Available online at www.sciencedirect.com

ScienceDirect

Progress in Natural Science 19 (2009) 1159–1163

Progress in Natural Science

www.elsevier.com/locate/pnsc

Short communication

Neuronal population dynamic model: An analytic approach

Wentao Huang [a,*], Licheng Jiao [a], Yuelei Xu [b], Shiping Ma [b], Jianhua Jia [a]

[a] *Institute of Intelligent Information Processing, Key Laboratory of Intelligent Perception and Image Understanding of Ministry of Education, Xidian University, P.O. Box 224, Xi'an 710071, China*

[b] *Department of Avionics Engineering, Engineering College of Air Force Engineering University, Xi'an 710038, China*

Received 12 October 2008; received in revised form 8 January 2009; accepted 14 January 2009

Abstract

A novel analytic approach is presented to study the population of excitatory and inhibitory spiking neurons in this paper. The evolution in time of the population dynamic equation is determined by a partial differential equation. A new function is proposed to characterize the population of excitatory and inhibitory spiking neurons, which is different from the population density function discussed by most researchers. And a novel evolution equation, which is a nonhomogeneous parabolic type equation, is derived. From this, the stationary solution and the firing rate of the stationary states are given. Last, by the Fourier transform, the time dependent solution is also obtained. This method can be used to analyze the various dynamic behaviors of neuronal populations.

Keywords: Analytic approach; Neuronal population; Dynamic model; Fourier transform

1. Introduction

The cerebral cortex is composed of a large number of neurons that are connected to an intricate network. In all small volumes of cortex, thousands of spikes are emitted at each millisecond. Each cubic millimeter of cortical tissue contains about 10^5 neurons. This impressive number also suggests that a description of neuronal dynamics in terms of a population activity is more appropriate than a description on the single-neuron level. Knight and his collaborators introduced a novel approach to the modeling and simulation of the dynamics of interacting populations of neurons [1–3]. In this approach, the dynamics of individual neurons, which are described by a state vector $\boldsymbol{v}$, determines the evolution of a density function as $\rho(\boldsymbol{v}, t)$ gives the probability that a neuron in the population is in state $\boldsymbol{v}$. The density function characterizes the behavior of the whole population. In its simplest form, the state vector is one dimensional and can be applied to leaky-integrate-and-fire (LIF) neurons. The evolution equation in this approach is a partial differential integral (PDE) equation, which describes the evolution of $\rho(\boldsymbol{v}, t)$ under the influence of neuronal dynamics and a synaptic input. So far, most approaches to solve this PDE numerically are based on finite difference schemes [3–6]. Sirovich [7] discussed the solutions of some solvable cases. Brunel [8] developed an analytical method to the sparsely connected networks of excitatory and inhibitory spiking neurons via the Fokker–Planck equation. Especially, there are many researchers engaging in research of the neuronal population model in recent years [9–14]. We present a novel view to the population evolution equation. A new population evolution equation is derived, and its analytical solution is given to analyze the firing rate in this paper.

2. The basic model

The population model on which this study is based derives from neuronal dynamics described based on the simple integrate-and-fire equation:

* Corresponding author. Tel./fax: +86 29 88207354.
E-mail address: wthuang@mail.xidian.edu.cn (W. Huang).

1002-0071/$ - see front matter © 2009 National Natural Science Foundation of China and Chinese Academy of Sciences. Published by Elsevier Limited and Science in China Press. All rights reserved.
doi:10.1016/j.pnsc.2009.01.007

$$\frac{\mathrm{d}v}{\mathrm{d}t} = -\lambda v(t) + s(t) \tag{1}$$

where the *trans*-membrane potential, $v(0 \leqslant v \leqslant 1)$, has been normalized so that $v = 0$ marks the rest state, and $v = 1$ the threshold for firing. When the latter is achieved v is reset to zero. λ, a frequency, is the leakage rate and $s(t)$, also having the dimensions of frequency, is the normalized current due to synaptic arrivals at the neuron.

