New Technique for analyzing stationary global activity in neural networks

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Abstract

To investigate the origin of spontaneous activity in the neuronal population dynamics and the mechanisms that keep it stable, we explore a new technique and methods for analyzing stationary global activity in large networks of integrate-and-fire neurons. Our technique is based on the diffusion approximation theory and probabilistic models. Under a given condition on the balance of excitation and inhibition, we find that stationary global activity deeply depends on major sources of inherent neuronal noise : background synaptic activity from other areas, thermal agitation, and ion channel stochasticity. In the case without this neuronal noise, population activity is exceedingly unstable even if we choose almost perfect balanced parameter regime by intention. We conclude that neuronal population, by making effective use of own neuronal noise, keep self-sustaining stable states.

Key words: Spontaneous activity, Integrate-and-fire neuron, Diffusion approximation, Poisson process, Neuronal noise

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1 Introduction

Neocortical neurons are spontaneously active in the absence of external input and the spontaneous firing is often considerd to be a noisy, stochastic process (9). Noise can have a significant impact on the response dynamics of nonlinear systems (7)(4)(8). Many studies have been devoted to reproducing the irregularity of the observed spike sequences by means of balanced inhibition in networks of integrate-and-fire (IF) neurons (1)(2)(3)(6)(5). In these theoretical research, stochastic approximation method (10) and Fokker-Planck equation are not only very useful but also one of the indispensable approch. What has to be noticed that there is an implicitly assumption : Spike dynamics of each neuron is a Poisson process. Assuming it to be true, the synaptic input of a neuron can be approximated by Gaussian stationary process : $(synaptic\ input) = (mean) + (fluctuation) = \lambda + \sqrt{\lambda}\xi(t)$. Here, λ is average input, and $\xi(t)$ is white Gaussian noise. It remains an unsettled question whether the irregular spike pattern in models of neural networks is a Poisson process or some other stochastic process. Without the assumption of Poisson process, only few attempts have so far been made to show the stability of spontaneous activity. The purpose of this paper is to consider self-sustaing stable states in networks of IF neurons within the framework of a wide class of diffusion processes for neuronal input. Amit and Brunel constructed a network model of IF neurons (1). They studied the problems of stability of spontateous activity in the model on the assumption of Poisson process. In the present study we look upon synaptic input from other areas (1) as inherent neuronal noise : background synaptic input + ion channel noise + thermal agiattion. We assume that the neuronal noise is in terms of the following expression: (*neuronal noise*) $= \mu + \sigma\xi(t)$. As in the diffusion approximation method, neurons receive a large number of spikes which can be approximated by an input consisting of a mean value (*drift term*) and noise (*diffusion term*). From this view point one may say that synaptic input from local area (*recurrent input*) is given as follows: (*recurrent input*) $= x + y\xi(t)$. We may recall that on the supposition that the input is Poisson process the above approximation is given as follows: (*recurrent input*) $= x+\sqrt{x}\xi(t)$. There is a strong restriction on the relation between *drift term* and *diffusion term*. Under the expression of *recurrent input* $= x + y\xi(t)$, we can estimate the stability of global spontateous activity within the wide class of diffusion processes. We apply the induction method to the population dynamics and show that under a given condition on the balance of excitation and inhibition, the spontaneous activity characterized by parameters of neuronal noise (x, y) is exceedingly stable.

2 The model

There are many models for the membrane dynamics for neurons. The IF model is the simplest one of them. This model can be written as,

$$\frac{dV}{dt} = -\frac{V}{\tau} + (input), \text{ if } V > \theta \text{ then } V \rightarrow 0.$$

where V represents the membrane potential, τ is the membrane time constant, and θ is the firing threshold. When V reaches θ, the neuron spikes and V is reset to zero; then the neuron turns into the refractory period γ. In this research, the input fall into two parts: a fixed neuronal noise part $= \mu + \sigma\xi(t)$ and a recurrent input part. Suppose that each neuron resceives excitatory postsynaptic

