

Existence of stable states of stochastic dynamics in a model of neocortex

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Abstract

We investigate stochastic dynamics of a spatially structured model of neocortex, which consists of numerous spiking neurons, both excitatory and inhibitory, interacting through a large number of synaptic connections. Analyzing sub-threshold voltage activity and recurrent input, we show the existence of stable basins of the dynamics which are independent of trials but dependent on the intensity of the Poisson external input and the connection structures of the network. Correspondences to experiments using voltage sensitive dye imaging are also discussed.

Key words: trial-to-trial variability, spacially structured model, stochastic dynamics, trial independently occurring states

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1 Introduction

On cortical dynamics, it is well known that the activity of neural populations shows high irregularity [1] and trial-to-trial variability in both spontaneous states and evoked ones [2]. On the other hand, the brain performs robust and reproductive information processing. In order to understand the fundamental strategy of information processing in neocortex, it is an important issue to investigate the properties of such stochastic dynamics.

Recent experimental studies using voltage sensitive dye imaging have shown the existence of spontaneously occurring states that correspond to cortical representations of orientations and characterize their dynamics; these states also occur during evoked activity [3] [4]. Here we theoretically study this property of cortical activity by the use of a model of neocortex. We have already shown that our model exhibits highly irregular firing of single neurons and globally asynchronous states [5] [6]. In this article, we focus on the trial independent properties of the dynamics. By computer simulation, we show the existence of stable states occurring independently of trials; these states are determined by the intensity of Poisson external input and the connection structures of the network. Correspondences to experimentally observed spontaneously occurring states are discussed in section 4.

2 The neural network model

Suppose that $i \in \Xi$ indicates a neuron in the network, where $\Xi := \{i = (i_1, i_2) | 1 \leq i_1, i_2 \leq N\}$; thus the network is two-dimensional and consists of N^2 neurons. To avoid boundary effect, we assume that boundaries of Ξ are

connected cyclically. We employ the leaky integrate-and-fire model: the voltage dynamics of neuron i obeys

$$\begin{aligned}\frac{dV_i}{dt} &= -\frac{1}{\tau}V_i + I_i(t) + I_i^{\text{ext}}(t), \\ I_i(t) &= \sum_{j \in \Lambda_i} J_j \sum_k \delta(t - t_j^{(k)} - d)\end{aligned}\tag{1}$$

below the firing threshold θ , where τ is the membrane time constant, $t_j^{(k)}$ is the timing of the k -th spike of neuron j , d is the spike transmission delay, J_j is the peak amplitude of post-synaptic potential induced by a single spike from pre-synaptic neuron j , and Λ_i is a set of pre-synaptic neurons of i . When V_i reaches θ , the neuron spikes and V_i is reset to zero; then the neuron turns into the refractory period with the length of ρ . In this model, in order to drive the network, each neuron receives Poisson spike input $I_i^{\text{ext}}(t)$ with intensity ν . We indicate a sample path of (1) by $V_i(t, \omega)$. In the following of part of this article, we call $V(t) = (V_i(t))_{i \in \Xi}$ *voltage activity*, $I(t) = (I_i(t))_{i \in \Xi}$ *recurrent input* and $\Lambda := \{\Lambda_i\}_{i \in \Xi}$ *connection structure*.

Based on anatomical results about the structure of neocortex, we introduce a statistical model of connection structures. In this article, we assume that each Λ_i obeys the following distribution:¹

$$\text{Prob}[j \in \Lambda_i] = \frac{1}{\Sigma} \exp\left(\frac{|i_1 - j_1| + |i_2 - j_2|}{\sigma}\right),\tag{2}$$

where Σ is the normalizing constant and σ is a parameter which decides the localization degree of connection distribution. We note that there are many possible connection structures obeying (2) even when σ is fixed. We indicate a sample structure by $\Lambda(\lambda)$. When we use the terms “different structures” or

¹ We also investigated Gaussian cases and obtained similar results. (Data is not shown.)

“detailed structures”, we intend to compare networks with different samples of Λ . In this article, we fix the parameter σ and focus on properties dependent on detailed structures. Properties which are dependent only on σ (i.e. independent of detailed structures) are discussed in [5], [6].

Here we summarize the parameters and the procedure of simulation. We set $N = 400$. The 80% of neurons randomly chosen from the network are set excitatory and the other 20% are inhibitory. Then we set $J_i = 0.15$ for excitatory neurons and Poisson external inputs, $J_i = -0.9$ for inhibitory neurons. The number of connections $\#\{\Lambda_i\} = 5000$ for every $i \in \Xi$. Initial state $V_i(0)$ is decided by Gaussian random variables with the mean of zero and the variance of 2.0. It should be noted that our result does not depend on this initial condition. Other parameters: $\theta = 15\text{mV}$, $\tau = 20\text{ms}$, $d = 2\text{ms}$, $\rho = 2\text{ms}$, $\sigma = 30$, the time increment is 0.1ms.