Under the statistical approach one considers a population of N neurons, each following Eq. (1), so that $N\rho(\mathbf{v}, t)\,\mathrm{d}v$ specifies the probable number of neurons, at time t, in the range of states $(v, v + dv)$. $\rho(\mathbf{v}, t)$, the probability density, may be shown to be governed by

$$\begin{aligned}\frac{\partial \rho}{\partial t} = & -\frac{\partial}{\partial v}J + \delta(v)r(t) = \frac{\partial}{\partial v}(-\lambda v\rho) + \sigma_e(t)\int_{v-h_e}^{v}\rho(v', t)\,\mathrm{d}v' \\ & - \sigma_e(t)\int_{v}^{v+h_i}\rho(v', t)\,\mathrm{d}v' + \delta(v)r(t-\tau) = \frac{\partial}{\partial v}(-\lambda v\rho) \\ & + \sigma_e(t)(\rho(v-h_e, t) - \rho(v, t)) + \sigma_e(t)(\rho(v+h_i, t) \\ & - \rho(v, t)) + \delta(v)r(t-\tau)\end{aligned} \tag{2}$$

where h_e and h_i are the membrane voltage jump due to an excitatory synapse spike arrival and an inhibitory synapse spike arrival, respectively, τ is the refractory period, $\sigma_e(t)$ and $\sigma_i(t)$ are the external excitatory neuronal input rate of spikes and the external inhibitory neuronal input rate of spikes, J is the neuronal flux in the state space and $r(t)$ is the firing rate of the population and is given by the flux of neurons leaving at the threshold value of the membrane potential

$$r(t) = J(v = 1, t) = \sigma_e(t)\int_{1-h_e}^{1}\rho(v', t)\,\mathrm{d}v' \tag{3}$$

Since the number of neurons is preserved, the flux of neurons leaving the interval must equal that entering at the resting state

$$J(\rho, t)_{v=0} = J(\rho, t-\tau)_{v=1} \tag{4}$$

From this it follows that probability is conserved,

$$\int_0^1 \rho(v, t)\,\mathrm{d}v + \int_{t-\tau}^{t} r(t')\,\mathrm{d}t' \equiv 1 \tag{5}$$

The second boundary condition is that

$$\rho(v = 1, t) = 0 \tag{6}$$

Eq. (2) is to be solved given initial data

$$\rho(v, t = 0) = q(v) \tag{7}$$

This model may be extended to membrane dynamics, a richer set of reversal potentials and stochastic effects, as well as more complicated neuronal models [3,4,6].

3. Analytical studying of a modified model

Sometimes we are more interested in firing rate $r(t)$ than $\rho(v, t)$. If we solved the firing rate $r(t)$ by Eqs. (2) and (3), the computational process would be discommodious and complicated. In order to overcome the difficulties, we use the following transformation first:

$$\begin{cases} P(v, t) = \int_{-\infty}^{v}\rho(v', t)\,\mathrm{d}v' \\ P(v, 0) = Q(v) = \int_{-\infty}^{v} q(v')\,\mathrm{d}v' \end{cases} \tag{8}$$

Integrating Eq. (2) from 0 to v on two sides, and substituting Eq. (8) into Eq. (2) derives

$$\begin{aligned}\frac{\partial P}{\partial t} - \lambda v\frac{\partial P}{\partial v} = & \sigma_e(t)(P(v-h_e, t) - P(v, t)) + \sigma_i(t)(P(v+h_i, t) \\ & - P(v, t)) + H(v)r(t-\tau)\end{aligned} \tag{9}$$

where $v \in [0, 1]$, and $H(v)$ is the Heaviside step function:

$$H(v) = \begin{cases} 0 & v < 0 \\ 1 & v \geqslant 0 \end{cases} \tag{10}$$

The firing rate $r(t)$ is

$$r(t) = \sigma_e(t)[P(1, t) - P(1-h_e, t)] \tag{11}$$

From the above, moreover, we can get the conditions

$$\begin{cases} P(0, t) = \frac{r(t-\tau)}{\sigma_e(t)} \\ P(1, t) = 1 - \int_{t-\tau}^{t} r(t')\,\mathrm{d}t' \end{cases} \tag{12}$$

and

$$\begin{cases} P(v, t) = 0 & v < 0 \\ P(v, t) \geqslant 0 & 0 < v \leqslant 1 \\ P(v, t) = P(1, t) & v > 1 \end{cases} \tag{13}$$

