A New Method for Measuring the Visuotopic Map Function of Striate Cortex: Validation with Macaque Data and Possible Extension to Measurement of the Human Map

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A NEW METHOD FOR MEASURING THE VISUOTOPIC MAP FUNCTION OF STRIATE CORTEX: VALIDATION WITH MACAQUE DATA AND POSSIBLE EXTENSION TO MEASUREMENT OF THE HUMAN MAP


The observation and measurement of the visuotopic map of primate visual cortex is a classical experimental activity. A number of psychophysical (e.g. vernier acuity, visual acuity, Panum's area, stereo acuity, motion thresholds) and anatomical (e.g. retinal cell densities) measurements bear at least a qualitative relationship to the presumed curve of cortical magnification. However, there is no accurate and direct method for estimating human magnification factor; and even for the case of monkeys, where micro-electrode and 2DG experiments have been performed, there is still uncertainty in this area. What is the correct functional form for the primate map? What is the variance of this estimate across a population?

In order to address these issues, we have constructed a computer generated planar approximation to the surface of Macaque striate cortex (median flattening error = 5%). This eliminates errors associated with cortical surface curvature. We then implemented a numerical algorithm which generates the unique isotropic map from the retinal hemisphere to the surface of the cortex, constrained by a single interior point (e.g. the representation of the optic disk) and a direction at this point. We used this algorithm to analyze three different hemispheres (one from our lab, computer flattened; and two from previously published data from other labs). The same analysis was used in each case, which was based on the assumption that the striate map is isotropic (i.e. conformal: this means that magnification factor does not depend locally on direction). Although the assumption that Macaque V1 is locally isotropic is the basis of this analysis, this is an assumption which is supported, at least approximately, by several recent experimental studies 2. We further support this conclusion by showing that the variance and range of map parameters generated by our numerical/anatomical method is comparable to those between existing microelectrode studies. In other words, given as data a flattened V1 and a single topographic location (and direction) within it, we are able to numerically estimate cortical magnification about as well as other existing methods.

Since our numerical-anatomical method is similar in its results to current micro-electrode measurements of V1 topography, it should be possible to apply this method to human visual cortex, and to obtain an estimate of the human map function with a precision which is comparable to current measurements of magnification factor in monkeys.

1E. Schwartz and B. Merker. IEEE Comp. Graph. and App. 6:36-44 (1986)
2A particular conformal map, based on the complex logarithm, has been stated to be a good approximation to the V1 map in a number of recent experiments: Dow et al, J. Neurosci. 5:890-902; Van Essen et al, Vis. Res. 24:429-448; Tootel et al, Science 227:1066.
3Supported by AFOSR #85-0235 and System Development Foundation

We have previously described an algorithm designed to flatten cortex with minimal distortion or error. This algorithm operates on a three dimensional polyhedral model of the surface of cortex, composed of perhaps several thousand small triangles. This level of detail is sufficient to provide a good approximation to the surface geometry of a cortical structure. However, the level of detail of a polyhedral model (e.g. roughly 0.5 mm²) is not sufficient to represent details such as the columnar pattern of V1.

In the present work, we describe an algorithm for constructing an image resolution flattening of Macaque visual cortex. We illustrate this algorithm with a specimen of (Macaque) striate cortex, stained for cytochrome oxidase following enucleation of one eye. The cytochrome oxidase data from coronal sections cut at 40 μ clearly indicated the ocular dominance column pattern. The design goal was to reconstruct this pattern, at the full 40 μ resolution of the digitized sections, in three dimensions. A polyhedral model of striate cortex was then constructed from these data and it was numerically flattened. This yielded a planar model of the cortex, for which the median distance error was 5%. Next, a three dimensional model of layer IV of the stained cortex was constructed. This procedure required the construction of the full three dimensional cortical model at image resolution, and then the use of a "brain peeler" or digital tangential microtome, to "peel" lamina of the model cortex until layer IV was isolated as a thin (40μ) three dimensional section. A computer graphic of a "peel" representing much of the occipital pole will be demonstrated. Finally, the 3D "brain peel", which is a digital image of stained layer IV of cortex, was image mapped into the flattened two dimensional model of the cortex. The result of these steps was a two dimensional image of the ocular dominance column pattern of striate cortex, at 40μ resolution, with 5% metric error. The cortical representation of the optic disk, as well as full details of the columnar pattern, are clearly produced.

This work represents the completion of a system of computer aided neuro-anatomy, which is adequate to manipulate cortical specimens on the scale of an entire occipital pole, at a level of detail sufficient to resolve functional architecture, in both three dimensions and two dimensions. This work allows questions related to the metric structure of visual cortical areas (e.g. topography, columnar geometry, etc.) to be studied with full quantitative rigor.


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Although topographic and columnar architectures are simple and basic features of visual cortex, they are not jointly well defined. The existence of columnar interlacing (e.g. ocular dominance columns) introduces periodic discontinuities due to the boundaries of the two or more map systems which are interlaced. How can one define a "map" made up of several complete maps warped into a single map, and how can one simulate the (stereo) images associated with such an architecture?

In order to simulate the combined effects of topography and columnar interlacing, it is necessary to first deal with the problem of topography, and to obtain to some reliable form of data concerning column boundaries. In this work, the topographic map problem is dealt with by two methods: complex logarithmic mapping, and numerical conformal mapping based on computerized flat mappings of macaque V-1. Both methods are in good agreement with existing cortical magnification data, as will be briefly discussed.