3 Simulation results

Firstly, we generated a sample connection structure $\Lambda(\lambda_0)$ from (2) and fixed it, then simulated three sample paths (referred by $\omega_1, \omega_2, \omega_3$) for every $\nu = 10, 15, 20, 25, 30\text{kHz}$. Under such conditions, dynamical states of the model are *asynchronous-irregular* [6] [7], which can be regarded as spontaneous activity of neocortex. Based on the analysis in [3] [4], we evaluate the average states as follows:

$$V^{\text{AS}} = V_{\nu}^{\text{AS}}(\omega) := \frac{1}{t_e - t_s} \int_{t_s}^{t_e} V_{\nu}(t, \omega) dt,$$

$$I^{\text{AS}} = I_{\nu}^{\text{AS}}(\omega) := \frac{1}{t_e - t_s} \int_{t_s}^{t_e} I_{\nu}(t, \omega) dt.$$

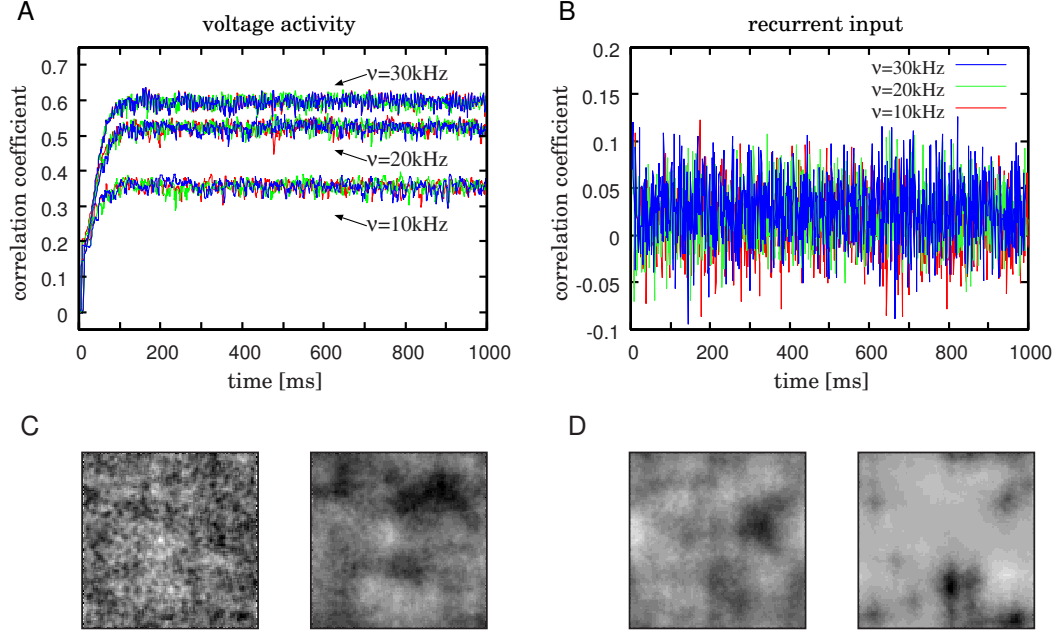


Fig. 1. (**Upper panels**) Time evolutions of correlation coefficient. A: Voltage activity. For every ν , three sample paths are plotted. Correlation coefficients quickly converge to stable levels independent of sample paths. B: Recurrent input. One sample path is plotted for each ν . Correlation coefficients fluctuate around zero. (**Lower panels**) Average pattern and a sample of instantaneous patterns. C: Voltage activity. The average pattern of a voltage activity (the left) and an instantaneous pattern at a certain time (the right). D: Recurrent input.

(To avoid the effects of initial transition, we use the data from $t_s = 2\text{s}$ to $t_e = 3\text{s}$ in simulation.) We chose $V^{\text{CS}} := V_{\nu=10\text{kHz}}^{\text{AS}}(\omega_1)$ as the criterion state (CS) of voltage activity and $I^{\text{CS}} := I_{\nu=10\text{kHz}}^{\text{AS}}(\omega_1)$ of recurrent input respectively. Then we evaluate spatial correlation coefficient between CS and the state at each time. That is to say, we compute time evolutions of $\text{CC}(V^{\text{CS}}, V(t))$ and $\text{CC}(I^{\text{CS}}, I(t))$ for all paths, where correlation coefficient is defined by $\text{CC}(v, w) = \frac{\langle v, w \rangle}{|v| \cdot |w|}$ for $v, w \in \mathbb{R}^{N^2}$. Results are shown in Fig.1. (In the figure, data of $\nu = 15$ and 25 are omitted.) On voltage activity, correlation coefficients keep their values with small fluctuations after quick approach to certain