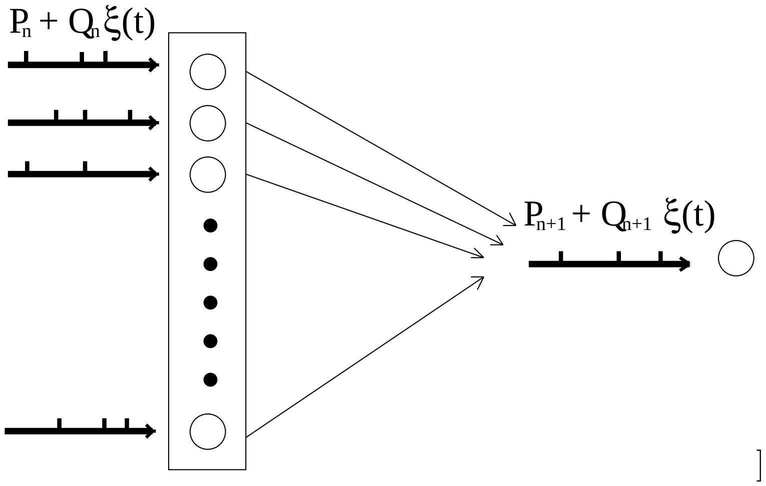

Fig. 1. Input output model for population dynamics. $P_n + Q_n\xi(t)$ is input for each neuron, and $P_{n+1} + Q_{n+1}\xi(t)$ is the sum of the total output of neuronal population and neuronal noise $\mu + \sigma\xi(t)$, where $\xi(t)$ is white Gaussian noise.

potentials (EPSPs) at N_E excitatory synapses and inhibitory postsynaptic potentials (IPSPs) at N_I inhibitory synapses. If spike process for each neuron can be approximated by $u + v\xi(t)$ then we can estimate the total inputs as folows: $(input) = P + Q\xi(t) = \mu + (N_E J_E + N_I J_I)u + \sqrt{\sigma^2 + (N_E J_E^2 + N_I J_I^2)v^2}\xi(t)$, where $J_E > 0$ and $J_I < 0$ are amplitude of each EPSP and IPSP, and we refer to P and Q as *drift term* and *diffusion term* respectively.

In order to analyze the stationary states of the above model (Figure 1) and the explicit relation between input and output of neurons, we restrict ourselves to the simple case: a nonleaky integrate and fire neurons without refractory period. If the total input is $P_n + Q_n\xi(t)$, then the neuronal spike process is approximated by $\frac{P_n}{\theta} + \frac{Q_n}{\theta}\xi(t)$, and by the above input formula we get $P_{n+1} + Q_{n+1}\xi(t) = \mu + (N_E J_E + N_I J_I)\frac{P_n}{\theta} + \sqrt{\sigma^2 + (N_E J_E^2 + N_I J_I^2)\frac{Q_n^2}{\theta^2}}\xi(t)$. To obtain the stationary state of this system, we apply the induction method $((P_n, Q_n) \to (P_{n+1}, Q_{n+1}))$ to the above formula and then we can get the general term and the limit values:

$$(P_n, Q_n) = \left(\frac{\mu}{1-\alpha} + \alpha^n \left(P_0 - \frac{\mu}{1-\alpha} \right), \sqrt{\frac{\sigma^2}{1-\beta} + \beta^n \left(Q_0 - \frac{\sigma^2}{1-\beta} \right)} \right),$$
$$(P_\infty, Q_\infty) = \left(\frac{\mu}{1-\alpha}, \sqrt{\frac{\sigma^2}{1-\beta}} \right)$$

where $\alpha = \frac{N_E J_E + N_I J_I}{\theta}$ and $\beta = \frac{N_E J_E^2 + N_I J_I^2}{\theta^2}$. This analytical expression indicate that the existence of the stable point and the irregularity of spike sequences. And we can also get the mean firing rate and the coefficient of variation (CV) of the output interspike interval at the limit state:

$$(\text{rate}) = \frac{\mu}{\theta(1-\alpha)}, \quad (\text{CV}) = \sigma \sqrt{\frac{1-\alpha}{(1-\beta)\mu\theta}}.$$

We have seen that there are global stationary states in the above simple case and the limit values relate to the neuronal noise $\mu + \sigma\xi(t)$. The question arises how the above behavior generalizes for the more realistic case that both leak currents and refractory period are present. It is difficult to get a analytical expression for the neuronal spike process by the total input $P_n + Q_n\xi(t)$. Therefore, we rely on numerical simulations for this case in the next section.