Generally, for the following quasi-linear first order partial differential equations:

$$\begin{cases} \frac{\partial\phi(v,t)}{\partial t} - av\frac{\partial\phi(v,t)}{\partial v} = -b(t)\phi(v, t) + g(v, t) \\ \phi(v, 0) = \Theta(v) \end{cases} \tag{14}$$

we can get its analytical solution:

$$\begin{cases} \phi(v, t) = \Theta(ve^{at})e^{-\eta(t)} + \int_0^t g(ve^{a(t-t')}, t')e^{\eta(t') - \eta(t)\,\mathrm{d}t'} \\ \eta(t) = \int_0^t b(t')\,\mathrm{d}t' \end{cases} \tag{15}$$

Then, from (9), we have

$$\begin{cases} P(v, t) = Q(ve^{\lambda t})e^{-\eta(t)} \\ \qquad + \int_0^t \left[\sigma_e(t')P(ve^{\lambda(t-t')} - h_e, t') + \sigma_i(t')P(ve^{\lambda(t-t')}\right. \\ \qquad \left. + h_i, t') + r(t'-\tau)\right]e^{\eta(t') - \eta(t)}dt' \\ \eta(t) = \int_0^t(\sigma_e(t') + \sigma_i(t'))\,\mathrm{d}t' \end{cases} \tag{16}$$

Eq. (16) gives an iterative approach to solve $P(v, t)$ for us. The value of current state $P(v, t)$ in each fixed position (v, t) is determined by the integrate value of previous states. From the point of view of signal processing, this can be regarded as a spatio-temporal recursion filter.

3.1. Approximate approach

However, the above method does not give an immediate analytical solution, and is inconvenient for us to apply.

When $h_e \to 0$ and $h_i \to 0$, let us consider the Taylor expansion

$$\begin{cases} P(v-h_e,t) \approx P(v,t) - h_e \frac{\partial P(v,t)}{\partial v} + \frac{h_e^2}{2}\frac{\partial^2 P(v,t)}{\partial v^2} \\ P(v-h_i,t) \approx P(v,t) - h_i \frac{\partial P(v,t)}{\partial v} + \frac{h_i^2}{2}\frac{\partial^2 P(v,t)}{\partial v^2} \end{cases} \tag{17}$$

But when $v < h_e$, $P(v-h_e,t)$, and $v > 1-h_i, P(v+h_i,t) = P(1,t)$, the influence of $P(v-h_e,t)$ and $P(v+h_i,t)$ vanish, then Eq. (17) cannot be used for estimating $P(v-h,t)$ and $P(v+h_i,t)$. We adopt

$$\begin{cases} P(v-h_e,t) \approx P(v,t) - h_e \frac{\partial P(v,t)}{\partial v} + \frac{h_e^2}{2}\frac{\partial^2 P(v,t)}{\partial v^2} + h(v,t) \\ P(v+h_i,t) \approx P(v,t) + h_i \frac{\partial P(v,t)}{\partial v} + \frac{h_i^2}{2}\frac{\partial^2 P(v,t)}{\partial v^2} + h'(v,t) \\ h(v,t) = -H_{h_e}(v)P(0,t) = -H_{h_e}(v)\frac{r(t-\tau)}{\sigma_e(t)} \\ h'(v,t) = -H(v-1+h_i)P(1,t) \\ \qquad = -H(v-1+h_i)\left(1-\int_{t-\tau}^{t} r(t')\,dt'\right) \\ H_{h_e}(v) = H(v) - H(v-h_e) \end{cases} \tag{18}$$

