STOCHASTIC MODELING OF THE PYRAMIDAL CELL MODULE

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ABSTRACT

The neuronal environment of the pyramidal cell module (PCM) is morphologically modeled as perhaps the most important example of a space-filling neuronal structure. PCMs are fundamental information processing units of the monkey striate cerebral cortex. The PCM is modeled as a cylinder, 1600 μm long and 31 μm in diameter, which contains approximately 142 cells, the majority of which are pyramidal cells. Granular cells, spiny stellate cells, and other inhibitory nonpyramidal cells have a minority presence. The influence of peripheral PCMs is modeled by considering a larger cylinder around the PCM in question. We assume a hexagonal packing of the PCMs inside the larger cylinder, much like rods in a chilled water nuclear reactor. A PCM has a six-layer architecture, and the number and type of cells varies from one layer to the other. The PCM is then modeled as a stack of coaxial wafers of varying thickness. The dendrite morphology of the constituent cells of the PCM, as derived from digital neuron tracing, is used to stochastically estimate distribution functions for wafer-to-wafer interactions. Translational and rotational invariance is invoked to simplify the functional form of the critical distribution functions.

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1. INTRODUCTION

Although Nissl-stained preparations show that the cell bodies of neurons in the cerebral cortex are arranged in horizontal layers, the more interesting architectural issue from the point of view of function is how the neurons are organized in vertically oriented units [2]. There is strong evidence for the existence of vertically oriented neuronal columns called *pyramidal cell modules* [2]. The pyramidal cell modules are the fundamental information-processing units of the monkey striate cortex. Our objective is to model the cylindrical environment in which these pyramidal cell modules develop, and demonstrate the feasibility of using stochastic L-systems [4] and ray-casting growth strategies [1] to model the pyramidal cell module as an example of a dense space-filling neuronal structure. Because of its computational complexity a detailed morphological model of the pyramidal cell module has not been hitherto attempted.

2. METHODS

2.1. The pyramidal cell module

Apical dendrites of pyramidal cells are organized into vertically oriented groups or clusters. Counts show that there are some 1270 clusters of layer V apical dendrites per mm^2 in the tangential plane. Thus, the clusters of apical dendrites have a center-to-center spacing of 31μm. These clusters represent the axes of modules of pyramidal cells. Since it is known that there are 1.8-1.9 $\times$ 10^5 neurons beneath 1 mm^2 of cortical surface, the pyramidal cell module is modeled as a cylinder 1600 μm long and 31 μm in diameter which contains approximately 142 cells, the majority of which are pyramidal cells [2]. Granular cells, spiny stellate cells, and other inhibitory nonpyramidal cells have a minority presence.

A pyramidal cell module has the following neuronal constituents: Kernel cell dendrites, peripheral dendrites, and ascending/descending axons. (1) *Kernel cell dendrites* are from dendritic arbors whose soma are within the pyramidal cell module. There are approximately 142 such soma within the pyramidal cell module. (2) *Peripheral dendrites* are dendrites that do not originate from soma within the the pyramidal cell module under consideration but enter from peripheral pyramidal cell modules. (3)*Ascending/descending axons* are of two principal types, the thalamocortical connections and the collaterals. The thalamocortical connections enter from outside the cerebral cortex and generally terminate in layer IV. The collaterals largely arise from axons of the pyramidal cell module under consideration and from neighboring pyramidal cells. These axons typically branch and then grow vertically upwards.

2.2. Design of the PCM modeling environment

A morphological model of the pyramidal cell module (PCM) and its connections is developed below. The model first embeds the PCM in a large cylindrical array of surrounding PCMs. Then each PCM is decomposed into submodules called wafers. The neuronal constituents of these wafers are then defined, and their distributions within the submodules estimated. Finally, detailed morphological modeling of these neuronal constituents is undertaken.

