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NEUROCOMPUTING
Neurocomputing 70 (2007) 2069–2073
www.elsevier.com/locate/neucom

Emergence of population synchrony in a layered network of the cat visual cortex

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Available online 16 November 2006

Abstract

Recently, a quantitative wiring diagram for the local neuronal network of cat visual cortex was described [T. Binzegger, R.J. Douglas, K.A.C. Martin, A quantitative map of the circuit of the cat primary visual cortex, J. Neurosci. 39 (24) (2004) 8441–8453.] giving the first complete estimate of synaptic connectivity among various types of neurons in different cortical layers. Here we numerically studied the activity dynamics of the resulting heterogeneous layered network of spiking integrate-and-fire neurons, connected with conductance-based synapses. The layered network exhibited, among other states, an interesting asynchronous activity with intermittent population-wide synchronizations. These population bursts (PB) were initiated by a network hot spot, and then spread into the other parts of the network. The cause of this PB is the correlation amplifying nature of recurrent connections, which becomes significant in densely coupled networks. The hot spot was located in layer 2/3, the part of the network with the highest number of excitatory recurrent connections. We conclude that in structured networks, regions with a high degree of recurrence and many out-going fibres may be a source for population-wide synchronization.

Keywords: Recurrent network; Layered-cortical network; Synchrony; Cat area 17

1. Introduction

Random network models have emerged as a useful tool to understand the dynamical properties of local cortical networks. At its simplest, the cortical networks are modeled as homogeneous networks of spiking model neurons. These simple models have been successful in characterizing the dynamics of cortical networks [5]. However the cortex is not a homogeneous network. It can be clearly identified as a structure composed of up to six layers in sensory cortices, with each layer differing in neuron types, their density and connection probability [11,4,6]. Even though the heterogeneous nature of cortical networks was known for long [2,6], only few studies have attempted to model this heterogeneity [8,12,7].

This small number of studies on heterogeneous network dynamics was primarily due to a lack of detailed information on the neuron type specific inter- and intra-layer connectivity. Recent advances in techniques have greatly increased the knowledge of the cortical neuro-anatomy and a quantitative wiring diagram of the local neuronal network of cat visual cortex was described [3], which provided the first realistic estimate of synaptic connections among various neuron types in different cortical layers. Here we numerically studied the dynamics of the resulting heterogeneous layered network of spiking integrate-and-fire neurons, connected with conductance-based synapses.

2. Network

Binzegger et al. [3] specified the total number of neurons in cat area 17 to be approx. 31×10^6. However, it is still not possible to simulate such large networks, so we downscaled the network to a size of $10,000$ or $50,000$ neurons. While downscaling the complete network of area 17, we conserved the proportion of excitatory (NE) and inhibitory

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doi:10.1016/j.neucom.2006.10.130

