Propagating Waves in Visual Cortex: A Large Scale Model of Turtle Visual Cortex

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Abstract—This paper presents a detailed model of the turtle visual cortex containing 750 cells from different cortical layers. Our model captures the basic geometry and temporal structure of the visual cortex and has been shown to generate propagating waves of activity that contain information about a moving stimulus. The simulation data have been analyzed using principal component analysis. © 2002 Elsevier Science Ltd. All rights reserved.

1. INTRODUCTION

Mammals have a cerebral cortex that embodies several, topographically organized representations of visual space. Extracellular recordings show that neurons in a restricted region of many visual cortices are activated when a visual stimulus is presented to a restricted region of visual space (the classical receptive field of the neuron). Neurons at adjacent points in the cortex are activated by stimuli presented at adjacent regions of visual space. There is, consequently, a continuous (but deformed) map of the coordinates of visual space to the (x, y) coordinates of the cortex. Early extracellular recordings from the visual cortex of freshwater turtles [1] produced a very different result. Neurons at each cortical locus are activated by visual stimuli presented at every point in binocular visual space, although the latency and shape of the response waveforms vary as the stimulus is presented at different loci in visual space. This suggests there may not be a simple map of the coordinates of visual space to the (x, y) coordinates of the visual cortex in turtles. Position in visual space is either not represented in the visual cortex, or is represented in some form other than a retinotopic map. Senseman and Robbins [2,3] supported this hypothesis. They used voltage sensitive dye methods to show that presentation of a visual stimulus to the retina of an *in vitro* preparation of the turtle eye and brain produces a wave of depolarization that propagates anisotropically across the cortex. They used a principal components method, the Karhunen-Loeve decomposition, to analyze the data. Individual waves could be represented as

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a weighted sum of as few as three eigenvectors which were functions of the (x, y) coordinates of the cortex. The dynamics of the wave could be represented as a trajectory in a phase space, A. Interestingly, presentation of different visual stimuli (such as spots of light at different points in visual space) produced waves represented by different trajectories in the A-space. This raises the possibility that visual information is coded in the spatiotemporal dynamics of cortical waves. Our presentation explores this possibility by describing a large-scale model of turtle visual cortex that has the qualitative features of the cortical waves seen in experimental preparations.

2. CONSTRUCTING THE MODEL

2.1. Modeling Individual Neurons

Turtle visual cortex contains at least 11 morphologically distinct types of neurons. The model contains the three types of neurons that are most numerous and are best characterized. These are two types of pyramidal cells (the lateral and medial pyramidal cells), stellate cells and horizontal cells. Pyramidal cells have somata located in the intermediate Layer 2 of the cortex and are glutaminergic. Stellate cells have somata in the outer Layer 1 and are GABAergic. Horizontal cells have somata in Layer 3 and are also GABAergic. Multiple compartmental models of each type of cell were constructed using standard methods, constrained by anatomical and physiological data and implemented in GENESIS.

2.2. Spatial Distribution of Neurons

Maps of the spatial distribution of neurons in each of the three layers of the cortex were constructed from coronal sections through visual cortex of a turtle. The maps were divided into a 8×56 array of rectangular areas. An algorithm was developed in MATLAB that constructed an array of neurons in each layer that preserved the ratios of cells between layers in the real cortex. Spatial coordinates of cells within each block were assigned assuming a uniform distribution of cells within the block. This algorithm is convenient as it can generate as many different models as needed, while retaining the information about the relative densities of cells. Figure 1 shows an example of cells distributed within a block. Most of our models have approximately 700 pyramidal cells, 40 stellate cells, and 20 horizontal cells. Figure 2 shows the spatial distribution of each of the four types of cells in the model.

