NEO-CORTICAL COLUMNAR ARCHITECTURES I: A GENERALIZED VORONOI DIAGRAM ALGORITHM FOR MULTI-COLUMN MAP SYSTEMS

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ABSTRACT

We define the proto-column of a cortical column as the pattern of afferents that are mapped into the cortical column. The proto-column is not determined by the shape of any single cortical column, but is rather a property of the local neighborhood of cortical columns. In determining the proto-columns for an experimentally observed set of cortical columns, we require that each point of the input mappings be accounted for in the proto-columns. Furthermore, the proto-columns must cover the input space with no overlap, fitting together like the pieces of a jigsaw puzzle. Last, we note that the generalized Voronoi diagram associated with a set of columns represents its set of proto-columns.

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Introduction

A common architectural feature of neo-cortex in cats, monkeys, and humans is the interlacing of multiple map systems, in the form of "columns," in a single two-dimensional layer. Examples are ocular-dominance columns (human and monkey V1; see Figure 1), orientation columns (cat and monkey V1), and direction columns (monkey medial temporal cortex). Column systems, which seem to be ubiquitous in neo-cortex, appear to be associated with the representation of more than two stimulus dimensions in a single two-dimensional cortical layer.

Although the ocular-dominance system represents a 2:1 interlacing of data from the left and right eyes into a single layer of striate cortex, other

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systems may have a higher valence. Thus, the orientation-column system of striate cortex may be thought of as an interlacing of perhaps 20:1, i.e., with one complete copy of the visual field for each orientation-column value. Although this is not the usual way of thinking about the orientation-column system, it is consistent with the approach of this report, as explained below.

Historically, little attention has been paid to the details of how an interlacing (for example, of data from the entire left and right eyes) might be produced in a single map, as in monkey V1 (ocular-dominance columns). In this report, we describe a simple algorithm that can interlace an arbitrary number of complete 2D maps into a single 2D layer, via columns. The columns can have an arbitrary polygonal shape. All pixels of the input map are assigned to a specific cortical column, and the boundaries of the proto-columns smoothly cover the input surface with no overlap.

**Proto-columns as “numerical HRP”**

The best way to understand the proto-column concept is to think of the experimental technique of horseradish peroxidase (HRP). HRP, when injected into a layer of cells, labels the distant cells that project to the HRP labeling site.

Consider the following “gedanken” experiment. Inject HRP in a series of very fine spots in each of the columns making up a cortical map. Then, in a laborious (and, in practical terms, impossible) procedure, map the site of origin for each cortical column. Thus, for a single-ocular dominance column, the result of this exercise would be the map of a columnar domain in the left (or right) retina. This columnar domain is what we call a retinal “proto-column.” By performing this experiment for all the
columns, we would obtain a set of "proto-columns" that covers both the left and right retina smoothly and completely.

Now, taken together with a global topographic map function (e.g., the complex log), the proto-column system would completely and unambiguously define the structure of the map of the two retinas to the single cortical surface.

Algorithmic assumptions: the nearest-neighbor rule for compression

Because the HRP experiment is impractical, if not impossible, we resort to the algorithm of this report in order to specify the proto-column map. However, we must first make some assumptions about the convergence, divergence, and overlap of the mapping systems. These assumptions amount to the statement that the migration of cells into column interlacings is based on a nearest-neighbor rule. We can best illustrate these assumptions in terms of a brief discussion of some of the known facts about the ocular-dominance-column system of macaque monkey striate cortex.

Full "proto-maps" exist before birth

Rakic (Rakic, 1983) has shown that before birth, monkey visual cortex contains two full visual maps, one each for the left and right eyes, at the level of striate cortex. We call these maps "proto-maps." About 13 weeks before birth, the cells in the two visual maps migrate together into a single map, forming the ocular-dominance column system. Thus, we can visualize the cortical proto-columns as existing in each of the cortical proto-maps (see Figure 2).