where $h(v,t)$ and $h(v,t)$ can be compensate function. Substituting (18) into (9) yields:

$$\begin{cases} \frac{\partial P}{\partial t} - \lambda v \frac{\partial P}{\partial v} = \mu_1(t)\frac{\partial P(v,t)}{\partial v} + \mu_2(t)\frac{\partial^2 P(v,t)}{\partial v^2} + f(v,t) \\ f(v,t) = H(v-h_e)r(t-\tau) - H(v-1+h_i)\sigma_i(t)\left(1-\int_{t-\tau}^{t} r(t')\,dt'\right) \\ \mu_1(t) = h_i\sigma_i(t) - h_e\sigma_e(t) \\ \mu_2(t) = \frac{h_e^2\sigma_e(t)}{2} + \frac{h_i^2\sigma_i(t)}{2} \end{cases} \tag{19}$$

3.2. Stationary solution

First, let us consider the stationary states. In this case, $\sigma_e(t) = \sigma_e^0$, $\sigma_i(t) = \sigma_i^0, \frac{\partial P(v,t)}{\partial t} = 0, P(v,t) = P_0(v), r(t) = r_0$, then, from (19) we get

$$\begin{cases} (\lambda v + \mu_1^0)\frac{dP_0(v)}{dv} + \mu_2^0 \frac{d^2 P_0(v)}{dv^2} + f_0(v) = 0 \\ f_0(v) = H(v-h_e)r_0 - H(v-1+h_i)\sigma_i^0(1-\tau r_0) \\ \mu_1^0 = h_i\sigma_i^0 - h_e\sigma_e^0 \\ \mu_2^0 = \frac{h_e^2\sigma_e^0}{2} + \frac{h_i^2\sigma_i^0}{2} \end{cases} \tag{20}$$

The solution of Eq. (20) is

$$\begin{cases} P_0(v) = -\int_0^v \exp\left(-\frac{(v_2-b)^2}{2a^2}\right)\int_0^{v_2} f_0(v_1)\exp\left(\frac{(v_1-b)^2}{2a^2}\right)dv_1\,dv_2 \\ \qquad + C_1\int_0^v \exp\left(-\frac{(v_1-b)^2}{2a^2}\right)dv_1 + C_2 \\ a = \sqrt{\frac{\mu_2^0}{\lambda}} \\ b = \frac{\mu_1^0}{\lambda} \end{cases} \tag{21}$$

where C_1, C_2 are constants and they satisfy

$$\begin{cases} P_0(0) = \frac{r_0}{\sigma_e^0} \\ P_0(1) = 1 - \tau r_0 \\ P_0(1) = P_0(1-h_e) = \frac{r_0}{\sigma_e^0} \end{cases} \tag{22}$$

Finally, we obtain

$$\begin{cases} r_0 = \frac{(\mu_2^0 - m_3\sigma_i^0)n_2\sigma_e^0}{n_1\mu_2^0 + n_2\mu_2^0 + \sigma_e^0(m_2n_1 - m_1n_2 + \tau n_2\mu_2^0) + \tau\sigma_i^0\sigma_e^0(m_4n_1 - m_3n_2)} \\ C_1 = \frac{r_0}{n_2\sigma_e^0} + \frac{r_0}{n_2\mu_2^0}(m_2 + m_4\tau\sigma_i^0) \\ C_2 = \frac{r_0}{\sigma_e^0} \end{cases} \tag{23}$$

