Spatiotemporal dynamics in a model of turtle visual cortex

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Abstract

This paper presents simulations of a small patch of the turtle's visual cortex with 20 pyramidal cells and four smooth stellate cells. 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. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

The visual cortex of freshwater turtles contains three layers. The intermediate layer 2 principally contains pyramidal cells with dendrites that extend into layers 1 and 3. The outer layer 1 and inner layer 3 contain mainly inhibitory interneurons. Geniculate afferents make excitatory synapses upon the dendrites and somata of pyramidal cells and the dendrites and somata of layer 1 neurons. Studies using both multiple electrode recording techniques [9] and voltage-sensitive dye techniques [7,8], demonstrate that visual stimuli produce waves of activity that propagate along the rostrocaudal and mediolateral axes of the cortex. These waves have been compared in the literature [3] to the waves generated in a vibrating membrane, such as a “drum” [8]. This study uses a minimal, or “toy” model of turtle visual cortex to study the cellular origin and properties of these propagating waves. The model is a rectangular array of 20

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pyramidal neurons and four inhibitory interneurons. Each neuron is a compartmental model with biophysically realistic conductances. The input to the model is an array of five geniculate inputs. The study demonstrates that

1. excitatory interactions within the cortex generate a propagating wave in the model that duplicates the general features of the propagating wave in the real cortex, and
2. the cortical dynamics in even this simple model are sufficient to capture the velocity of a drifting square wave grating.

2. Model description

The model represents a 2 × 12 mm, rectangular region of turtle visual cortex. It contains 20 pyramidal neurons, organized in 4 × 5 matrix array (Fig. 1). Four inhibitory neurons are interspersed between the pyramidal cells. Each pyramidal neuron makes excitatory synapses on each of its nearest neighbors (Fig. 2). These include synapses upon both pyramidal neurons and inhibitory neurons. Inhibitory neurons make inhibitory synapses upon all neurons within their spheres of influence (Fig. 3). Five geniculate axons run across the cortex, from medial to lateral, consistent with the known anatomy of the system [5]. Each geniculate afferent makes excitatory synapses upon each pyramidal neuron and each inhibitory neuron along its trajectory. Each neuron is represented by a 16-compartment model based on the anatomy of real pyramidal neurons and inhibitory interneurons (Fig. 4). Each compartment is represented by a standard membrane equation. All compartments contain a leakage conductance. The soma compartments of both types of neurons contain fast sodium and delayed rectifier conductances which are specified by the Hodgkin–Huxley kinetic schemes. Geniculocortical synapses are known to be glutaminergic and access the
AMPA subtype of glutamate receptor [4]. Corticocortical synapses are also glutaminergic but access both AMPA and NMDA subtypes of glutamate receptors. In this initial study, only the AMPA conductance is included. Inhibitory interneurons are GABAergic and access both GABAa and GABAb subtypes of GABA receptors, but only GABAa conductances are included in this model. Propagation times between neurons are calculated using the distance between a pair of neurons and conduction velocities. The conduction velocity for geniculate afferents in turtle visual cortex has been measured at 0.18 m/s [2]. Corticocortical connections are given conduction velocities of 0.05 m/s, consistent with measurements of propagating waves in turtle visual cortex [7] and the conduction velocities for axons of inhibitory interneurons in rat cortex [6]. Visual stimuli have been simulated by activating
3. Activation of a single geniculate afferent produces a propagating wave of activity in the model cortex

Presentation of a visual stimulus in a localized region of visual space is simulated by activating a single geniculate afferent. Activation of a single channel generates several action potentials in all of the cortical neurons postsynaptic to the geniculate afferent and produces a wave of activity that propagates initially in both rostral and caudal directions. However, the inhibitory interconnections are strong enough to damp the system and limit the extent of the propagation. Sequences of inputs with constant time delays represent stimuli moving with specific velocities and produce richer outputs. Fast velocity signals do not produce significant propagating cortical activity because developing cortical activity is damped by intracortical inhibition. Slow velocity
signals demonstrate how geniculate inputs and internal cortical inputs interact to produce a wave of activity that travels along the cortex (Fig. 5). Certain sets of parameters cause a secondary wave of activity that travels across the cortex in the opposite direction. This phenomenon is a reflection, similar to reflections that have been observed in turtle visual cortex [8] and in the slice preparation of cat and rat cortex [1]. Certain velocities produce large reflected waves, resulting in a particularly strong response (Fig. 6). Very slow velocity signals produce a network response that equals the sum of the individual responses.

4. The model cortex codes the velocity of moving spatial patterns

The response of the model to a moving spatial pattern has been studied using a drifting half-wave-rectified square luminance grating (Fig. 7). The small size of the model did not permit the use of sinusoidal gratings as input stimuli. The luminance, spatial frequency and velocity of the square wave grating are given in dimensionless units because the model is not calibrated to units of visual arc. The spectral composition of the stimulus is characterized by taking the absolute value
of its Fourier transform as a function of both spatial and temporal frequencies (Fig. 8). The response of the model to an input stimulus drifting with a certain velocity is represented as absolute value of Fourier transforms of the membrane potentials produced by all of the neurons in the model. Initial simulations indicate that variations in the output signal along the trajectories of the geniculate afferents are not significant. So responses along each geniculate afferent have been averaged prior to calculating the Fourier transforms. The Fourier transform shows a significant peak on a line with a slope equal to the velocity of the signal. There is also a DC offset and other major peaks that result from interactions between neurons within the cortex (Fig. 8).

5. Conclusion

This study shows that a very simple model of a cortical structure that captures the basic geometry and temporal structure of visual cortex can generate propagating waves of activity that contain information about the speed of a small moving stimulus or a patterned stimulus, such as a square wave grating. We are now working on building a larger and more complex model of turtle visual cortex that will contain explicit representations of all three layers based on detailed maps of the spatial distributions of neurons in real cortices. The responses of this model can then be compared to propagating waves of activity obtained from real turtle cortices using
Fig. 8. The Fourier transforms of the input signal (A), and cortical response (B). Top view of the signal from figure (A), showing that the peak lies on the line $v = u$, where $v$ is the drifting velocity of the input signal (C). Top view of the signal from figure (B), showing the secondary peak lying on the same line (D).

Voltage sensitive dyes. This large-scale model will also be used to study the responses of the cortex to more complex visual stimuli.

References