Of course, it is not necessary for the proto-maps to exist in the adult; but visualizing them is a useful exercise, and they do indeed exist for
monkeys before birth. Now, consider the case of the ocular-dominance columns before they have formed: how does a given cell "know" which column to migrate toward? The simplest rule is based on proximity: the cell would simply migrate to the nearest column-to-be. This assumption is the basis of our "proto-column" algorithm.

Earlier attempts to simulate ocular-dominance-column patterns

Two previous simulations of ocular-dominance-column patterns have been published (Schwartz, 1977, Hubel and Freeman, 1977). In both these simulations, the actual cortical ocular-dominance-column pattern (not the proto-column pattern!) was mapped back to the retina. This resulted in the loss of half the visual field from each eye. That is, wherever a left-eye column occurs in the cortex, there was no right-eye input to map back to the retina, and vice-versa for the right-eye columns.

However, when we close one eye, we do not lose the half of the visual field that corresponds to the cortical pattern of the closed eye's columns. In order to take into account of the true complexity of this situation, we must construct the proto-column boundaries of the left and right eyes as well as the actual column boundaries (see Figure 2).

The proto-column algorithm: Voronoi regions

The concept of Voronoi regions, also known as "Dirichlet regions," is familiar from both crystallography and computational geometry. Briefly, the notion of Voronoi regions is that given a distribution of points in a plane, we can divide up the plane such that:

⇒ Each point is contained within its own region

⇒ Each region contains the set of points closer to it than any other.
The border between the regions about neighboring points x and y is a segment of the perpendicular bisector of xy. In our application, an important characteristic of Voronoi regions is that Voronoi polygons assume shapes that reflect the local spatial distribution of points. For example, the Voronoi neighbors of a point are not necessarily its nearest neighbors. This is so because distant points may be accepted as neighbors on a sparsely populated side, whereas relatively close points on a dense side may be rejected if they occur "behind" other, closer points.

Thus, connecting a point to each of its Voronoi neighbors provides an efficient triangulation of the point set. Figure 3 shows how the lines of the triangulation are the perpendicular bisectors of the borders of the Voronoi regions.

**Generalized Voronoi regions and generalized Voronoi diagrams**

If we start with polygons instead of points, we can construct a generalization of the Voronoi diagram described above. Thus, the locus of points that are nearest to a given polygon forms a region. The boundary of this region is the generalized Voronoi region of the polygon. In our terminology, it is also the *proto-column*.

Let T represent the polygon defining a particular column, and S the region surrounding the column. Then the generalized Voronoi region of this polygon is defined as:

\[ V(T) = \{ p : \exists v \in T, \forall w \in S - T, \text{dist}(p,v) < \text{dist}(p,w) \} \]

Now, consider a collection of columns (polygons) in a plane. The union of the generalized Voronoi regions of these polygons is a generalized Voronoi diagram of the column system, as shown in Figure 2.
In the case of cortical systems, we perform the following construction. We take a given cortical area, which by assumption is a continuous two-dimensional sheet. If \( n \) column systems are interlaced in that area, we make \( n \) copies of the cortical sheet. In the \( n^{th} \) sheet, we color black the column system parameterized by \( n \), and color the others white (i.e., we erase their boundaries).

Thus, the generalized Voronoi diagram corresponding to the \( n^{th} \) column system corresponds to the proto-map of that column parameter. The union of all the generalized Voronoi regions in that proto-map will smoothly cover the area of the proto-map, with no overlap, and every pixel in the proto-map region will be assigned to one of the proto-columns.

**An efficient algorithm to find Voronoi regions**

Let us start with a definition of a column system in terms of labeled pixels (e.g., black and white regions). For concreteness, we assume the black regions represent left-eye afferents for cortical ocular-dominance columns (see Levay et al., 1975, and Figure 1).

Focusing attention on, say, the white columns, we detect each column (for example, by applying a connected-components algorithm), and label each column with a unique integer. For simplicity, we actually "color" the column with this integer, and can then display this color-coded image on a computer monitor. We then apply a standard contour-follower to isolate the boundaries of the columns.

