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Universal analyses of neuron models based-on a concept of potential with active areas

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Abstract—We present various bursting wave forms which are obtained from a simple model of the Hodgkin-Huxley type. The model is a typical example whose characteristics can be discussed through the concept of potential with active areas. A potential function is able to provide a global landscape for dynamics of a model, and the dynamics are explained in relation to the disposition of the actives area on the potential. We obtain the potential functions and the active areas for the Hindmarsh-Rose model, the Morris-Lecar system, and the Hodgkin-Huxley system, and hence we are able to discuss the common properties among these models based on the concept of potential with active areas.

1. Introduction

While artificial neural networks may appear to make them ideal candidates for meeting the increasing demand for intelligent information processing, there are many residual problems in the formational study for the active brain architecture. Although, various neuron models have been introduced, there are not so many studies concerning with networks based on the interconnection of active neuron units[1] because of complex properties. The analyses of the models may often provide us with novel dynamical systems possessing interesting properties in their component oscillators or in the nature of the interconnections. Nonlinear systems are usually able to display different dynamic behaviors depending on system parameters and external input. When these are slightly modified in the vicinity of a critical point, an abrupt qualitative change or transition in the dynamics occurs. Hence, these dynamics have been minutely investigated in each individual model based on the bifurcation theory[2] where we can discuss the characteristics around a critical point and the perturbation in its vicinity. These models which typically take the form of ordinary nonlinear differential equations of several dimensions commonly display two main types of dynamics firing spikes at regular intervals and bursting of spikes interwoven with periods of quiescence. The pattern of spiking is of great importance because it is believed that it codifies the information transmitted by neurons. Numerous types of spiking and bursting regimes are classified based on bifurcations of the quiescent state and of a limit cycle involved[3]. The universality of the dynamic characteristics of these models, which has been mainly discussed through a canonical model[3], is of further importance to apply active neuron units to the networks for intelligent information processing. Many important aspects of this situation are poorly understood and lack the satisfying universality of the structural stability discussion among the various models because of nonlinearity. One of the candidates for comparable characteristics among the models is a potential function which is able to provide a global landscape for dynamics of the models. The shape of the potential function and its modification with parameters are able to indicate the stability conditions. Furthermore, we can also discuss the stability in relation to the active or passive property on the potential, for example, a negative resistance or viscosity. The concept of potential with active areas is able to provide the new view of the analyses of the nonlinear system in addition to the bifurcation theory.

In this paper we establish each potential function for typical neuron models, and simultaneously the active areas on the potentials are obtained according to the linear stability theory Hurwitz's theorem. Particularly, we propose a simple model consisting of three first-order nonlinear differential equations of the Hodgkin-Huxley type[4], and then explain the various types of bursting phenomena and firing modes of the model through the analytical and numerical results which may suggest the similar characteristics of the other well-known models. Consequently, we are able to investigate both the correlation among the models and the characteristics of each individual model in a systematic manner.

2. Equilibrium Points

Neuron models typically take the form of ordinary nonlinear differential equations of several dimensions. In this paper we address the models where the set of the ordinary nonlinear differential equations can be transformed into a higher order and single nonlinear differential equation with one variable x,

$$\frac{d^{n}x}{dt^{n}} + b_{n-1}\left(x, \frac{dx}{dt}, \cdots, \frac{d^{n-1}x}{dt^{n-1}}\right) \frac{d^{n-1}x}{dt^{n-1}} + \cdots + b_{1}\left(x, \frac{dx}{dt}\right) \frac{dx}{dt} = f(x, \theta),$$
(1)

where $x = x(t) \in \mathbf{R}$ and θ is a constant input. It is assumed that $f(x, \theta)$ in Eq. (1) is a continuous and differentiable function of variable x only. The equilibrium points of Eq. (1) are obtained from $f(x, \theta) = 0$. Therefore, letting $f(x, \theta) = -\partial Un(x, \theta)/\partial x$, $Un(x, \theta)$ is a kind of potential function. We mainly address the models of three dimensions (n = 3) in Eq. (1) where $b_1 dx/dt$, $b_2 d^2 x/dt^2$, and $d^3 x/dt^3$ are regarded as forces originated from the velocity, the acceleration, and the change of acceleration, respectively. Hence, it is expected that b_1 is a nonlinear coefficient of viscosity, and $b_2 d^2 x/dt^2$ is related to inertia. In order to discuss the stability of the equilibrium points, letting $x = x_0 + \delta$ and $\delta = A \exp(\lambda t)$ we obtain the following characteristic equation after the linearization in terms of δ ,

$$\lambda^{3} + b_{2} \left(x_{0}, \frac{dx}{dt} = 0, \frac{d^{2}x}{dt^{2}} = 0 \right) \lambda^{2}$$
$$+ b_{1} \left(x_{0}, \frac{dx}{dt} = 0 \right) \lambda - \frac{\partial f(x_{0}, \theta)}{\partial x} = 0.$$
(2)