where

$$\begin{cases} m_1 = \int_0^1 \exp\left(-\frac{(v_2-b)^2}{2a^2}\right)\int_0^{v_2} H(v_1-h_e)\exp\left(\frac{(v_1-b)^2}{2a^2}\right)dv_1\,dv_2 \\ m_2 = \int_{1-h_e}^1 \exp\left(-\frac{(v_2-b)^2}{2a^2}\right)\int_0^{v_2} H(v_1-h_e)\exp\left(\frac{(v_1-b)^2}{2a^2}\right)dv_1\,dv_2 \\ m_3 = \int_0^1 \exp\left(-\frac{(v_2-b)^2}{2a^2}\right)\int_0^{v_2} H(v_1-1+h_i)\exp\left(\frac{(v_1-b)^2}{2a^2}\right)dv_1\,dv_2 \\ m_4 = \int_{1-h_e}^1 \exp\left(-\frac{(v_2-b)^2}{2a^2}\right)\int_0^{v_2} H(v_1-1+h_i)\exp\left(\frac{(v_1-b)^2}{2a^2}\right)dv_1\,dv_2 \\ n_1 = \int_0^1 \exp\left(-\frac{(v_1-b)^2}{2a^2}\right)dv_1 \\ n_2 = \int_{1-h_e}^1 \exp\left(-\frac{(v_1-b)^2}{2a^2}\right)dv_1 \end{cases} \tag{24}$$

From Eq. (23) we know that the firing rate r_0 increases with the increase in external excitatory input rate σ_e^0 and the increase in inhibitory excitatory input rate σ_i^0. When $\sigma_e^0 \to \infty$ and $\sigma_i^0 \to \infty$, we have

$$r_0 = \begin{cases} \lim\limits_{\sigma_i^0 \to \infty} \frac{(\mu_2^0 - m_3\sigma_i^0)n_2\sigma_e^0}{n_1\mu_2^0 + n_2\mu_2^0 + \sigma_e^0(m_2n_1 - m_1n_2 + \tau n_2\mu_2^0) + \tau\sigma_i^0\sigma_e^0(m_4n_1 - m_3n_2)} = \frac{1}{\tau} \\ \lim\limits_{\sigma_i^0 \to \infty} \frac{(\mu_2^0 - m_3\sigma_i^0)n_2\sigma_e^0}{n_1\mu_2^0 + n_2\mu_2^0 + \sigma_e^0(m_2n_1 - m_1n_2 + \tau n_2\mu_2^0) + \tau\sigma_i^0\sigma_e^0(m_4n_1 - m_3n_2)} = 0 \end{cases} \tag{25}$$

3.3. Time dependent solution

Next, we discuss how to solve Eq. (19). It can be expressed as a nonhomogeneous parabolic type equation

$$\begin{cases} \frac{\partial P}{\partial t} - \lambda v \frac{\partial P}{\partial v} = \mu_1(t)\frac{\partial P(v,t)}{\partial v} + \mu_2(t)\frac{\partial^2 P(v,t)}{\partial v^2} + f(v,t), \quad v \in (0,1) \\ P(v,0) = Q(v) \\ P(0,t) = \frac{r(t-\tau)}{\sigma_e^0(t)}, \quad P(1,t) = 1 - \int_{t-\tau}^{t} r(t')\,dt' \end{cases} \tag{26}$$

This is a mixed problem that possesses initial value and boundary value simultaneously. It is a challenge for us to solve. We adopt the following assumption:

$$Y(v,t) = P(v,t)[H(v) - H(v-1)] = \begin{cases} P(v,t), & v \in [0,1] \\ 0, & v \notin [0,1] \end{cases} \tag{27}$$

and

$$P'_v(0,t) = \frac{\partial P(0,t)}{\partial v} = 0, \quad P'_v(1,t) = \frac{\partial P(1,t)}{\partial v} = 0 \tag{28}$$

From Eqs. (27) and (28) we can get

$$\begin{cases} \frac{\partial Y(v,t)}{\partial v} = \frac{\partial P(v,t)}{\partial v}[H(v) - H(v-1)] + [P(0,t)\delta(v) - P(1,t)\delta(v-1)] \\ \frac{\partial^2 Y(v,t)}{\partial v^2} = \frac{\partial^2 P(v,t)}{\partial v^2}[H(v) - H(v-1)] + [P(0,t)\delta'(v) - P(1,t)\delta'(v-1)] \end{cases} \tag{29}$$

