Globally Coupled Resonate-and-Fire Models

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We analyze globally coupled resonate-and-fire neuron models. We analytically explain the stability of asynchronous states in the limit of large number of neurons and calculate a phase diagram. The results of our theory coincide with those of numerical simulations. Our theory is applicable to any excitable units coupled with finite strength.

§1. Introduction

The oscillations of the local field potentials (LFP) are reported in the brain. To examine the origin of macroscopic oscillations, we study the asynchronous states for a large neural network. An asynchronous state is a state where total activity of the network is constant over time. In this paper, we calculate the phase diagram for the stability of asynchronous states for two dimensional resonate-and-fire models. While one dimensional models can be considered as a normal form near the saddle node bifurcation, the resonate-and-fire model can be considered as a normal form near the Hopf bifurcation. Therefore some difference might appear in the stability.

§2. Model

We consider all-to-all coupled resonate-and-fire models:[2),3)]

$$\begin{cases} \frac{dx_i}{dt} = -bx_i - \omega y_i + I_{ex} + g\sum_{j,k}\alpha(t-t_{jk}), \\ \frac{dy_i}{dt} = \omega x_i - by_i, \end{cases} \tag{2·1}$$

where x_i and y_i are internal state variables of the i-th neuron ($i = 1...N$) and t_{jk} denotes the k-th firing time of the j-th neuron. If y exceeds the threshold ($y = 1$), the internal state is reset to $(0, -1)$. $\alpha(t) = \alpha^2 te^{-\alpha t}$ is the alpha function. We can set $b = 1$ by scaling t without loss of generality. In what follows, we use $b = 1$ and $\omega = 10$ for which the property of single neuron dynamics has been investigated in detail.[2)] The external current (I_{ex}) and the coupling strength (g) are uniform. Note that all the neurons receive the same input at any time.

§3. Asynchronous states

An asynchronous state is a state where firing rate of a network is constant over time.[4)–6)] In noiseless case, it is also called a merry-go-round state where all neurons fire in turn at regular intervals.

Self consistency equation can be expressed as $f(g/T + I_{ex}) = 1/T$, where $f(I)$ denotes the f-I curve and T denotes a firing period of single neurons. Since the resonate-and-fire model is solvable, $f(I)$ can be obtained analytically (Eq. (4·3)). Therefore, if two of g, T, I_{ex} are given, the other is automatically determined.

§4. Stability of asynchronous states

The stability of asynchronous states can be determined analytically by using the phase reduction.

4.1. *Phase reduction*

We perform the phase reduction following the general theory.[1)] We assume that the state is almost asynchronous and the synaptic inputs can be split into a stationary part ($\frac{1}{T}$) and an infinitesimal perturbation ($e(t)$). Since neurons are firing repetitively, we assume that there exists a limit cycle as an orbit of a single neuron. $\phi(x, y)$ is defined around the limit cycle so that the points which converge each other in the limit of infinite time have the same value. Because the resonate-and-fire model has a threshold, the points which will exceed the threshold at the same time have the same value of ϕ. Note that ϕ increases constantly without perturbation. The evolution of ϕ can be written as

$$\dot{\phi} = \frac{\partial \phi}{\partial \overrightarrow{X}} \frac{d\overrightarrow{X}}{dt} = \frac{\partial \phi}{\partial \overrightarrow{X}} (\overrightarrow{F_0}(X) + \overrightarrow{g}\epsilon(t)) = \frac{1}{T} + \frac{\partial \phi}{\partial x}(X) g\epsilon(t) \simeq \frac{1}{T} + \mathit{\Gamma}(\phi)\epsilon(t), \quad (4·1)$$

where F_0 is a evolution equation for x and y without perturbation. The phase response curve ($\mathit{\Gamma} \equiv \frac{\partial \phi}{\partial x} g$) can be evaluated on the limit cycle in the lowest-order approximation and can be obtained analytically as a function of ϕ and T. Note that the evolution equation has a closed form in ϕ.