According to Hurwitz's theorem the equilibrium point x_0 is stable, if

$$b_0(x_0) = -\frac{\partial f(x_0, \theta)}{\partial x} = \frac{\partial^2 U3(x_0, \theta)}{\partial x^2} > 0, \qquad (3)$$

$$b_1(x_0, 0) > 0,$$
 (4)

$$b_2(x_0, 0, 0) > 0, \tag{5}$$

and

$$B_1(x_0) = b_2(x_0, 0, 0)b_1(x_0, 0) - b_0(x_0) > 0.$$
 (6)

Therefore, *x* converges on x_0 as the motion on the potential in the vicinity of the equilibrium point. Eq. (3) means that the curvature b_0 of the potential *U*3 is positive at x_0 .

If $b_1(x, 0) > 0$, $b_2(x, 0, 0) > 0$, and $B_1(x) > 0$ for $-\infty < \infty$ $x < \infty$, the stability of an equilibrium point x_0 depends only on the potential curvature $b_0(x_0)$. Accordingly, when we have *m* number of equilibrium points $x_1 < x_2 < \cdots < x_n$ $x_{m-1} < x_m$, it is expected that x always converges on one of the stable equilibrium points without divergence if the curvatures $b_0(x_1)$ and $b_0(x_m)$ are both positive. The global curvature of the potential U3(x) in this case is positive, and hence $f(x,\theta) < 0$ for $x_m < x$. Therefore, if the velocity dx/dt and the acceleration d^2x/dt^2 were both positive for $x_m < x$, the increment of the acceleration would be negative $(d^3x/dt^3 < 0)$ on condition that $b_1 > 0$ and $b_2 > 0$ for $x_m < 0$ x according to Eq. (1). It leads to the negative acceleration and the negative velocity in the long run without resulting in divergence. The similar discussion is available for x < x x_1 . Therefore, no divergent solutions exist. This conclusion is supported by the results of simulations in the succeeding section.

However, the behavior of the system is no more a motion on the potential in the interval of x where $b_1(x, 0) \le 0$ or $b_2(x,0,0) \leq 0$ or $B_1(x) \leq 0$ is satisfied. The disposition of the equilibrium point can be controlled by the external input θ according to Eq. (1), and hence, when an equilibrium point with $b_0 > 0$ is within one of these intervals, the equilibrium point is unstable because the requirement of Hurwitz's theorem for stability is not fulfilled. If there are no any other equilibrium points which satisfy Eqs. (3)-(6), a dynamical motion will occur. However, it is considered from the above discussion that no divergent solutions exist, if the global curvature of the potential is positive, and if the intervals with negative $b_1(x, 0)$ or $b_2(x, 0, 0)$ or $B_1(x)$ are localized. Consequently, it causes an oscillation which may be a periodic or nonperiodic limit cycle or a chaotic motion. These intervals are regarded as active areas in analogy with the BVP model which corresponds to Eq. (1) with n = 2. If the global curvature of the potential is positive, each one of these active areas $X_{[b1<0]}, X_{[b2<0]}$, and $X_{[B1<0]}$, which are obtained from Eq. (1) with n = 3 by using $b_1(x, 0) < 0$ or $b_2(x,0,0) < 0$ or $B_1(x) < 0$, causes an oscillation with a different frequency due to three time constants in the system as shown in the next section. It is a bifurcation that the potential curvature b_0 of an equilibrium point changes its sign, or an equilibrium point crosses an edge of active areas with changing parameters. The relations between the three active areas and the oscillation frequencies are shown in the next section. The relations and the disposition of the active areas concern directly the states of spiking and bursting appeared in neuron models.

3. Models

3.1. Hindmarsh-Rose model

The Hindmarsh-Rose equations[5] define a recognized model for the bursting-spiking dynamics of the membrane potential x(t). The equations of the model written in dimensionless form read

$$\dot{x} = y + 3x^2 - x^3 - z + I, \tag{7}$$

$$\dot{y} = 1 - 5x^2 - y,$$
 (8)

$$\dot{z} = -r\left\{z - 4\left(x + \frac{8}{5}\right)\right\}.$$
(9)

The equations can be transformed into the one-variable equation,

$$\ddot{x} + \left\{3(x-1)^2 + r - 2\right\}\ddot{x} + 6(x-1)\dot{x}^2 + \left\{3(1+r)x^2 + 2(2-3r)x + 5r\right\}\dot{x} = -r\left(x^3 + 2x^2 + 4x + \frac{27}{5} - I\right).$$
(10)

