Random Retinal Waves are Sufficient to Establish Retinotopy in a Knowledge–seeking Model of Primary Visual Cortex

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Abstract

It has been argued that the retinotopic organization of primary visual cortex must be genetically determined rather than learned, because cortical retinotopy is fully established before the onset of patterned vision. However, retinal waves of traveling burst spiking characterize the embryonic previsual retina. These randomly directed retinal waves may carry sufficient information to establish cortical retinotopy. Here we show that a simple, well-known knowledge-seeking neural network model (Kohonen's self-organizing map algorithm) can extract full retinotopic organization from the previsual information contained in embryonic retinal waves, lending support to the neuronal empiricism hypothesis of cortical organization.

Key Words: Retinal waves, Self-organizing map, Primary visual cortex, Retinotopic organization.

1   Introduction

The venerable nature vs. nurture argument continues to resurface in neurobiology in many systems and under many guises. Here we focus on one particular example, the development of the primate visual cortex. In terms of the detailed wiring of the mammalian visual system, it has been argued that the retinotopic organization of the primary visual cortex must be established at least approximately by genetic mechanisms, because such organization is present long before the visual system becomes functional.

Retinal Waves   This view has been challenged by the discovery of organized previsual retinal activity that is probably initiated by amacrine cells but propagated by ganglion cells [7]. These are waves of coordinated burst firing that originate at random locations on the retina and then proceed to propagate away from the site of origin across the retina. Thus, ganglion cells in the developing previsual retina systematically fire in bursts of activity that are synchronized and move across the retina in locally correlated periods of activity.

These retinal waves spread in unpredictable directions, but do not re–enter regions that have recently supported bursting activity. Retinal waves appear only in early development

and cease just prior to the onset of patterned vision. This coincides with the developmental period in which organized retinotopic projections from the retina to the lateral geniculate and primary visual cortex are established [7].

It is now clear that retinal wave activity certainly affects the development of the monocularly specific areas of the lateral geniculate nucleus. The LGN, in addition to maintaining a retinotopically organized pattern, divides itself into a series of six layers that are strictly monocular, responding to either the right or the left retina, but not both. This organization develops during the period of retinal wave activity, which—of course—is completely uncorrelated in the two eyes.

Further, it has recently been shown experimentally that the relative size of the right– and left–responsive layers is determined solely by the relative amount of retinal wave activity generated by the right vs. the left retina [6]. This finding is in perfect accord with the neuronal empiricism hypothesis [1].

Retinal waves contain a great deal of spatial information, perhaps enough to establish retinotopy in both the lateral geniculate nucleus (LGN) and the primary visual cortex (PVC), if such structures embody a knowledge-seeking unsupervised learning algorithm.

We explicitly tested this hypothesis using a well-known unsupervised learning method, Kohonen's self-organizing map (SOM) algorithm with simplified projections from retinal ganglia cells, relayed but not modified by the LGN to the PVC. Such a knowledge–seeking model of cortical computation generates a retinotopic cortical representation of retinal spatial relations spontaneously and without contrivance [1].

2   Methods

The previsual retina was simulated by a 40×40 matrix of retinal ganglion cells, which, in the absence of a retinal wave, were quiescent. A series of 1600 static retinal waves of excitation were simulated by selecting each ganglion cell in the simulated population as the point of origin for the wave. Static retinal waves are appropriate for testing the SOM model since it embodies no explicit time dependencies.

A small Gaussianly ($\sigma = 3$) distributed field of excitation was then created around the selected cell. This method provides the cortical model with a minimal subset of the spatial information contained in biologically generated retinal waves.

The Self-Organizing Map Algorithm   The knowledge-seeking learning algorithm that we employed is Kohonen's self-organizing map algorithm [2, 3]. We created a model of cerebral cortex containing 1,600 map vectors, also arranged as a 40×40 matrix. Initially this model was not retinotopically organized. However, receptive fields of the cortical model were modified by experience with the retinal waves. In this model, self-organization of the map takes place by competitive learning over a large number of training trials. On each trial, the weights of the cortical vectors are modified as follows:

$$m_i(t + 1) = m_i(t) + h_{ci}(t)\left[x(t) - m_i(t)\right] \tag{1}$$

where $t = 0, 1, 2\ldots$ and is a discrete function of time, here the presentation of randomly positioned retinal waves for processing by the SOM algorithm, m_i is a cortical map vector, $x(t)$ is the data vector representing one retinal wave, and h_{ci} is the model's adaptation
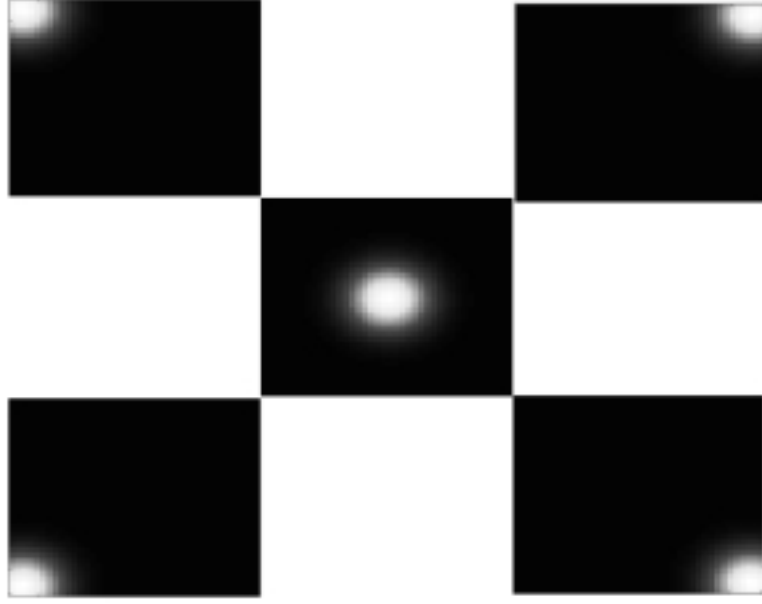
Figure 1. Retinotopic Organization in the Self–organized Map. The receptive fields of five of the 1,600 cortical self-organizing map vectors, extracted from the four corners and the center of the self-organizing map after 1,000,000 iterations of Kohonen's algorithm.

kernel. On each of the 1 million iterations of the model, one of the 1,600 possible retinal waves is presented to the model.