We have found that any given inter-column pixel is generally no farther than an average column-width from the nearest column. We construct a small mask, or window, this size or slightly larger, and build a
look-up table of all the distances from the center of the mask to its own boundaries. We then use this look-up table of distances to "pass" the mask over all intercolumn pixels. This way, we can easily determine which inter-column pixels "belong" to a particular column, based on nearness. We then label each pixel with the "color" of the column to which it belongs.

Using the look-up table of distances in a mask greatly reduces the potentially enormous amount of computation that this algorithm might otherwise require. Furthermore, by running the mask over every intercolumn pixel, we classify each of the inter-column pixels according to its nearest column. After we have examined all such inter-column pixels, every pixel in the image has been assigned to one or another of the original columns and has been marked with the color of its column. Thus, each set of marked pixels forms the proto-column of the correspondingly colored column.

Performance and applications of the algorithm

We have run this algorithm on a typical ocular-dominance-column pattern (see Figure 3) with an image size of 480x512. The execution time for the algorithm on a Sun 2 workstation is about 2 minutes.

After this algorithm is used to find the proto-columns associated with ocular-dominance columns, the known cortical-map function can be used to find the retinal proto-columns. This application is discussed elsewhere (Loris et al., 1986).

As noted above, this kind of algorithm might well be used on other columnar systems. Consider the orientation-column pattern of striate cortex. Assume that the cortical surface has been divided up into "columns"
according to the subject's responses to a set of 20 orientations. Any cell in the cortex is classified by the orientation to which it responds best. The boundaries of these regions will then delineate the "orientation columns." All of the cortical cells, possibly including an "unoriented" class of cells, will belong to one or another of these columns.

Now, assume that immediately beneath this cortical layer there is a layer of unoriented cells, and that these cells project up to their neighbors to form, somehow, the orientation-column system. We assume that every orientation column in one layer receives a projection from all of the cells beneath it. (In other words, there are no "blind spots" in the orientation layer.)

Thus, we take 20 copies of the unoriented layer and run the proto-column algorithm for each copy, once for each orientation. The result will be a simple nearest-neighbor model for the boundaries of the afferent projections into the orientation columns, based on an observation of their columnar boundaries. Similar applications can be made for other column systems, such as the direction columns in MT (medial temporal) cortex.

Discussion

The proto-column algorithm of this paper performs a necessary extension of the concept of a "cortical map." Because most cortical layers consist of two or more "copies" interlaced together in complex fashion, the simple concept of a "regular" or "continuous" map of $R^2 \rightarrow R^2$ is not sufficient or satisfactory.

A simple nearest-neighbor rule for multi-column systems leads to the definition of the proto-column regions associated with the observable columnar boundaries. A simple algorithm can then find these regions.
Without knowledge of these proto-column regions, accurate simulations of multi-column systems are impossible. Conversely, however, with good knowledge of a global, regular topographic map (e.g., the complex log), and knowledge of proto-column boundaries, accurate simulations can be performed.

In a companion report (Loris et al., 1986), we show an application of this method that leads to the first accurate simulation of the primate ocular-dominance-column system in both retina and cortex.
Figure Captions

Figure 1. This image of the ocular-dominance-column pattern of macaque striate cortex is reprinted from (LeVay et al., 1975). The black areas correspond to cortical cells that receive input from the (missing) left eye, while the white areas correspond to cortical cells that receive input from the (present) right eye.

Figure 2. This figure shows the construction of "proto-columns" from the material in Figure 1. The colored areas represent the territory of each proto-column. This territory corresponds to the actual cortical column (shown by a solid line) that it contains.

Figure 3. This figure shows the Voronoi regions and the Voronoi triangulation associated with a distribution of points in a plane. The generalized Voronoi regions of the columns in Figure 1 are the proto-columns in Figure 2.
References