2.3. Interconnecting Neurons in the Model

Pyramidal cells and stellate cells receive direct inputs from the dorsal lateral geniculate complex (LGN). The model contains 800 geniculate afferents. Each LGN cell is modeled as a single compartment spike generator and an axon, modeled as a delay line that extends across the cortex from lateral to medial. The geometry of the geniculate afferents and the distribution of synapses (varicosities) along the length of the axons were based on anatomical data [4]. Figure 3 shows the distribution of geniculate axons and the distribution of varicosities used. Geniculate axons intersect lateral and medial pyramidal cells in characteristic patterns. Figure 4 shows the spatial distribution of geniculocortical synapses upon these two types of cells. Geniculate synapses were modeled as AMPA synapses, consistent with experimental data. Pyramidal cells were connected to stellate cells, horizontal cells, and other pyramidal cells located within spherical domains. Pyramidal cell synapses were modeled as mixed AMPA and NMDA synapses. Stellate cells were connected to pyramidal cells located within spherical domains. Their synapses were modeled as mixed GABAa and GABAb synapses.

Horizontal cells are connected to pyramidal cells within spherical domains. Their synapses were modeled as mixed GABAa and GABAb synapses.
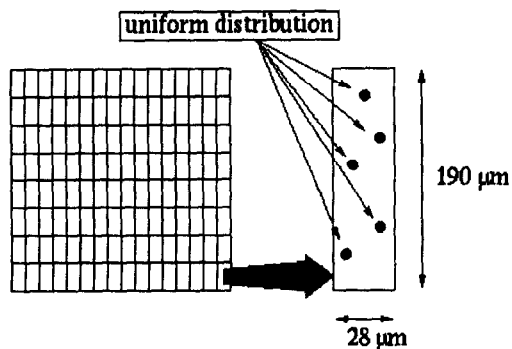
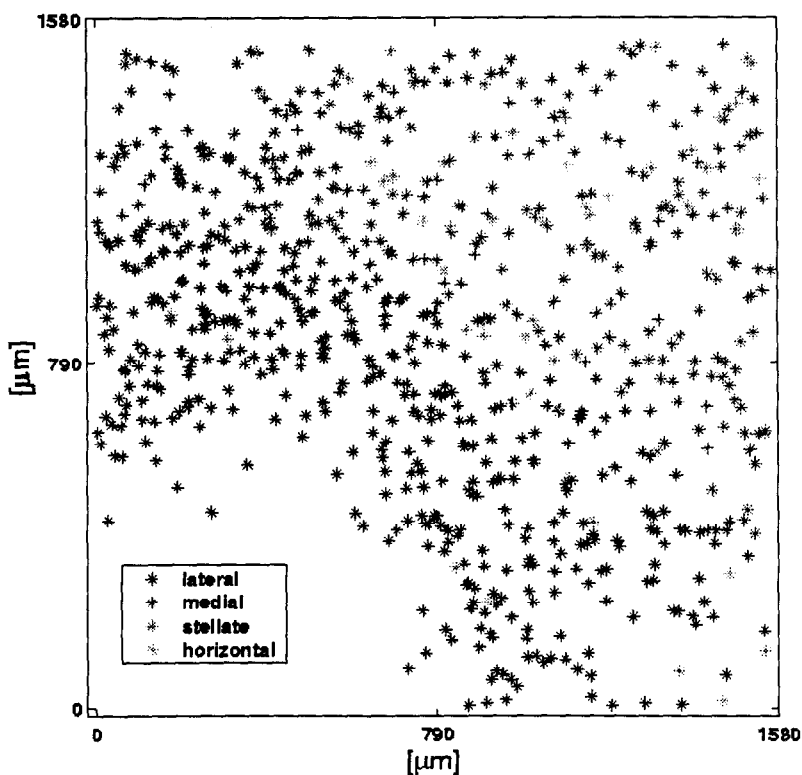Figure 1. The algorithm distributes the cells within each block.

Figure 2. The spatial distribution of particular cells.