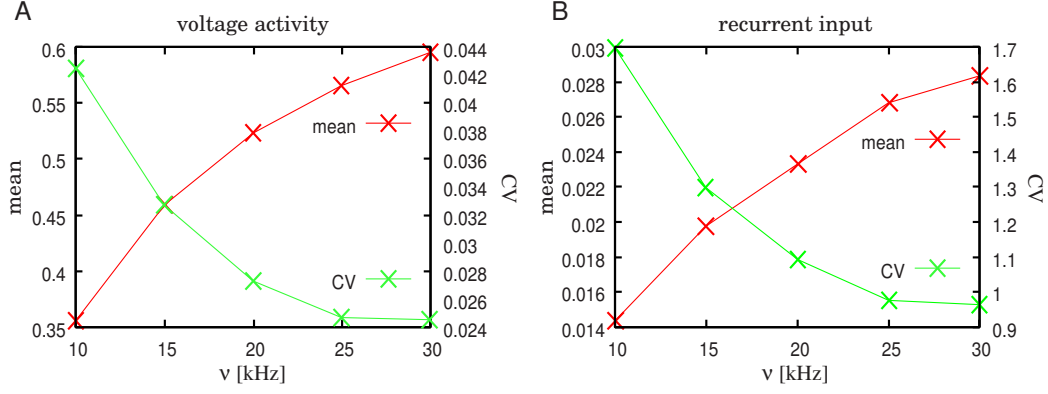


Fig. 2. Mean and coefficient of variation of correlation coefficients. Each point was estimated from three sample paths on the time interval $[2s, 3s]$. A: voltage activity. B: recurrent input. The mean increases along with ν and CV decreases in both panels.

positive levels independent of trials. On the other hand, correlation coefficients of recurrent input fluctuate around zero. This implies that there exist trial independent stable states of dynamics (discussed in section 4). We should note that the result in Fig.1 does not depend on the choice of the criterion states: even when we used different average states as criteria, estimations were almost same.

In order to estimate dependency on the intensity ν of Poisson input, we evaluated the mean and the coefficient of variation (CV) of the correlation coefficients. As shown in Fig.2, the mean increases along with ν and CV decreases in both cases of voltage activity and recurrent input.

Next we investigate the dependency of dynamical states on connection structures. For this purpose, we simulated again with connection structures $\Lambda(\lambda_k)$ ($k = 1, 2$) different from $\Lambda(\lambda_0)$. Similar results as shown in Fig.1 and Fig.2 were also obtained in all cases. Then we estimate correlation coefficient between criteria: $CC(V^{\text{CS}}(\lambda_k), V^{\text{CS}}(\lambda_l))$ was almost equal to zero for every $k \neq l$.

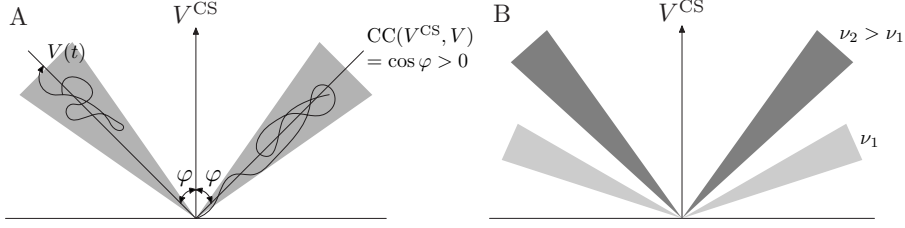


Fig. 3. Stable states of voltage activity. A: Illustration of a stable basin of voltage dynamics. Since correlation coefficient between V^{CS} and $V(t)$ remains in a certain level, $V(t)$ is attracted into a basin illustrated in the panel and never escapes from the region. B: Dependency of stable states on the input intensity ν . When ν increases, stable state becomes more close to V^{CS} .

This implies that the connection structures of the network strongly influence dynamical states.

4 Discussion

In Fig.1.A, correlation coefficients $\text{CC}(V^{\text{CS}}, V(t))$ quickly converge to certain levels independent of sample paths and then keep their values with small fluctuations. This implies the existence of trial independent stable states of voltage activity. It can be explained as follows: we can consider correlation coefficient is the cosine of the angle between two vectors by the definition: $\text{CC}(v, w) = \frac{\langle v, w \rangle}{|v| \cdot |w|} = \cos \varphi$. Thus stable correlation coefficient means the existence of a stable basin as illustrated in (Fig.3.A), which is independent of trials; $V(t)$ is attracted into the basin and never escapes from that area.

In contrast, correlation coefficient of recurrent input fluctuates around zero (Fig.2.B) and its mean is slightly positive (Fig.2.B). This property of recurrent input seem to stabilize voltage activity. Here we note that the time evolution of recurrent input (Fig.1.B) is consistent with experimentally observed results in

[3] [4], because voltage sensitive dye imaging emphasizes the synaptic current more than the voltage at the soma, and the synaptic current corresponds to recurrent input of our model. Thus we think stable states in our result probably correspond to the spontaneously occurring states in [4].

In Fig.2, the mean and CV of correlation coefficient changes along with the intensity ν of Poisson inputs; therefore the basin of dynamics also changes along with ν . Nevertheless, average direction of basins is stable for changes of ν because results in Fig.1 do not depend on the choice of the criterion; cf. Fig.3.B. On the other hand, connection structures of the network have greater effects on the stable states. Typically, stable basins with different structures are orthogonal (the last paragraph in section 3). These two dependency of activity are summed up to the following schema similar as in [2].

$$\begin{aligned} \text{dynamics} &= \text{connection dependent stable dynamics} \\ &+ \text{external input (stimulus dependent dynamics)}. \end{aligned}$$

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