The Gaussian Adaptation Kernel We used a standard Gaussian adaptation kernel in our cortical model, which weighs the extent of adaption of each map unit by a decreasing neighborhood function of its distance from the cortical node most similar to the retinal data.

$$h_{ci} = \alpha(t) \cdot \exp\left(-\frac{\| \, loc_c - loc_i \, \|^2}{2\sigma^2(t)}\right) \qquad (2)$$

where α is a learning rate factor, σ defines the width of the Gaussian adaptation kernel, loc_c is the location of the winning or best–fitting map vector and loc_i is the location of the i_{th} map vector, both in two–dimensional cortical space [5].

Both α and σ are decreasing functions of time. In our simulation, α was initially set to 0.2 and decreased to 0.0 on the last trial. Similarly, σ was set initially to 30 and decreased to 1 on the last training trial. This is typical of Kohonen-style training algorithms [2]. In point of fact, the Kohonen algorithm is surprisingly insensitive to exact model parameters [4].

3 Results and Discussion

The spatial information contained in Gaussian retinal waves is sufficient to establish cortical retinotopy if the model of the cortex embodies the SOM algorithm or something like it.
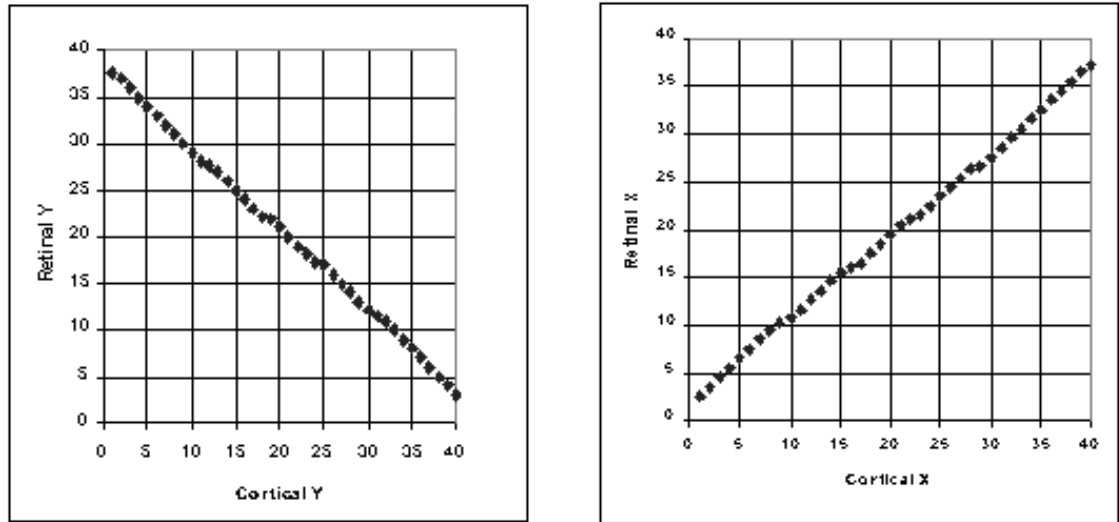
Figure 2. Vertical and Horizontal Retinal Registration on the Cortical Self-organizing Map. Left: A plot of retinal vs. cortical azimuth. This relationship happens to be inverse because of the arbitrary assignment of vertical orientation in the cortical SOM. The important point is that the retinal and cortical organization is in near–perfect registration. Right: A plot of retinal vs. cortical eccentricity.

This is most clearly shown by examining the receptive field (RF) weights of selected cortical elements. Figure 1 presents the RF weights for 5 cortical units, four at the corners of the cortical map and one in its center. Lightened regions of the retinal surface correspond to high weights and dark regions to low. This qualitative snapshot of the self–organized cortical map suggests that a high degree of retinotopy has been captured by the model.

This conclusion is demonstrated more quantitatively in Figure 2. Here, we asked what the average value of the retinal azimuth or eccentricity was for each column or row of the cortical map. The results are very clear. Both the retinal X and Y coordinates are transferred faithfully to the cortical map. The variance of these means is extremely small, often zero.

These findings establish empirically that simple, biologically realistic unsupervised learning algorithms are sufficient to account for many of the apparently complex organizational properties of the primate cerebral cortex. They suggest that the primary visual cortex may already be retinotopically segregated before the onset of patterned vision. One might imagine that the development of orientation columns and modules builds upon the retinotopic anatomical segregation provided by retinal wave input during a critical stage of cortical development [7].

More generally, our results lend support to the neuronal empiricism hypothesis, which argues that many important features of cortical neurons are learned from their inputs, not specifically genetically determined [1]. These findings, and others like them, raise the exciting possibility that all neocortex may utilize the same computational algorithm and that the functional differences observed between cortical areas are simply the result of differences in connections and the properties of the information that each individual area receives.

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