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Dynamic Characteristics of Neuron Models and Active Areas in Potential Functions

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Abstract

We present a simple neuron model that shows a rich property in spite of the simple structure derived from a simplification of the Hindmarsh-Rose, the Morris-Lecar, and the Hodgkin-Huxley models. 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 is explained in connection with the disposition of the active areas on the potential, and hence we are able to discuss the global dynamic behaviors and the common properties among these realistic models.

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1. Introduction

There have been many researches of various neuron models that typically take the form of ordinary nonlinear differential equations of several dimensions. Nonlinear systems are usually able to display different dynamic behaviors depending on system parameters and an external input. The pattern of neuronal spiking is of great importance because it is believed that it codifies the information transmitted

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by neurons. These dynamics have been thoroughly investigated in each individual model based on the bifurcation theory, where we can discuss the characteristics around a critical point and the perturbation in the vicinity of equilibrium points. However, many important aspects of the situation are poorly understood and lack the satisfying universality of the structural stability discussion and the global dynamic behavior of the models.

2. Burst ID model

We have proposed a concept of potential with active areas to discuss a global landscape for dynamics of various models [1], [2]. For example, let us consider the following Hodgkin-Huxley type equations with three variables,

$$\tau_x dx/dt = u + z - g(x), \quad (1)$$

$$\tau_z dz/dt = z_\infty(x) - z + \theta, \quad (2)$$

$$\tau_u du/dt = u_\infty(x) - u, \quad (3)$$

where τ_x , τ_z , τ_u , and θ are time constants of x , z , u , and an external input, respectively. We can rewrite Eq. (1) in the following form,

$$dx/dt = -\partial U_1(x, z, u) / \partial x, \quad (4)$$

where $\partial U_1 / \partial x = \tau_x^{-1} (g(x) - z - u)$. $U_1(x, z, u)$ can be read as a potential function for variable x ; however, $U_1(x, z, u)$ varies with time because of $z = z(t)$ and $u = u(t)$. Equations (1), (2), and (3) can be transformed into the following two-variable (x, u) system,

$$d^2x/dt^2 + \eta(x) dx/dt = -\partial U_2(x, u, \theta) / \partial x, \quad \tau_u du/dt = u_\infty(x) - u, \quad \eta(x) = g'(x) / \tau_x + 1 / \tau_z, \quad (5)$$

$$\partial U_2(x, u, \theta) / \partial x = (1 / \tau_x \tau_z) \{ g(x) - z_\infty(x) - u_\infty(x) \tau_z / \tau_u - \theta - (1 - \tau_z / \tau_u) u \}, \quad (6)$$

where $\eta(x)$ is a damping factor, $g'(x) = \partial g(x) / \partial x$, and $U_2(x, u, \theta)$ can be read as a potential function for variable x , however $U_2(x, u, \theta)$ varies with time because of $u = u(t)$. Equations (1), (2), and (3) can be also transformed into the following one-variable (x) system,

$$d^3x/dt^3 + b_2(x) d^2x/dt^2 + b_1(dx/dt, x) dx/dt = -\partial U_3(x, \theta) / \partial x, \quad (7)$$

$$b_2(x) = (1 / \tau_x) \{ g'(x) + \delta \} = \eta(x) + 1 / \tau_u, \quad \delta = \tau_x / \tau_z + \tau_x / \tau_u, \quad (8)$$

$$\partial U_3(x, \theta) / \partial x = (1 / \tau_x \tau_z \tau_u) \{ g(x) - z_\infty(x) - u_\infty(x) - \theta \}, \quad (9)$$

$$b_1(dx/dt, x) = (1 / \tau_x) g''(x) dx/dt + (1 / \tau_x) [\{ g'(x) - z'_\infty(x) \} / \tau_z + \{ g'(x) - u'_\infty(x) \} / \tau_u + \tau_x / \tau_z \tau_u], \quad (10)$$