4.2. *Phase response curve*

A phase response curve shows the shift of firing times in response to an infinitesimal input current. Here we consider $\frac{\partial \phi}{\partial x}$ because current inputs enter in the x direction. The phase response curve can be obtained as follows.

The orbit of the resonate-and-fire model can be obtained analytically as a function of time owing to its linearity.[3)] We consider the following orbit. First, a neuron is reset. Next, it evolves for time t_1 and receives the infinitesimal pulse input with amplitude δK. Then, it evolves for $t_2 + \delta t_2$ and arrives at the threshold. The orbit satisfies $y(t_1, \delta K, t_2 + \delta t_2) = 1$, where t_2 denotes the firing time without the input. Taking the lowest order term of δK and δt_2, the phase response curve becomes

$$\mathit{\Gamma} = -\frac{1}{T}\frac{dt_2}{dK} = \frac{g}{T}\frac{\exp(t_1)\sin(\omega t_2)}{\cos(\omega(t_1+t_2)) + I_0 \sin(\omega(t_1+t_2)) + \omega \sin(\omega(t_1+t_2))}, \quad (4·2)$$

where $\frac{1}{T} = \frac{1}{t_1+t_2}$ is multiplied so that the phase ranges from 0 to 1. I_0 is a total stationary current input which can be obtained as a function of T from the self-consistency equation:

$$I_0 = I_{ex} + \frac{g}{T} = \frac{(1+\omega^2)e^{-T}\cos\omega T + (1+\omega^2)}{\omega - e^{-T}\sin\omega T - \omega e^{-T}\cos\omega T}. \tag{4·3}$$

Using $T = t_1 + t_2$ and $\phi = \frac{t_1}{t_1+t_2}$, the phase response curve can be rewritten as

$$\Gamma(\phi) = \frac{g}{T}\frac{e^{T\phi}\sin(\omega T(1-\phi))}{\cos(\omega T) + I_0\sin(\omega T) + \omega\sin(\omega T)}. \tag{4·4}$$

4.3. *Linear stability of density equation*

We consider the limit of large number of neurons and define a phase density function as the fraction of neurons in the interval $[\phi, \phi + d\phi]$. This density evolves via the advection equation:

$$\frac{d\rho}{dt} = -\frac{\partial(\rho(\phi)\dot{\phi})}{\partial\phi}. \tag{4·5}$$

When the perturbation is infinitesimal, the phase density can be split into two parts: $\rho(\phi) = 1 + \delta\rho(\phi)$. Simultaneously, let the synaptic input and the total current input as

$$E(t) = 1/T + \epsilon(t), \tag{4·6}$$

$$I = I_{ex} + gE(t) = I_{ex} + \frac{g}{T} + g\epsilon(t). \tag{4·7}$$

Linearization of the density equation leads to the equation for $\delta\rho$:

$$\frac{d\delta\rho}{dt} = -\frac{1}{T}\frac{\partial\delta\rho}{\partial\phi} - \frac{\partial\Gamma}{\partial\phi}e(t). \tag{4·8}$$

The density function can be discontinuous at the boundary while the flux J cannot be discontinuous due to the mass conservation law. For example, if $\dot{\phi}$ is discontinuous, ρ is also discontinuous because $J = \rho\dot{\phi}$. Therefore we consider the equation for δJ so that the boundary condition is tractable.

$$\dot{\delta J} = \Gamma(\phi)\dot{\epsilon}(t) - \frac{1}{T}\frac{\partial\delta J}{\partial\phi}. \tag{4·9}$$

The synaptic input with the alpha coupling becomes

$$\epsilon(t) = \int_{-\infty}^{t}\alpha(t-t_*)\delta J(t_*)|_{\phi=1}dt_* = \frac{\alpha^2}{(\lambda+\alpha)^2}\delta J(t)|_{\phi=1}. \tag{4·10}$$