A pyramidal cell module is influenced by other such modules around it, and the radius of influence of such peripheral modules can be determined. The influence of such peripheral PCMs is modeled by considering a larger cylinder around the PCM under consideration. We

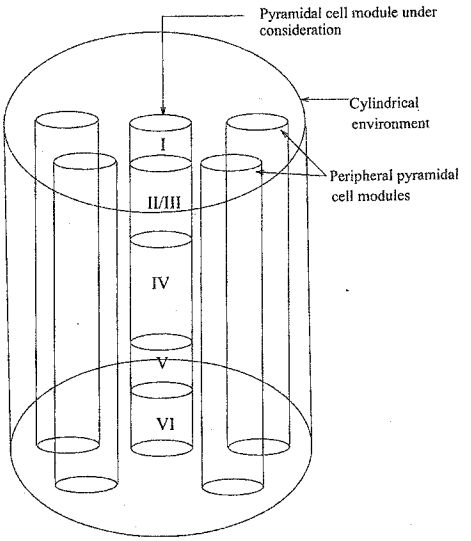

Figure 1. The modeling environment for a PCM [1, 3]

assume a hexagonal packing of the PCMs inside the larger cylinder, much like rods in a chilled water nuclear reactor. A diagrammatic representation of this modeling environment is shown in Figure 1 [1, 3]. In our model the pyramidal cell module under consideration is the *sink* which receives the neuronal constituents originating in the peripheral PCM which form the *sources*. The model described here can be used for modeling the information flow by reversing the designations *source* and *sink*.

The number of peripheral dendritic segments increases exponentially as the distance from the module's cylindrical axis increases and is assumed to drop to zero at a distance R_0. This is modeled by considering a large cylinder of radius R_0, called the "radius of influence" around the PCM under consideration (see Figure 2). The radius of influence R_0 depends upon the cell type.

2.3. Decomposition into wafers

A pyramidal cell module (PCM) has a six-layered architecture, and the number of cells varies from one cortical layer to the other. This is an important consideration in modeling the PCM. Each cortical layer can be modeled as one or more wafers. The PCM is then a collection of wafers of varying thickness. The layered model of the distribution of cells in the PCM used in this work is based on the estimates made by Peters [2].

Figure 2 shows the modeling environment at the wafer level. Here, the index l refers to the PCM under consideration and the index k refers to a peripheral PCM. The sub-index i refers to individual wafers within the peripheral PCM and the sub-index j refers to individual wafers within the PCM under consideration.

2.4. Wafer-to-wafer connections

Our model makes some simplifying assumptions about the dendritic segment distribution within a PCM. (1) The distribution function is invariant under translation in the tangential X-Y

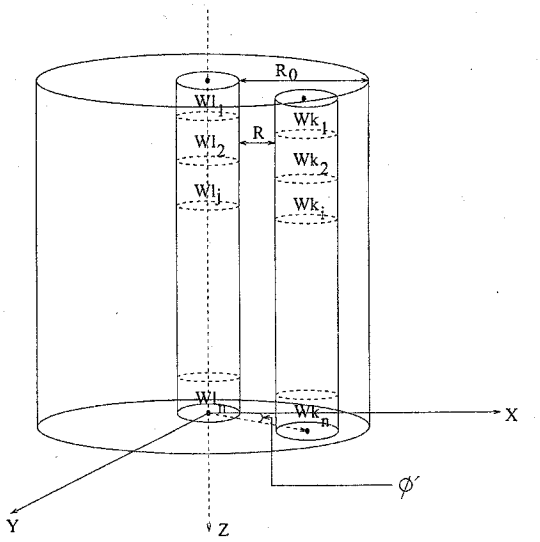

Figure 2. The modeling environment at the wafer level [1, 3]

plane, that is, the pyramidal cell module under consideration could be translated in the plane to an adjacent PCM and this would not affect the stochastic distribution functions. (2) The distribution function is also invariant under rotation in a plane, that is, the peripheral pyramidal cell modules can be rotated around the PCM under consideration and, if the fibers inside the PCM under consideration are appropriately rotated, then this again would not affect the distribution function. The above assumptions hold only within a common architectonic area of the cortex. The distributions could be different in different architectonic areas or on the boundaries between adjacent areas.

Our interest is in estimating the distribution of dendritic segments within a wafer (for example, wafer W_j in Figure 3). Such wafers will be referred to as the wafer-of-interest. There are two sources of the dendritic segments within the wafer-of-interest:

- Wafers in peripheral PCMs (for example, wafer W_i in Figure 3). Such wafers will be referred to as peripheral wafers.
- Ascending/descending dendrites from wafers within the same pyramidal cell module

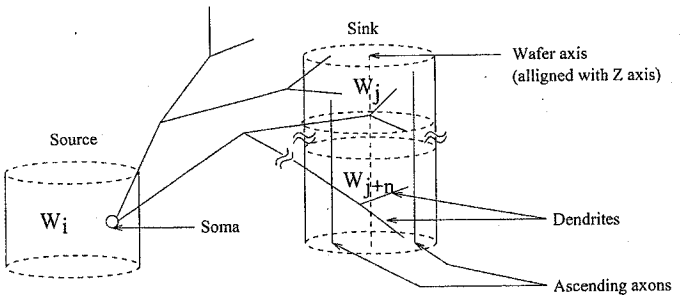

Figure 3. Interaction at the wafer level [1, 3]