3. SIMULATING RESPONSES OF THE CORTEX TO SPOTS OF LIGHT PRESENTED ON THE RETINA

Spots of light produce waves of depolarizing activity in the cortex. Presentation of a spot of light on the retina was simulated by presenting a 50 msec square current pulse to a set of adjacent geniculate neurons. This produced a train of action potentials in the geniculate afferents. Presentation of a spot of light produced a wave of depolarization that originated near the rostral pole of the cortex and propagated anisotropically across the cortex. Figure 5 shows several frames from such a movie.

4. WAVES ARE ANALYZED USING A TWO-STEP KL DECOMPOSITION

Waves were analyzed using a KL decomposition [3,5]. Figure 6 shows the first four eigenfunctions obtained from this method. The waves of activity can be represented as a weighted sum of
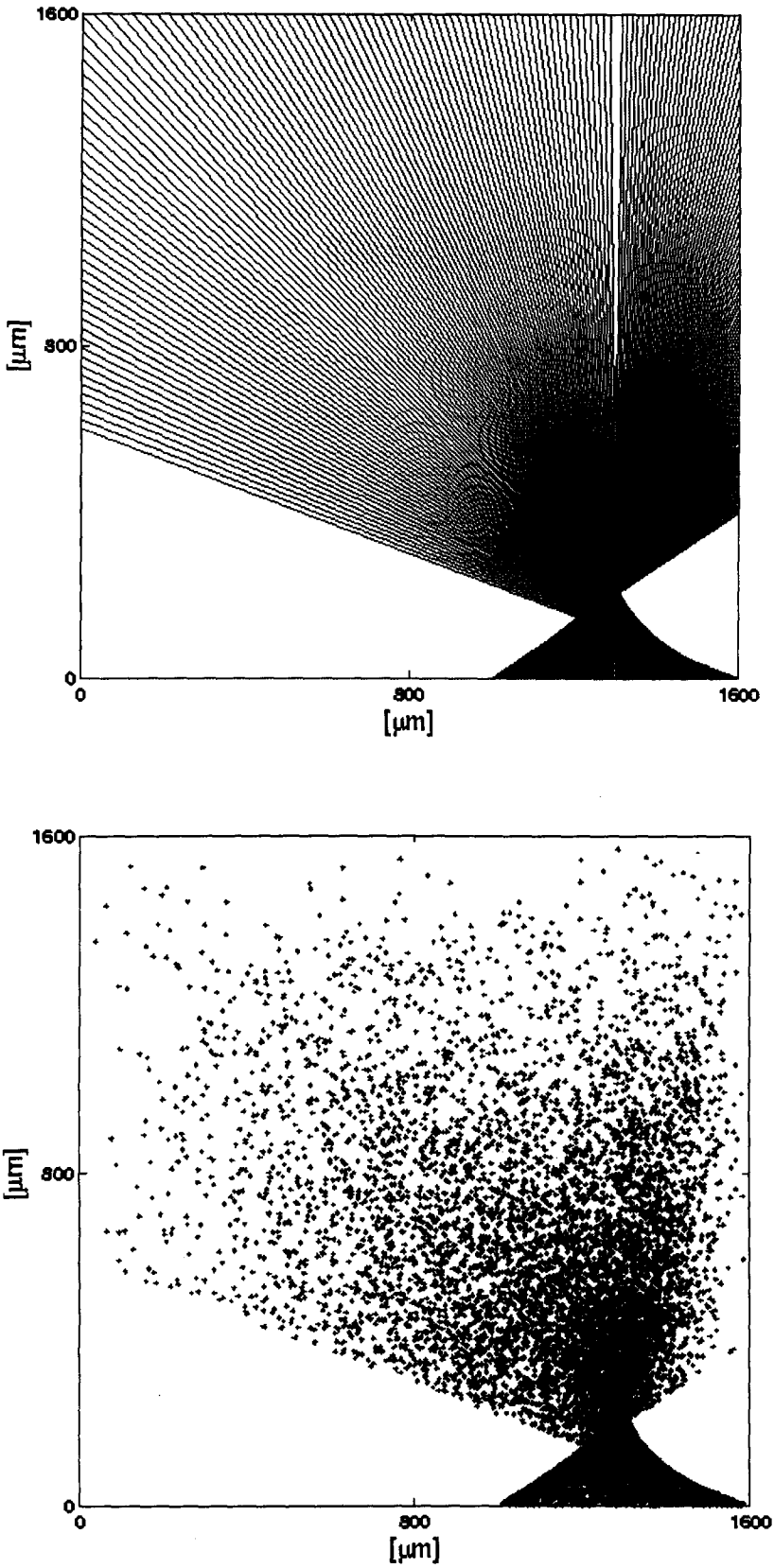
Figure 3. The spatial distribution of LGN axons (top) and varicosities (bottom).
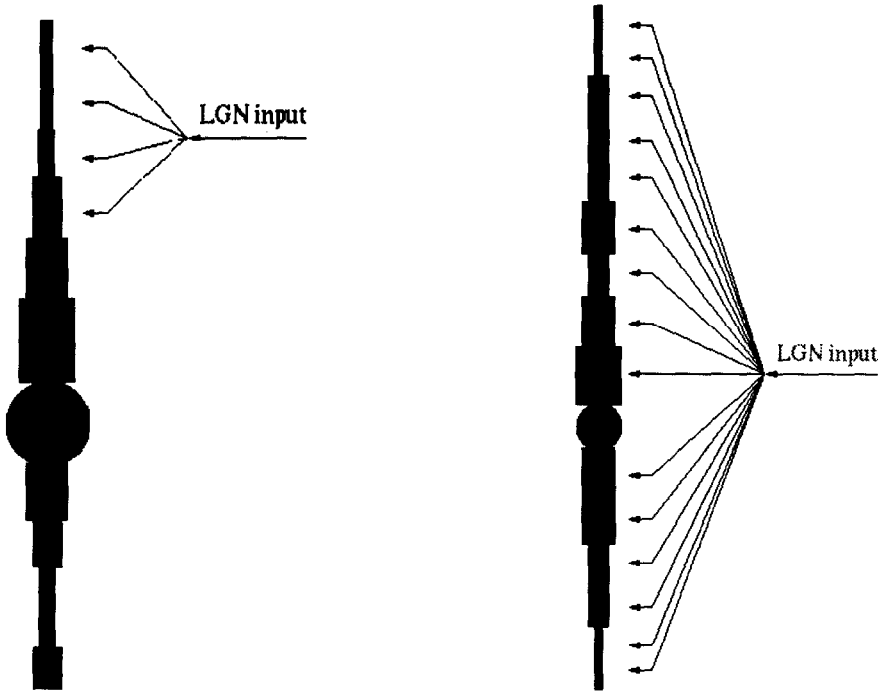
Figure 4. The spatial distribution of LGN synapses upon both types of pyramidal cells.