Here we assume the time dependence as $e^{\lambda t}$ and replace $\frac{d}{dt}$ by λ. Then $e(t)$ can be eliminated by substituting Eq. (4·10) into Eq. (4·9). The equation for δJ is linear and can be integrated by ϕ under the periodic boundary condition:

$$\frac{1}{T}(e^{\lambda T} - 1)(\lambda+\alpha)^2 = \alpha^2\lambda\int_0^1 d\phi\Gamma(\phi)e^{\lambda\phi T}. \tag{4·11}$$

Here we consider the condition of neutral stability and set $\lambda = i\beta$.

There are two equations to solve because this spectral equation has the real part and the imaginary part. The variables included in the equations are five: β, I_{ex}, g, T, and α. As has been stated before, if two of g, T, I_{ex} are given, the other is automatically determined from the self-consistency equation Eq. (4·3). Therefore there are two degrees of freedom. When I_{ex} is fixed, α can be obtained as a function of g as shown in Fig. 1.

§5. Result

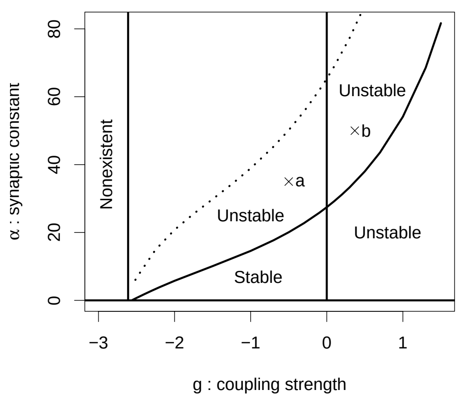

Fig. 1. Phase diagram for $I_{ex} = 10.1$. In "Stable" region, all modes of perturbation attenuate.

Figure 1 shows the phase diagram for $I_{ex} = 10.1$. α is the inverse of the synaptic time constant included in the alpha coupling. $I_{ex} = 10.1$ is a critical amplitude. For $I_{ex} > 10.1$, there is no fixed point and a neuron finally fires from any initial states. For $g < g_c = -2.61$, the inhibitory coupling is so strong that the network cannot sustain the asynchronous firing. The asynchronous state is marginally stable for $g = 0$ because there is no coupling. The stability for any mode switches across the line, $g = 0$.

For inhibitory couplings, as α increases, the synaptic input tends to be jaggy and the asynchronous state becomes unstable at a critical value. While every mode has its own critical value of α, the first mode always destabilizes first according to numerical simulation. Note that the spectral equation has multiple solutions corresponding to each mode.

The solid and dotted lines denote the critical values of α for the first and second mode. At point a in Fig. 1, the first mode is unstable while the second mode is stable. Then, the initial bimodal state evolves to the unimodal state as shown in Fig. 2. The neurons are sorted according to y-value and the deviations from the asynchronous state are plotted. Similarly, at point b, only the first mode is stable. In the numerical calculation in Fig. 3, the initial unimodal state evolved to the bimodal state.

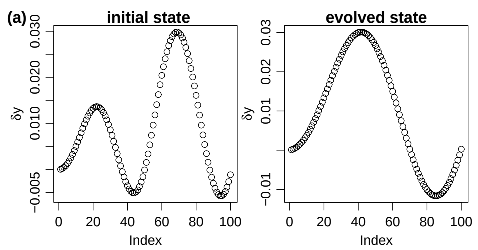

Fig. 2. Evolution of perturbation at point a.

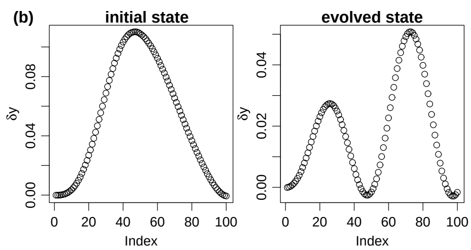

Fig. 3. Evolution of perturbation at point b.

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