Afferent Geometry in the Primate Visual Cortex and the Generation of Neuronal Trigger Features*

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Abstract. In previous work, it was suggested that the sequence regularity property of cortical neurons could be accounted for if the local geometric structure of the cortex were a recapitulation of the global complex logarithmic structure of the retinotopic mapping. This model is developed in detail: the excitatory and inhibitory structure of cortical receptive fields may be approximated by a complex logarithmic local geometry, coupled with an intra-cortical lateral inhibition operator which may flow unidirectionally yet still create “rotating” receptive field structure. The direction of intra-cortical lateral inhibition follows the borders of cortical ocular dominance columns, which are the approximate images under the global complex logarithmic mapping, of exponentially spaced, horizontal straight lines in the visual field. Two different topological structures are discussed for the local cortical manifold. The binocular trigger features of cortical neurons follow from the same geometric model, and the ratio of binocular to monocular cortical cells is related to the size and shape of cortical dendritic tree’s by an application of integral geometry. Recent results in optical pattern recognition are cited to suggest that the rotation and size invariant properties of the cortical map are essential to any cross-correlational basis for stereopsis. Finally, a meromorphic function is presented which is both locally and globally complex logarithmic in its structure, and therefore represents the model presented in this and previous papers in a concise mathematical form. This function is closely related to the description of a Karman vortex pattern, in fluid mechanics, and leads to the suggestion that the boundary conditions of layer IV of the cortex (i.e. periodic ocular dominance columns) are causally related to the existence of sequence regularity in the cortex. The developmental implications of this statement are that the specification of neural connections in the cortex may follow directly, both locally and globally, from the detailed nature of the cortical boundary conditions (i.e. anatomy), coupled with general physico-mathematical considerations of continuity and differentiability in the neural fiber flow.

Introduction

The global analytic structure of the retinotopic mapping of the primate cortex has been characterized by a complex logarithmic mapping of the retinal surface to the cortical surface; the receptotopic structure of the secondary and medial visual cortex, the inferior pulvinar nucleus, and the somatotopic mapping (cortical area S-1) have a similar analytic structure (Schwartz, 1976, 1977a). In this work, it was pointed out that the description of neuronal mappings via analytic functions (conformal mappings) has a simple developmental interpretation: analytic functions, such as the complex logarithm, represent “potential flow” on surfaces, subject to boundary conditions imposed by the “shape” of the surface. Thus, the development of specific neuronal mappings may be “encoded” by minimal rules such as those describing the flow of fluids, the diffusion of chemical substances, etc. This idea was developed in detail in subsequent work (Schwartz, 1977b) where Dirichlet's Principle was used to demonstrate that the minimization of the average magnitude of the anatomical magnification factor (per unit area) is sufficient to encode the structure of a detailed receptotopic mapping, based on the shape or boundary conditions of the available tissue surfaces. In the monkey, this follows from the demonstration that the density of retinal ganglion cells implies an annular domain which is logarithmically structured, as originally suggested (in the cat) by Fischer (1973). The cortical domain is characterized as a rectilinear strip, and the retinal annulus is conformally equivalent to the cortical strip.
under the complex logarithmic mapping. In the goldfish, the retina may be characterized as a disk (constant cell density) and the optic tectum as an ellipse. The unit disk is mapped to an ellipse by a certain Jacobian elliptic conformational mapping, and the level lines of this function are in agreement with the experimentally determined retino-tectal mappings of the goldfish. Specific experimental tests of this theory are outlined in the same paper. The present paper is a detailed development of a second suggestion presented in Schwartz (1976, 1977a). The sequence regularity property of the visual cortex of the primate (and the cat) suggests that the local structure of the cortical map is also described by the complex logarithm function: the cortex is a concatenated logarithmic map. This follows because the angle of orientation tuning of cortical cells rotates through equal angular increments as an electrode traverses equal linear steps across the surface of the cortex. Since the complex logarithm function assigns a polar angle in the visual field to a linear coordinate in the cortex, it is intuitively evident that dendritic summation of an afferent input to the cortex that is locally logarithmic in its structure would provide this sequence regularity property. The detailed presentation of this statement requires a discussion of intra-cortical inhibition, the nature of the images of the dendritic tree's of cortical cells, the topological structure of the local cortical mapping, and a model for the "packing" of adjacent hypercolumn mappings in the cortex.