Figure 5. Several frames showing the propagation.

these functions, with time dependent weighting coefficients

$$I(x, y, t) = \alpha_1(t)\, M_1(x, y) + \alpha_2(t)\, M_2(x, y) + \alpha_3\,(t) M_3(x, y) + \cdots,$$

where $M_i(x, y)$ is the ith spatial mode of spatio-temporal signal $I(x, y, t)$ and $\alpha_i(t)$ is the projection of the spatio-temporal signal on the ith mode. Given that all the movies are projected to the same set of basis functions, a so-called global basis, the individual waves can actually be represented as a phase trajectory in the A-space. Figure 7 shows an example of trajectories produced by presenting spots of light at three different points in visual space.

A second KL decomposition was used to compare trajectories produced by different stimuli [6]. Each trajectory was represented by a vector of coefficients in a second space, B. These coefficients are constant while the eigenfunctions are functions of time. Therefore, each complex cortical wave is represented by a point in B-space

$$\begin{pmatrix} \alpha_1(t) \\ \alpha_2(t) \\ \alpha_3(t) \end{pmatrix} = \beta_1\, \phi_1(t) + \beta_2\, \phi_2(t) + \beta_3\, \phi_3(t) + \cdots,$$

where $\phi_i(t)$ represents the ith basis function, and β_i is the projection of the trajectory on the ith basis function.

5. CONCLUSION

Our hypothesis is, thus, that position in visual space is coded by the spatio-temporal dynamics of the propagating cortical waves. Figure 8 supports this hypothesis by showing the results of
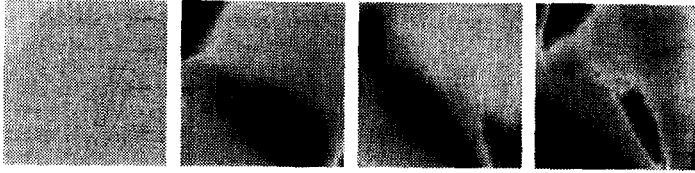
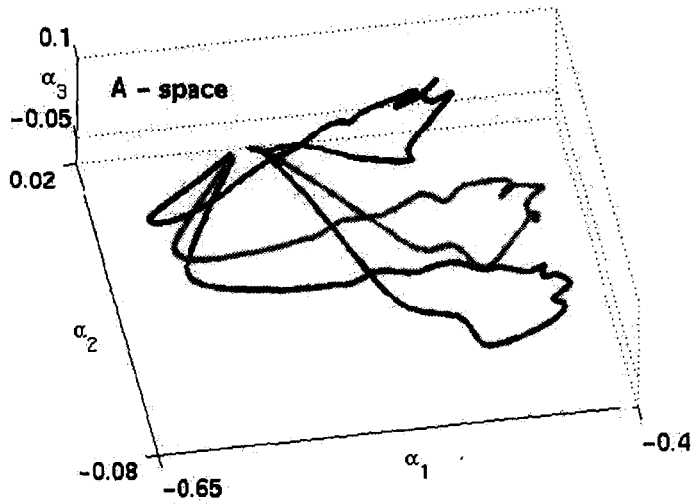Figure 6. Modes corresponding to first four eigenvalues.

Figure 7. The same stimulus applied at three different locations produce three different phase trajectories.
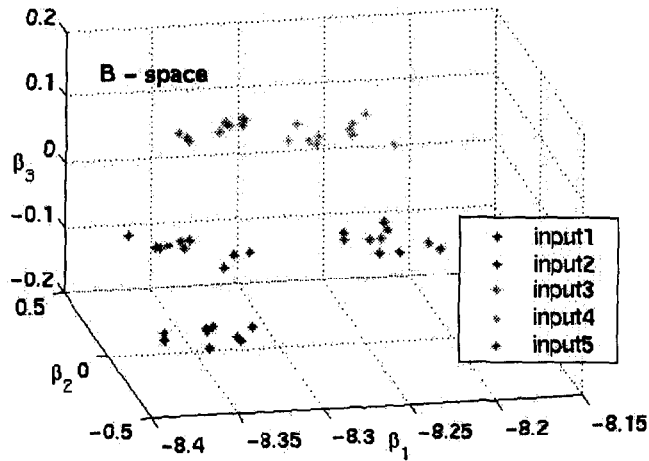

Figure 8. Clusters of points resulting from ten presentations of a stimulus at each of five loci in visual space.

simulations produced by presenting spots at five individual loci in visual space. The same stimulus was presented ten times at each locus in visual space. The variability in the cortical response is coming from the variability in the coordinates of cortical neurons. This results in clusters of points in the B-space, effectively mapping the visual space to the B-space. It seems likely that position in visual space can be inferred from the coordinates of the B-space. An important caveat, however, is we do not yet know if the turtle uses the information in the cortical wave.

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