Substituting (29) into (26) yields:

$$\begin{cases} \frac{\partial Y(v,t)}{\partial t} - \lambda v \frac{\partial Y(v,t)}{\partial v} = \mu_1(t) \frac{\partial P(v,t)}{\partial v} + \mu_2(t) \frac{\partial^2 P(v,t)}{\partial v^2} + F(v,t) \\ Y(v,0) = Y_0(v) = Q(v)[H(v) - H(v-1)] \end{cases} \tag{30}$$

where

$$\begin{cases} F(v,t) = [H(v-h_e) - H(v-1)]r(t-\tau) \\ \qquad -[H(v-1+h_i) - H(v-1)] \\ \qquad \times \sigma_i(t)\left(1 - \int_{t-\tau}^{t} r(t')\,\mathrm{d}t'\right) + g(v,t) \\ g(v,t) = -\mu_1(t)[P(0,t)\delta(v) - P(1,t)\delta(v-1)] - \mu_2(t) \\ \qquad \times [P(0,t)\delta'(v) - P(1,t)\delta'(v-1)] \end{cases} \tag{31}$$

Applying the Fourier transform to (30) yields

$$\begin{cases} \frac{\partial \widetilde{Y(s,t)}}{\partial t} + \lambda s \frac{\partial \widetilde{Y(s,t)}}{\partial s} = (-\lambda + \mu_1(t)js - \mu_2(t)s^2)\widetilde{Y}(s,t) + \widetilde{F}(s,t) \\ \widetilde{Y}(s,0) = \widetilde{Y}_0(s) \end{cases} \tag{32}$$

Solving the quasi-linear first order partial differential equations obtains

$$\begin{cases} \widetilde{Y}(s,t) = \widetilde{Y}_0(se^{-\lambda t})e^{\eta(s,t)} + \int_0^t \widetilde{F}(se^{-\lambda(t-t')},t')e^{\eta(s,t)-\eta(s,t')}\,\mathrm{d}t' \\ \eta(s,t) = -\lambda t - jse^{-\lambda t}\int_0^t \mu_1(l)e^{\lambda t}\,\mathrm{d}l - s^2 e^{-2\lambda t}\int_0^t \mu_2(t)e^{2\lambda t}\,\mathrm{d}l \end{cases} \tag{33}$$

The inversion of the Fourier transform of $\widetilde{Y}(s,t)$, i.e. $Y(v,t) = F^{-1}[\widetilde{Y}(s,t)]$ is

$$\begin{cases} Y(v,t) = Y_0(ve^{\lambda t}) * L^{-1}[e^{\eta(s,t)}] + \int_0^t F(ve^{\lambda(t-t')},t') * L^{-1}\left[e^{\eta(s,t)-\eta(s,t')}\right]dt' \\ \eta(s,t) = -\lambda t - jse^{-\lambda t}\int_0^t \mu_1(l)e^{\lambda l}\,\mathrm{d}l - s^2 e^{-2\lambda t}\int_0^t \mu_2(t)e^{2\lambda l}\,\mathrm{d}l \end{cases} \tag{34}$$

where * is the convolution operator. Due to

$$\begin{cases} F^{-1}[e^{\eta(s,t')}] = F^{-1}[e^{-\lambda t + jsc_1(t)}] * F^{-1}[e^{-s^2 c_2(t)}] \\ \quad = e^{-\lambda t}U(v + c_1(t), t) \\ F^{-1}[e^{\eta(s,t)-\eta(s,t')}] = e^{-\lambda(t-t')}U'(v + c_1(t) - c_1(t'), t, t') \end{cases} \tag{35}$$