$$b_0(x) \equiv \partial^2 U_3(x, \theta) / \partial x^2 \quad (11)$$

$$= \{ g'(x) - z'_\infty(x) - u'_\infty(x) \} / \tau_x \tau_z \tau_u, \quad (12)$$

$$\partial U_2(x, u, \theta) / \partial x = \tau_u \partial U_3(x, \theta) / \partial x + (1 - \tau_z / \tau_u) \{ u_\infty(x) - u \} / \tau_x \tau_z, \quad (13)$$

where $b_0(x)$ is the curvature of the potential $U_3(x, \theta)$ at an equilibrium point $x = x_0$, which is stable when $b_2(x_0) > 0$, $b_1(dx/dt = 0, x_0) > 0$, $b_0(x_0) > 0$, and $B_1(x_0) = b_2(x_0) b_1(dx/dt = 0, x_0) - b_0(x_0) > 0$ according to Hurwitz's theorem. We can define three active areas b_2 -active area, b_1 -active area, and B_1 -active area where $b_2(x) < 0$, $b_1(dx/dt = 0, x) < 0$, and $B_1(x) < 0$, respectively. We can discuss the global dynamics of neuron models in terms of the shape of the potential and the disposition of active areas in the potential. For simplicity, let us assume the potential $U_3(x, \theta)$ has the following form,

$$U_3(x, \theta) = (x^4 - 2\gamma x^2 - \theta x) / \tau_x \tau_z \tau_u, \tag{14}$$

$$\partial U_3(x, \theta) / \partial x = \{4x(x^2 - \gamma) - \theta\} / \tau_x \tau_z \tau_u, \quad \partial^2 U_3(x, \theta) / \partial x^2 = b_0(x) = (12x^2 - 4) / \tau_x \tau_z \tau_u, \tag{15}$$

$$\text{and hence, } \partial U_2(x, u, \theta) / \partial x = (4x^3 - 4\gamma x - \theta) / \tau_x \tau_z - (1 - \tau_z / \tau_u) \{u_\infty(x) - u\} / \tau_x \tau_z, \tag{16}$$

where the potential $U_3(x, \theta)$ has a double or single well shape depending on the sign of γ , and hence there are three equilibrium points $x = 0$ and $x = \pm \sqrt{\gamma}$ when $\gamma > 0$ and $\theta = 0$.

To have control of a center and a width of an active area independently each other, let $b_2(x)$ and $b_1(dx/dt = 0, x)$ have the following forms,

$$b_2(x) = \{(x - c_2)^2 - \beta_2\} / \tau_x, \quad b_1(dx/dt = 0, x) = \{(x - c_1)^2 - \beta_1\} / \tau_x, \quad B_1(x) = b_2(x)b_1(x) - b_0(x). \tag{17}$$

The center and width of b_2 -active area are c_2 and $2\sqrt{\beta_2}$, respectively, and those of b_1 -active area are c_1 and $2\sqrt{\beta_1}$, respectively. Thus, we obtain the following equations,

$$g'(x) = (x - c_2)^2 - \alpha, \quad \alpha = \beta_2 + \tau_x(1/\tau_z + 1/\tau_u), \quad g(x) = x^3/3 - c_2x^2 + (c_2^2 - \alpha)x, \tag{18}$$

$$z'_\infty(x) = -\tau_x \tau_u [b_2(x) - \tau_z b_1(x) + \tau_z^2 b_0(x) - 1/\tau_z] / (\tau_z - \tau_u), \tag{19}$$

$$u'_\infty(x) = \tau_x \tau_z [b_2(x) - \tau_u b_1(x) + \tau_u^2 b_0(x) - 1/\tau_u] / (\tau_z - \tau_u), \tag{20}$$

$$z_\infty(x) = \tau_z \tau_u [\{4/\tau_u + (1 - \tau_z)/3\tau_z\}x^3 + (c_1 - c_2/\tau_z)x^2 - \{4\gamma/\tau_u - (c_2^2 - \beta_2)/\tau_z + c_1^2 - \beta_1 + \tau_x/\tau_z^2\}x] / (\tau_u - \tau_z), \tag{21}$$