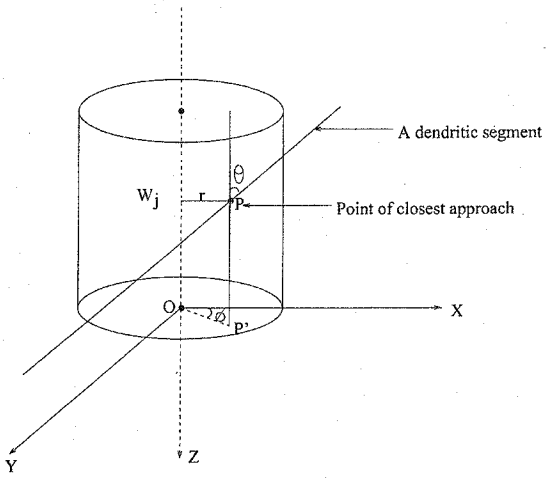

Figure 4. Spatial distribution of dendritic segments within a wafer [1]

(for example, wafer W_{j+n} in Figure 3).

2.5. Distribution Functions for Peripheral Dendrites

The length of the dendritic segment is ignored in this model. An important consideration here is that its point of closest approach **P** to the cylindrical axis is unique (Figure 4). The probability density function of the dendritic segments within a wafer is given by:

$$f(\mathbf{P},\theta|R,\phi')d\mathbf{P}d\theta RdRd\phi'. \tag{1}$$

where $\mathbf{P} \equiv (r,\phi,Z)$ is the point of closest approach on the dendritic segment and is specified by cylindrical co-ordinates (r,ϕ) and the depth Z from the top of the PCM. Here θ is the angle the dendritic segment makes with the vertical Z-axis; R is the cylindrical radial distance of the peripheral PCM in which the peripheral wafer (and hence the soma of the peripheral dendrites arise) lies; and ϕ' is the azimuthal angle of the peripheral PCM containing the peripheral wafer. Substituting in Equation 1 we have:

$$f(\mathbf{P},\theta|R,\phi') = f(r,\phi,Z,\theta|R,\phi'). \tag{2}$$

Because of rotational invariance we can say that:

$$f(r,\phi,Z,\theta|R,\phi') = f(r,\phi-\phi',Z,\theta|R) \tag{3}$$

which by symmetry is an even function of $\phi-\phi'$. Since we are considering interaction at the wafer level we can ignore Z*. Equation 1 can now be simplified to:

$$f(r,\phi,\theta|R). \tag{4}$$

The closest-approach points **P** of the dendritic segments entering the wafer-of-interest at a particular azimuthal angle ϕ lie along a straight line (Figure 5). If R (i.e., the cylindrical

*More accurately, a wafer can be modeled by many sub-wafers thereby eliminating the dependence on Z.

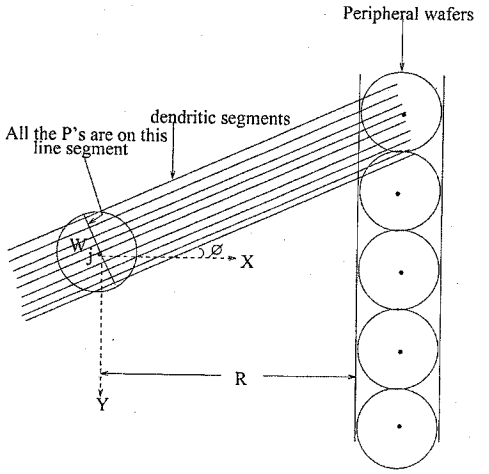

Figure 5. The uniform distribution in r of dendritic segments [1]

radial distance between the wafer-of-interest and the peripheral wafers) is large the distribution of such dendritic segments is uniform in R (the shortest distance between the wafer-axis and the dendritic segment). This follows because when R is large the peripheral wafers can be considered to be arranged in a straight row. Assuming that the kernel cells in these peripheral wafers are uniformly distributed, it can be easily seen that dendritic segments entering the wafer-of-interest at a particular azimuthal angle ϕ will be uniformly distributed in r.

In summary, the probability distribution function for dendritic segments from peripheral wafers reduces to $f(\phi, \theta|R)$.

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