There is little data currently available concerning within-column topography, but we show recently re-constructed computer flattened models of the macaque V-1 ocular dominance column system. We supplement this data with a computational assumption: the existing columnar map in V-1 is the result of a minimal distortion that allows the two full (left and right) retinal maps to "warp" into the observed pattern of ocular dominance columns. This idea is developed into an algorithm which provides a well defined model of the binocular cortical image. This work is illustrated with the simulation of a stereo representation of two slightly different views of the same scene, as it would be represented at the level of layer IV of macaque V-1.

This work provides a well defined basis for topographic maps, in the presence of columns, and also provides a clear example of how a computational approach to visual architecture is necessary to clarify even as basic a concept as topographic mapping.


--- Supported by AFOSR 85-0235 and the System Development Foundation ---
THREE DIMENSIONAL COMPUTER RECONSTRUCTION OF THE OCULAR DOMINANCE COLUMN PATTERN OF MACAQUE STRIATE CORTEX: DEMONSTRATING A DIGITAL TANGENTIAL MICROTMOMETER

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Recently, we have measured the surface curvature of the opercular surface of macaque striate cortex and demonstrated methods to optimally flatten cortical surfaces (1,2). In this abstract, we demonstrate the construction of a "digital tangential microtome", and apply it to the visualization of the pattern of ocular dominance columns across the surface of macaque striate cortex.

Serial sections (40µm) through the occipital pole of a one-eyed cynomolgous were stained for cytochrome oxidase, digitized and aligned as previously described (1,2). Each digitized section was thresholded to yield a black and white image of the section. These data were then used to reconstruct the surface of striate cortex in 3D. This surface consists of a sheet of 80 µ3 volume elements (voxels). By recursively repeating this process on the sections after the surface sheet of voxels is discarded, a set of tangential cortical "shells" are generated at increasing depth from the original cortical surface. Finally, these abstract cortical shells are "colored" with the original gray scale data (i.e. the density of cytochrome oxidase stain) to produce high resolution images, in 3D computer graphics, of stained cortex at successive depths.

This method makes it possible to reconstruct and display whole brain patterns of differential staining or autoradiographic labeling at columnar resolution obtained from serial sections, without any hand tracing.

In combination with our algorithm for optimal cortical flattening (2), this method provides a general computer based approach to the study of patterns of cortical functional architecture.

1.) Merker and Schwartz, ARVO, 1985 2.) Schwartz and Merker, Neuroscience Soc.,1985

--- Supported by the System Development Foundation and AFOSR 85-0341 ---
Orthogonal stimuli, whose boundary curvature varies sinusoidally, are called Fourier Descriptor or FD stimuli (1). They provide a convenient metric for computer pattern recognition, single unit studies in infero-temporal cortex (2), and psychophysical studies of human shape perception (1).

Since there is an amplitude and a phase for each of the (curvature) frequency components, an analogy might be drawn to (conventional) spatial frequency analyses, in that a similar experimental approach can be adopted.

Prolonged (15-30 min) adaptation effects to FD stimuli have previously been described (1). We now report that this adaptation is frequency specific: human subjects selectively adapt to stimuli of one FD frequency, while showing much less adaptation to neighboring frequencies. Inverted "U" shaped tuning curves to FD adaptation as a function of frequency have been obtained over a range of FD frequencies.

We have also obtained evidence for complementary aftereffects between FD stimuli of opposite phase. Adaptation, with both adapting and test stimuli at the same frequency, resulted in baseline elevation for same phase, but facilitation for opposite phase, FDs. It is possible to cancel the adaptation effect by interpolating the complementary (i.e. opposite phase) FD between adapting and test FDs in the same phase. This suggests that mutually inhibitory interactions are generated by complementary FD stimuli. It also indicates an important role for inhibition in FD adaptation.

FD frequency specificity implies the existence of neuronal sub-populations with frequency-specific properties in the curvature domain. Since curvature is based on non-local orientation comparisons or changes, we would expect these populations to be located in extrastriate cortex. Infero-temporal cortex, in particular, has been shown to have populations of cells with curvature frequency selectivity (2).

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FREQUENCY SPECIFICITY AND INHIBITORY INTERACTIONS FOR FOURIER DESCRIPTORS OF BOUNDARY CURVATURE. Isabelle Alter and Eric L. Schwartz, Brain Res. NYU Med. Ctr. 550 1st Ave NY NY 10016

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The functional architecture of striate cortex may be regarded as determining one of the data formats upon which later visual processing is performed. In this abstract, a series of computer images will be presented which illustrate several aspects of cortical mapping of images: 1) the conformal map log(z+a) provides a convenient one parameter fit to primate two dimensional topography, which is in reasonably good agreement with current experimental data. The constant "a" in this fit has received a variety of different estimates. In order to illustrate the significance of these variations, real scenes mapped according to different current estimates of this parameter will be shown. 2) The pattern of ocular dominance columns of striate cortex may be re-mapped to the visual field, using this methodology. Stereo pairs will be shown, both as they would appear on the opercular surface of striate cortex, and in the visual field. 3) Multiple eye fixations of a visual scene are "blended" to produce a composite multiple-resolution view of the scene. This provides a graphic illustration of the maximum spatial information available over scan paths, and suggests some insight into the nature of visual world stability. 4) A simulation of local orientation domains will be shown, and this will be combined with the ocular dominance column and topographic simulations to provide an image, as it would appear on the surface of striate cortex, contingent on these three major aspects of functional architecture.

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