In the present paper, a geometric model for the local structure of the afferent input to the visual cortex is presented; this model accounts in a logically consistent way for a variety of anatomical and physiological features of the visual cortex, and leads to the following statements: 1) The borders of the ocular dominance columns in the primate are the approximate mapping under the complex logarithm of horizontal, exponentially spaced lines in the visual field; 2) The images of the dendritic tree's of cortical cells, under the local logarithmic mapping, are not particularly elongated, in agreement with experimental data from the cat and the primate, which implies: 3) Intra-cortical inhibition must be responsible for the existence of "linear tuning" and inhibitory sidebands, as suggested by Creutzfeld et al. (1974), and Schiller et al. (1976b). However, since the angle of both the excitatory center and the inhibitory surround rotates (sequence regularity), the intra-cortical connections responsible for this lateral inhibition must be highly "tangled", unless; 4) The local structure of the cortical mapping is a recapitulation of the global logarithmic structure, which causes the afferent input to effectively "rotate", allowing intra-cortical inhibitory connections to lie parallel to one another. This directional intra-cortical inhibition is mathematically modeled by a modification of the Laplacian operator (which becomes a "directional derivative"), and the direction of this inhibition is suggested to lie parallel to the ocular dominance column boundaries; 5) Orientation columns are therefore a joint product of directional lateral inhibition, and the locally logarithmic structure of the cortex: they need not have an observable anatomical substrate as "columns". 6) A simple application of integral geometry ("Buffon's Needle") allows a calculation of the ratio of binocular to monocular cortical cells, which is in good agreement with experiment, and which makes definite predictions for the perimeter of the dendritic tree's of cortical "S" and "CX" type cells. 7) The topological structure of a cortical hypercolumn is discussed, and the possibility is raised that the standard cylindrical Riemann surface of the logarithm function may have to be modified to a nonoriented cylinder for the local cortical map, in order to achieve a symmetric hypercolumn structure. This gives some insight into Werner's (1970) demonstration of the non-oriented topological structure of the somatosensory cortex: higher topological structure, in a biological context, may arise from the need to satisfy simple boundary conditions and symmetry requirements. 8) The binocular trigger features of the primate cortex, as measured by Hubel and Wiesel (1970), follow from the model of cortical geometry. A formula is derived relating binocular disparity to the cortical magnification factor, the amount of shift of neighboring receptive fields, and the size of a "hypercolumn". The large magnification factor for the parafoveal striate cortex predicts values of binocular disparity tuning that are extremely small, possibly explaining the lack of observed disparity tuning in the primate striate cortex. 9) Since the monocular and binocular trigger features of the visual cortex may be accounted for by a simple geometric structuring of the afferent input, then the identification of the psychological process of "feature extraction" with the neuronal trigger features is called into question. The relationship between structure and function in the cortex might be more aptly described in terms of "computational geometry" rather than "neuronal feature extraction". This (Gestalt) approach to the psychology of the visual cortex is supported by 10) Recent results in optical pattern recognition which indicate that if stereopsis is to depend on cross-correlation between the left and right eye input, then the size and rotation invariant properties of the complex logarithmic retinotopic mapping (Chaikin and Weiman, 1977; Casasent and Psaltis, 1977; Schwartz, 1977a) are critical to maintaining a reasonable signal to noise ratio. 11) A meromorphic function is presented which represents a concatenated complex logarithmic map, i.e. it is locally and globally logarithmic. This map concisely summarizes the geometric model presented in this paper, and represents a convenient mathematical