$$u_\infty(x) = \tau_z \tau_u [(4/\tau_z + (1 - \tau_u)/3\tau_u)x^3 + (c_1 - c_2/\tau_u)x^2 - \{4\gamma/\tau_z - (c_2^2 - \beta_2)/\tau_u + c_1^2 - \beta_1 + \tau_x/\tau_u^2\}x] / (\tau_z - \tau_u) \tag{22}$$

$$U_2(x, u, \theta) = [\{2\tau_u/\tau_z + (1 - \tau_u/12)\}x^4 + (c_1\tau_u - c_2)x^3/3 - \{8\gamma\tau_u/\tau_z - (c_2^2 - \beta_2) + \tau_u(c_1^2 - \beta_1) + \tau_x/\tau_u\}x^2/2 + \tau_u\{(1 - \tau_z/\tau_u)u - \theta\}x/\tau_z] / \tau_x \tau_u, \tag{23}$$

where we take integral constants to be zero.

3. Result and discussion

The model shows burst oscillations in a wide range of parameter values, for example, $c_2 = 0.3$, $\alpha = 2.2$ ($\beta_2 = 1.195$), $c_1 = 0$, $\beta_1 = 0.5$, $\gamma = 0.5$, $\tau_x = \tau_z = 2.0$, $\tau_u = 200$, and $\theta = 0$ with the initial condition $x(t = 0) = 0.01$ and $u(t = 0) = z(t = 0) = 0$. On the other hand, it also shows chaotic oscillations for some parameter values, for example, $c_2 = 0.55$, $\alpha = 0.5825$ ($\beta_2 = 0.02$), $c_1 = -0.45$, $\beta_1 = 0.08$, $\gamma = 0.56$, $\tau_x = 0.5$, $\tau_z = 1.0$, $\tau_u = 8.0$, and $\theta = 0$ with the same initial condition.

Figure 1(a) shows the burst output $x(t)$ on the contour map of time series of the potential function Eq. (23) with the active area where $\eta(x) < 0$. Figures 1(b) and 1(c) show bird's eye views of the burst oscillation shown in Fig. 1(a) and the chaotic oscillation on the potential $U_3(x, \theta = 0)$ with the active areas. In Fig. 1(a) black line, red line, blue line, and gray area denote the output, trajectories of the equilibria with a positive curvature, a trajectory of the equilibria with a negative curvature, and the active area, respectively. In Figs. 1(b) and 1(c), red lines, purple and blue areas denote the outputs, the b_2 -active areas, and the b_1 -active areas, respectively.

The characteristics of the b_1 -active area is explained as an area where a quasi-particle obtains an oscillatory component through a time dependent potential $U_2(x, u)$ not to receive only one-way acceleration. The b_1 -active area connects the slow dynamics of the burst oscillation because of the large

value of τ_u . On the other hand, the b_2 -active area connects the fast dynamics of the burst oscillation. The dynamic characteristics of neuron models including chaotic behaviors are connected with a shape of a potential and a disposition of active areas.

