conceptual template of a hemifield representation for V1 and adjacent quarter-field representations for V2 and V3 (both dorsal and ventral to V1); the criteria for subsequent areas are discussed in the main text. The boundaries between areas are drawn slightly inside the phase-reversal line in order to maintain distinct color-coding, and are not intended to represent a non-coded strip between areas. It should be noted that, although the retinotopy stimuli are advancing very slowly across the visual field (a total cycle time of 36 *s*), there are still small phase lags in the BOLD signal, which

has a peak lag time of about 4 *s* depending on the observer. Any lag time does not, however, affect the estimation of area boundaries because they are defined by the reversals in the phase function, which do not shift their location with variations in the absolute phase lag. The V5/hMT+ motion complex was identified using a low-contrast expanding and contracting motion vector field of white dots on a black background, alternating with static dots.

The fMRI (BOLD) response was analyzed by extracting the Fourier fundamental of the time series at every voxel at the stimulus alternation rate of 1/24 Hz. But phase relationships at this level should be considered statistically significant only when confirmed over many adjacent voxels. The initial response transient to stimulus onset was excluded by beginning dummy visual stimulation 9 *s* before the experimental stimulus sequence was initiated. A statistical correction for multiple occurrences was applied to the criterion for significant response, in terms of the amplitude of the Fourier fundamental. A coherence level of 0.3 provided a significance level of $p < 0.01$ in each voxel. Responses below this level do not represent significant activation in amplitude terms, although analysis of the signal phase was analyzed under the assumption that there was activation in each retinotopic voxel but the goal was the best estimate of its phase. This procedure allowed the phase to be used down to a coherence level of 0.15 ($p < 0.05$ in each voxel) for the ROIs defining visual projection area from the retinotopy scans (see Fig. **4**).

Observers

These conceptualizations are based on the analysis of 16 observers scanned in all conditions, eleven male and five female ranging in age from 20 to 60. They all had normal or corrected-to-normal vision, wearing prescription goggles in the scanner in the latter case.

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