Figure 1 shows the potential and active areas of the Hindmarsh-Rose model for I=0. The stable equilibrium



Figure 1: Potential and active areas of the Hindmarsh-Rose model. U3, dU3, b1, b2, B1 and B2 denote $500U3_{HR}(x, I = 0) - 15, 10^5 dU3_{HR}(x, I = 0)/dx, b_{1_{HR}}(x), b_{2_{HR}}(x), B_{1_{HR}}(x)$, and $B_{2_{HR}}(x) = b_{0_{HR}}(x)B_{1_{HR}}(x)$, respectively.

point is without active areas. It goes into the active areas with increasing external current I. The Morris-Lecar system[7] and the Hodgkin-Huxley system[4] are also able to be transformed into the one-variable equation with appropriate approximations, and hence, we are able to obtain potentials and active areas for them.

3.2. Burst ID model

3.2.1. Equations

Many burst models have been presented and analyzed, the Burst ID model is the extended version of Inverse function Delayed (ID) model[6] which is the slight modification of the BVP model. Let us make the ID model burst to add the third variable z as simple as possible[1],

$$\tau_x \dot{x} = u + z - g(x), \tag{11}$$

$$\tau_z \dot{z} = z_{\rm ex}(x) - z + \theta, \qquad (12)$$

$$\tau_u \dot{u} = W x - u, \tag{13}$$

where the external input θ is constant and $\tau_u \gg \tau_z \ge \tau_x$ is assumed. Eqs. (11) and (12) can be transformed into the equation

$$\ddot{x} + \eta_{BID}(x)\dot{x} = -\frac{\partial U2_{BID}(x,u)}{\partial x},$$
(14)

where

$$\eta_{\scriptscriptstyle BID}(x) = \frac{1}{\tau_x} \frac{dg(x)}{dx} + \frac{1}{\tau_z},\tag{15}$$

$$\frac{\partial U2_{_{BID}}}{\partial x} = \frac{g(x) - \frac{\tau_z}{\tau_u} W x - z_{\infty}(x) - \frac{\tau_u - \tau_z}{\tau_u} u - \theta}{\tau_x \tau_z}.$$
 (16)

 $\eta_{BID}(x)$ in Eq. (14) is a nonlinear function which has negative parts depending on g(x). Therefore, Eq. (14) shows oscillatory outputs even if u is constant. This oscillation whose basic angular frequency is related to $1/\sqrt{\tau_x \tau_z}$ from

Eq. (14) is fast one because of $\tau_u >> \tau_z \ge \tau_x$, and hence $\eta_{\scriptscriptstyle BID}(x)$ relates to the fast oscillation. Since *u* is a slow variable, we might regard it as a parameter in $U2_{\scriptscriptstyle BID}(x, u)$. Then Eq. (14) represents a motion on the potential $U2_{\scriptscriptstyle BID}(x, u)$. *u* follows *x* slowly according to Eq. (13), and hence, $U2_{\scriptscriptstyle BID}(x, u(t))$ changes with time due to the u(t)x term. It is expected in analogy with the ID (BVP) model that the change of the potential may cause the second oscillation which is a slow one because of $\tau_u >> \tau_z \ge \tau_x$. The basic angular frequency of the slow oscillation is related to $1/\sqrt{\tau_x \tau_u}$. A new negative resistance different from $\eta_{\scriptscriptstyle BID}(x)$ is expected for the second oscillation.

Eqs. (13) and (14) can be transformed into the one-variable equation

$$\begin{aligned} \ddot{x} + \left\{ \eta_{BID}(x) + \frac{1}{\tau_u} \right\} \ddot{x} + \left[\frac{1}{\tau_x \tau_z} \left\{ \frac{dg(x)}{dx} - \frac{dz_{\infty}(x)}{dx} - \frac{\tau_z}{dx} \right\} \right] \\ -\frac{\tau_z}{\tau_u} W + \frac{1}{\tau_u} \eta_{BID}(x) + \frac{d\eta_{BID}(x)}{dx} \dot{x} \\ \end{bmatrix} \dot{x} = -\frac{\partial U \mathcal{B}_{BID}(x)}{\partial x}, \quad (17) \end{aligned}$$

where

$$\frac{\partial U3_{_{BID}}(x)}{\partial x} = \frac{g(x) - z_{\infty}(x) - Wx - \theta}{\tau_x \tau_z \tau_u}.$$
 (18)

The third term of Eq. (17) is related to the new negative resistance. Eq. (17) corresponds to Eq. (1) with n = 3.