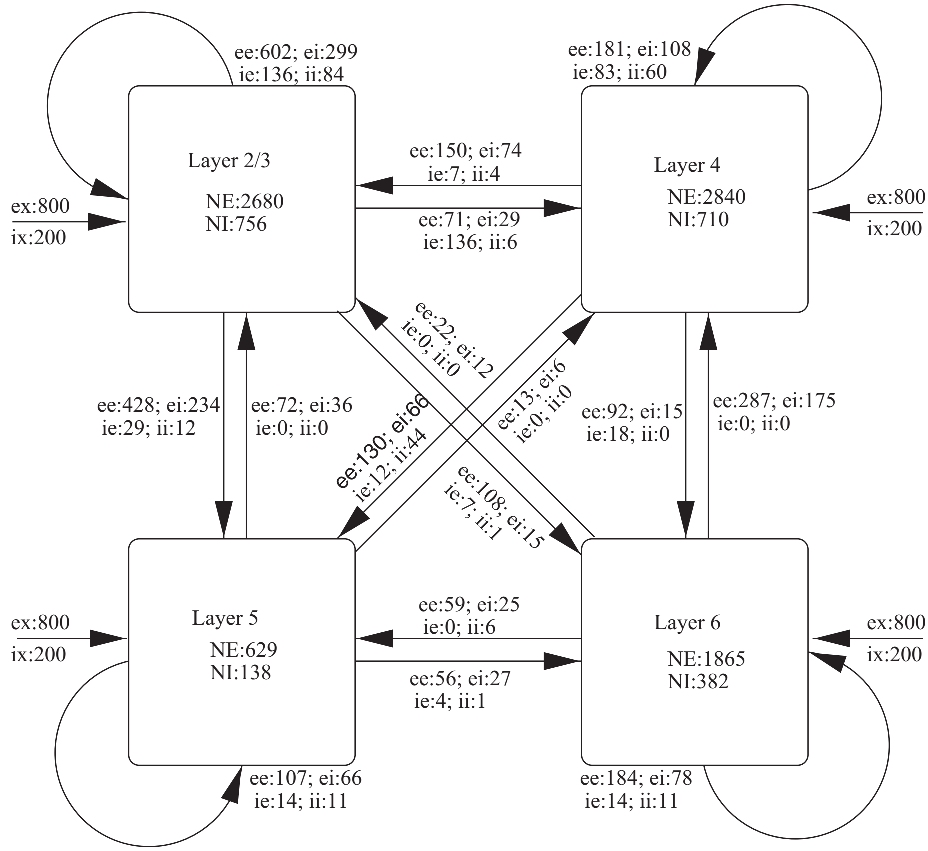

Fig. 1. *Schematic diagram of the network:* NE and NI are the numbers of excitatory and inhibitory neurons, respectively. The labels $xy\{\varepsilon\ \mathrm{ee}, \mathrm{ei}, \mathrm{ie}, \mathrm{ii}\}$ for each arrow indicate the number of synapses of type x projecting onto a neuron of type y, where e stands for 'excitatory' and i for 'inhibitory'.

(NI) neurons across the layers. The number of synapses within a layer was restricted to have a maximum network connectivity (fraction of possible couplings that are realized) of $\varepsilon = \frac{K}{N} = 0.1$. As neurons in different layers received different numbers of synapses due to layer-specific wiring, the resulting connectivity ε was also different in all layers. The neurons were modeled as point neurons with leaky-integrate-fire dynamics. All neurons had identical parameters (membrane capacitance 250 pF, leak conductance 16.7 nS, spike threshold 15 mV above rest). Besides the inter and intra layer connectivity, neurons also received a balanced external input ($\nu_{\mathrm{extGround}}$), mimicking the cortico-cortical inputs the area 17. Synaptic inputs were modeled as conductance transients using the same α-functions (time constant 0.3 ms) for excitation and inhibition. Fig. 1 shows the resulting circuit of a network with 10^3 neurons. The simulations were performed using a parallel kernel of NEST [10].

3. Network dynamics

3.1. Descriptors of network activity dynamics

To characterize the activity states of the network both at population level and single neuron level we used the following state descriptors:

Synchrony in the network was measured by pair wise correlations (PwC)

$$\mathrm{PwC}[C_i, C_j] = \mathrm{Cov}[C_i, C_j] / \sqrt{\mathrm{Var}[C_i]\mathrm{Var}[C_j]}, \tag{1}$$

where C_i and C_j are the joint spike counts.

Mean firing rate was estimated from the spike counts collected over 1 s simulation time, averaged over all neurons in the network.

Irregularity of individual spike trains was measured by the squared coefficient of variation of the corresponding inter-spike interval (ISI) distribution. Low values reflect more regular spiking, a clock-like pattern yields $\mathrm{CV} = 0$. On the other hand, $\mathrm{CV} = 1$ indicates Poisson-type behaviour.

3.2. Dynamics of network activity

In vivo the cortical activity is characterized by irregular spike trains of individual neurons and with a low pairwise correlation among neurons in the network [1]. The membrane potential of individual neurons is close to threshold, and the spikes are elicited by synaptically induced membrane potential fluctuations. In our simulations we excited the network with a balanced input ($\nu_{\mathrm{extGround}}$) to a uniform asynchronous-irregular (AI) activity state [5] with similar average firing rates in each