where

$$\begin{cases} U(v,t) = F^{-1}[e^{-s^2 c_2(t)}] = \frac{1}{\sqrt{4\pi c_2(t)}} e^{\frac{v^2}{4c_2(t)}} \\ U'(v,t,t') = F^{-1}[e^{-s^2(c_2(t)-c_2(t'))}] = \frac{1}{\sqrt{4\pi(c_2(t)-c_2(t'))}} e^{\frac{v^2}{4(c_2(t)-c_2(t'))}} \\ c_1(t) = e^{-\lambda t}\int_0^t \mu_1(l)e^{\lambda l}\,\mathrm{d}l \\ c_2(t) = e^{-2\lambda t}\int_0^t \mu_2(l)e^{2\lambda l}\,\mathrm{d}l \end{cases} \tag{36}$$

Eq. (34) changes to

$$\begin{aligned} Y(v,t) &= e^{-\lambda t}Y_0(ve^{\lambda t}) * U(v + c_1(t), t) \\ &\quad + \int_0^t e^{-\lambda(t-t')}F(ve^{\lambda(t-t')}, t') * U'(v + c_1(t) \\ &\quad - c_1(t'), t, t')\,\mathrm{d}t' \end{aligned} \tag{37}$$

This is a significant result. If we assume that $Y_1(v,t)$, $Y_2(v,t)$ and $Y_2'(v,t)$ satisfy the following equations:

$$\begin{cases} \frac{\partial Y_1(v,t)}{\partial t} - \lambda v \frac{\partial Y_1(v,t)}{\partial v} = F(v,t) \\ Y_1(v,0) = Y_0(v) \end{cases} \tag{38}$$

and

$$\begin{cases} \frac{\partial Y_2(v,t)}{\partial t} = \left(-\lambda + \frac{\mathrm{d}c_1(t)}{\mathrm{d}t} + \frac{\mathrm{d}c_2(t)}{\mathrm{d}t}\right)\frac{\partial^2 Y_2(v,t)}{\partial v^2}, \quad v \in (0,1) \\ Y_2(v,0) = \delta(v) \\ Y_2(0,t) = 0, \quad Y_2(1,t) = 0 \\ \frac{\mathrm{d}Y_2(0,t)}{\mathrm{d}t} = 0, \quad \frac{\mathrm{d}Y_2(1,t)}{\mathrm{d}t} = 0 \end{cases} \tag{39}$$

and

$$\begin{cases} \frac{\partial Y_2'(v,t)}{\partial t} = \left(-\lambda + \frac{\mathrm{d}c_1(t)}{\mathrm{d}t} + \frac{\mathrm{d}c_2(t)}{\mathrm{d}t}\right)\frac{\partial^2 Y_2'(v,t)}{\partial v^2}, \quad v \in (0,1) \\ Y_2'(v,0) = e^{-\lambda t'}U(v + c_1(t'), t') \\ Y_2'(0,t) = 0, \quad Y_2'(1,t) = 0 \\ \frac{\mathrm{d}Y_2'(0,t)}{\mathrm{d}t} = 0, \quad \frac{\mathrm{d}Y_2'(1,t)}{\mathrm{d}t} = 0 \end{cases} \tag{40}$$

then

$$\begin{cases} Y_1(v,t) = Y_0((1-v')e^{\lambda t}) + \int_0^t F\left(ve^{\lambda(t-t')}, t'\right)\mathrm{d}t' \\ Y_2(v,t) = e^{-\lambda t}U(v + c_1(t), t) \\ Y_2'(v,t) = e^{-\lambda(t-t')}U'(v + c_1(t) - c_1(t'), t, t') \end{cases} \tag{41}$$