The active areas should localize on the potential to avoid the divergence of the output *x*. It means $\eta_{BID}(x)$ should have a positive curvature. For simplicity, we take the lowest degree for $\eta_{BID}(x)$, accordingly, the function is

$$\gamma_{\scriptscriptstyle BID}(x) = 3\left\{ (x - \alpha)^2 - \beta \right\},\tag{19}$$

where the central position and the width of the negative part of $\eta_{BID}(x)$ are $x = \alpha$ and $2\sqrt{\beta}$, respectively. Therefore, Eqs. (15) and (19) give

$$g(x) = \tau_x \left\{ x^3 - 3\alpha x^2 + \left(3\alpha^2 - 3\beta - \frac{1}{\tau_z} \right) x \right\}.$$
 (20)

In order to discuss the characteristics of the model concerning about the position of active areas on the potential, it is appropriate to make $U3_{BID}(x)$ independent of g(x). Therefore, we choose,

$$z_{\infty}(x) = g(x) - x^3 + \gamma x - \delta W x.$$
⁽²¹⁾

3.2.2. Active areas

The active area $X_{BID}[b2<0]$ of the Burst ID model is

$$\left[\alpha - \sqrt{\beta - \frac{1}{3\tau_u}}, \alpha + \sqrt{\beta - \frac{1}{3\tau_u}}\right],\tag{22}$$

where $\beta > 1/3\tau_u$. The active area causes the fast oscillation, and is nearly equal to the negative part of $\eta_{BID}(x)$.

If $\tau_z/\tau_u = \delta \sim 0$ and $\gamma > 3\delta\alpha^2/(1+\delta) - 3\delta\beta$, we have

$$X_{BID[b1<0]} = \left[-\sqrt{\frac{\gamma}{3}}, \sqrt{\frac{\gamma}{3}}\right]$$
(23)



Figure 2: Time series of the output x(t) for the Burst ID model with W = -0.35, $\alpha = 0.2$, $\beta = 0.5(a)$, $\beta = 0.05(b)$, and $\gamma = 0.5$. (a) and (b) correspond to FB and SB in Fig. 2, respectively.

which does not depend on α and β . $X_{BID}[b1<0]$ represents the new negative resistance which causes the slow oscillation.

The third active area $X_{BID}[B1<0]$ is obtained from

$$B_{1_{BID}}(x) = b_{2_{BID}}(x)b_{1_{BID}}\left(x, \frac{dx}{dt} = 0\right) - b_{0_{BID}}(x) < 0.$$
(24)

The slow oscillation will occur, if both of the equilibrium points are within $X_{BID[b1<0]}$. If $\delta \sim 0$, it leads $-W < \gamma < -3W/2$ which agrees with simulations.

The Burst ID model satisfies the necessary condition for bursting [2], because of the possibility of two oscillations slow and fast which relate to the active areas $X_{BID}[b1<0]$ and $X_{BID}[b2<0]$, respectively. However, it does not always show bursting. The characteristics of the model depend on the positioning relation between the active areas and the equilibrium points with the positive potential curvature as well as the shape of the potential.

Figure 2 shows the time series of the output x(t) for the Burst ID model with W = -0.35, $\alpha = 0.2$, $\beta = 0.5$, and $\gamma = 0.5$. We can obtain the phase diagram on the $\alpha - \beta$ plane where we can see the various types of bursting phenomena and firing modes, for example, the bursting with and without the spike undershoot. We can also obtain the number of spikes per burst as a function of α and β [8]. Therefore, the set of theoretical and numerical results for the phase diagram of the Burst ID model appears valuable as the basis for research on the coding of information by neuron systems.

4. Conclusions

In this paper we discussed the universality of the dynamic characteristics of several neuron models by using the concept of a potential function with active areas which were directly derived from the model equations. We are able to discuss the stability of the models in relation to the shape of the potentials and the disposition of the active areas. The active areas relate with the stability condition obtained from the Hurwitz's theorem. The disposition of the active areas on the potential is of importance to display various firing modes including bursting. In order to show the characteristics clearly, we introduced a simple model (Burst ID model) of the Hodgkin-Huxley type. The model displays a variety of oscillatory behavior including the various types of bursting and spiking which are obtained through the numerical simulations. The different dispositions between more than two active areas are required in addition to two different frequencies for the genesis of bursting oscillations. They are also required to show the Class I neural excitability as shown in the simulation of the model. The result as the number of spikes per burst depends on the system parameters α and β may be relevant to the block structured dynamics[9] and hence the neural code.

If outputs of the other units in a artificial neural network are applied as the external input for the unit, we may solve the combinatorial optimization problems according to Hopfield. If we can set active areas on every local minimum excluding global minima, the network is able to converge on the global minimum only. The global minima are ordinarily set at the vertices of the output space, and hence local minima are expected to be inside of the space. Therefore, we are able to obtain the result for solving combinatorial optimization problem to set active areas on the space excluding vertices[6] by using the presented technique.

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