Here we summarize the parameters. We set for simulations $N_E = 8000, N_I = 2000, J_E = 0.09, J_I = -0.365, \theta = 20\text{mv}, \tau = 20\text{ms}, \gamma = 2\text{ms}$. In the nonleak currents case with neuronal noise, we choose $\mu = 0.15, \sigma = 0.59$, and in the leak currents case with neuronal noise, we choose $\mu = 0.58, \sigma = 1.2$

3 Simulation results

Firstly, we examine whether numerical simulation of the above simple case can reproduce the stable state obtaind by theoretical analysis. The left and right panels of Figure 2A (upper panels) show the inductive transition of the drift term P_n and the diffusion term Q_n in the simple IF model case. The theoretical analysis for P_n and Q_n is practically reproduced by the numerical simulations. The left and right panels of Figure 2B (lower panels) shows the inductive transition of P_n and Q_n in the more realistic case. In ether case there exists global spontaneous activity and this activity is exceedingly stable. The left panel of Figure 3 shows the evolution of population activity on its

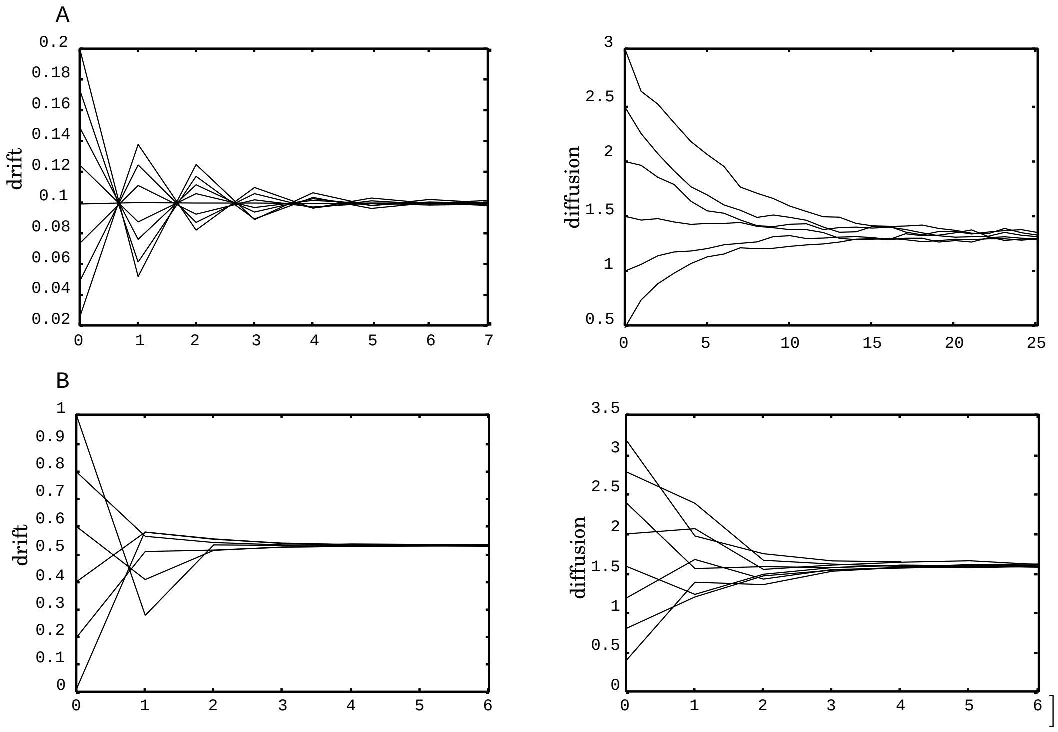

Fig. 2. The inductive transition of the drift term P and the diffusion term Q for nonleaky (upper panels) and leaky (lowwer panels) models of varying the initial values (P_0, Q_0).