These show that $Y(v,t)$ is given by the combination of the convolution of $Y_1(v,t)$, $Y_2(v,t)$ and $Y_2'(v,t)$. From (12) and (37), we can get the firing rate $r(t)$

$$\begin{aligned} r(t) &= \sigma(t)[Y(1,t) - Y(1-h,t)] \\ &= \sigma(t)\left[\int_{-\infty}^{\infty} e^{-\lambda t}[Y_0((1-v')e^{\lambda t}) - Y_0((1-h-v')e^{\lambda t})]\right. \\ &\quad \times (v' + c_1(t), t)\mathrm{d}v' + \int_0^t \int_{-\infty}^{\infty} e^{-\lambda(t-t')}\left[F\left((1-v')e^{\lambda(t-t')}, t'\right)\right. \\ &\quad \left.\left. -F\left((1-h-v')e^{\lambda(t-t')}, t'\right)\right] \times U'(v' + c_1(t) - c_1(t'), t, t')\mathrm{d}v'\mathrm{d}t'\right] \end{aligned} \tag{42}$$

Eqs. (12), (31) and (42) give the relation between the firing rate $r(t)$ and time t.

4. Summary

In this paper we have presented a novel analytical approach to study the population of excitatory and inhibitory spiking neurons. For computing the firing rate expediently, we adopt a transformation to the density function and obtain the state function. We derive a new evolution equation from the original equation which is a nonhomogeneous parabolic type equation, and give the approach that deduces its analytical solution. We propose a method to solve the approximative solution, which derives a nonhomogeneous parabolic type equation and gets a relation of the computing firing rate. Furthermore, we study the stationary solution and give the firing rate of the stationary states.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (Grant Nos. 60703107 and 60703108), the National High Technology Research and Development Program of China (Grant No. 2006AA01Z107), the National Basic Research Program of China (Grant No. 2006CB705700) and the Program for Cheung Kong Scholars and Innovative Research Team in University (PCSIRT, IRT0645).

References

[1] Knight B, Manin D, Sirovich LY. Dynamical models of interacting neuron populations in visual cortex. In: Symposium on robotics and cybernetics: computational engineering in systems applications. France: Lille; 1996.
[2] Knight BW. Dynamics of encoding in neuron populations: some general mathematical features. Neural Comput 2000;12(3):473–518.
[3] Omurtag A, Knight BW, Sirovich L. On the simulation of large populations of neurons. J Comput Neurosci 2000;8(1):51–63.
[4] Casti ARR, Omurtag A, Sornborger A, et al. A population study of integrate-and-fire-or-burst neurons. Neural Comput 2002;14(5): 957–86.
[5] de Kamps M. A simple and stable numerical solution for the population density equation. Neural Comput 2003;15(9):2129–46.
[6] Nykamp DQ, Tranchina D. A population density approach that facilitates large-scale modeling of neural networks: analysis and an application to orientation tuning. J Comput Neurosci 2000;8(1):19–50.
[7] Sirovich L. Dynamics of neuronal populations: eigenfunction theory; some solvable cases. Network: Comput Neural Syst 2003;14(2):249–72.
[8] Brunel N. Dynamics of sparsely connected networks of excitatory and inhibitory spiking neurons. J Comput Neurosci 2000;8(3):183–208.
[9] Huang W, Jiao L, Tan S, et al. Response analysis of neuronal population with synaptic depression. Advances in neural information processing systems, vol. 18. Cambridge (MA): MIT Press; 2006. p. 523–30.
[10] Huertas MA, Smith GD. A two-dimensional population density approach to modeling the dlgn/pgn network. Neurocomputing 2006;69(10–12):1286–90.
[11] Rudolph M, Destexhe A. Analytical integrate-and-fire neuron models with conductance-based dynamics for event-driven simulation strategies. Neural Comput 2006;18(9):2146–210.
[12] Kriener B, Tetzlaff T, Aertsen A, et al. Correlations and population dynamics in cortical networks. Neural Comput 2008;20(9):2185–92.
[13] Ly C, Tranchina D. Critical analysis of dimension reduction by a moment closure method in a population density approach to neural network modeling. Neural Comput 2007;19(8):2032–92.
[14] Sirovich L. Populations of tightly coupled neurons: the rgc/lgn system. Neural Comput 2008;20(5):1179–210.