course through induction map $(P_n, Q_n) \to (P_{n+1}, Q_{n+1})$ is described by the trajectory in the 2-dimensional state space, spanned by P (drift term) and Q (diffusion term). The state-space portrait exhibits only one fixpoint: an stable attractor. The right panel of Figure 3 indicates that the fixpoint is a spontaneous activity at the firing rate $\nu = 5$Hz and the coefficient of variation of the output interspike interval CV $= 0.85$. In the above simulation, the popu-

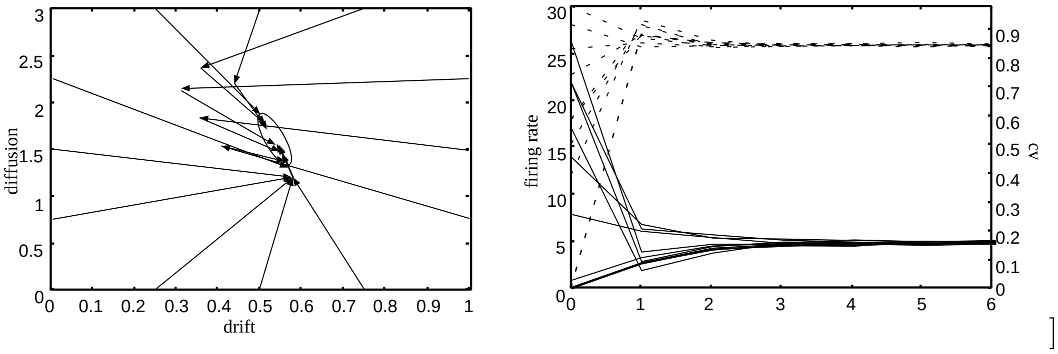

Fig. 3. (Left panel) State-space analysis of the inductive transition (P_n, Q_n). (Right panel) The inductive transition of the mean firing rate (solid lines) and the coefficient of variation (CV) of the output interspike interval (dash lines).

lation dynamics in the network is driven by neuronal noise and the recurrent input. The simulation in Figure 4 is made using only the recurrent input and the other conditions are equivalent to ones in the case of Figure 3. The state space exhibits two stable point: One point is an inert state, and another point is an explosive state.

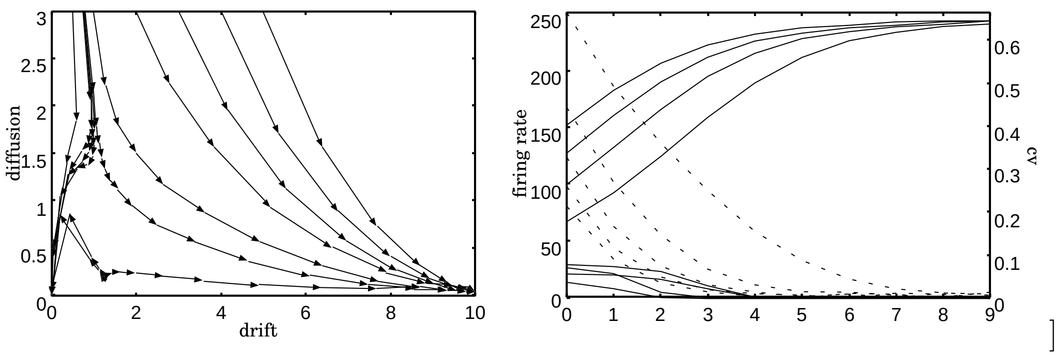

Fig. 4. (Left panel) State-space analysis of the inductive transition without neuronal noise. (Right panel) The inductive transition of the mean firing rate (solid lines) and the coefficient of variation (CV) of the output interspike interval (bash lines).

4 Discussion

The membrane potential of neocortical neurons in vivo is continuously fluctuating due to the presence of the synaptic background activity and biological noise sources. The spike process is approximatively expressed by (*mean firing rate*) + (*fluctuation*) $= u + v\xi(t)$. This approximative formula is useful to investigate the stable population activity in networks. By this simple assumption, we can get the powerful method to analyze stationary global activity in networks of IF neurons. Our results showed that there are two extremes of stable population activity in the noiseless case. On the other hand, under a given condition on the balance of excitation and inhibition, as we have seen, the spontaneous activity characterized by neuronal noise parameters (x, y) is exceedingly stable.

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