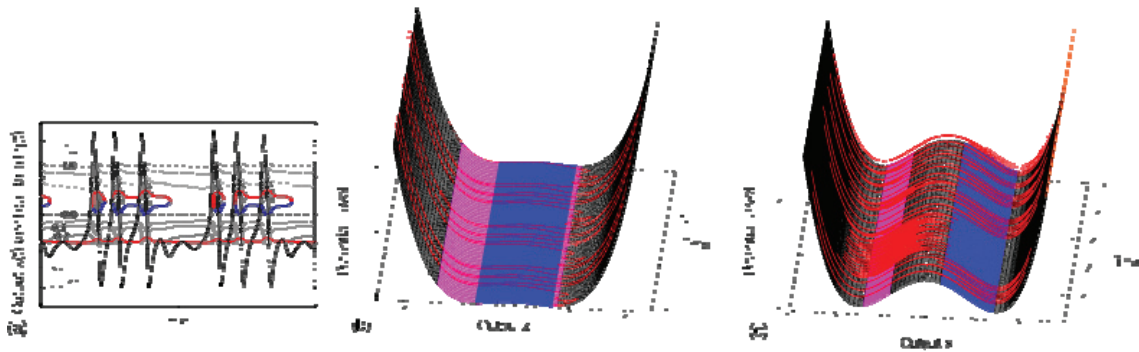


Fig. 1. Bursts (a), (b) and a chaotic oscillation (c) bound by the potential with the active areas

If we assume the time constants to be $\tau_u \gg \tau_z \gg \tau_x \doteq 1$, we can expect the dynamic behavior of the Burst ID model with $\theta = 0$ as follows in outline. For a moment, we may read z and u to be constant in the potential $U_1(x, z, u)$ because of the above condition among the time constants. According to Eqs. (4) and (18), $\partial U_1(x, z=0, u=0) / \partial x$ is an N-shaped function and has two equilibrium points which are $x_{2\pm} = C_2 \pm \sqrt{\beta_2 + \delta} \doteq C_2 \pm \sqrt{\beta_2}$ obtained from $\partial^2 U_1 / \partial x^2 = \tau_x^{-1} g'(x) = 0$, and hence the number of the roots of $\partial U_1 / \partial x = 0$ ($g(x) = z + u \doteq \text{const.}$) is one or two or three. The only root of $g(x) = z + u$ is stable, and the outside and central roots are stable and unstable, respectively, for the three roots that correspond to the two stable equilibrium points and the one unstable equilibrium point of the potential U_1 . For $z + u = 0$, for example, the solution sets are $x = 0$ and $x = 3C_2/2 \pm \sqrt{\{3(\beta_2 - C_2^2/4) + 3\delta\}}$. The solution sets for the two roots are $x_{2+} = C_2 + \sqrt{\beta_2 + \delta}$ and $x_{2T-} = C_2 - 2\sqrt{\beta_2 + \delta}$, or $x_{2-} = C_2 - \sqrt{\beta_2 + \delta}$ and $x_{2T+} = C_2 + 2\sqrt{\beta_2 + \delta}$.

In a gradient system, the motion is always toward a local minimum, accordingly, Eqs. (2) and (3) indicate that z and u are slowly toward $z_\infty(x)$ and $u_\infty(x)$, respectively, when the output x is at a stable equilibrium point obtained from $g(x) = z + u \doteq \text{const.}$ If $z_\infty(x) + u_\infty(x) < 0$ for $x \geq C_2 + \sqrt{\beta_2 + \delta}$, Eq. (1) indicates that the output x is toward $x_{2+} = C_2 + \sqrt{\beta_2 + \delta}$, and on the other hand, if $z_\infty(x) + u_\infty(x) > 0$ for $x \leq C_2 - \sqrt{\beta_2 + \delta}$, the output x is toward $x_{2-} = C_2 - \sqrt{\beta_2 + \delta}$. The output x consequently reaches to $x_{2\pm} = C_2 \pm \sqrt{\beta_2 + \delta}$ at last and successively switches toward $x_{2T\mp} = C_2 \mp 2\sqrt{\beta_2 + \delta}$ as the one of two stable equilibrium points of the potential U_1 disappears. We can obtain the restriction among C_2 , β_2 , and γ from the above discussion; however, it seems to be a weak restriction, because the above discussion just outlines the dynamics of the model. When $C_2 = 0$ and $\gamma = 0$, for example, we can obtain $z_\infty(x) + u_\infty(x) = -(11x^2/3 + \beta_2 + \delta)x = \mp 14 \{\sqrt{\beta_2 + \delta}\}^3 / 3$ from Eqs. (21) and (22) for $x = \pm\sqrt{\beta_2 + \delta}$, that is, $z_\infty(x) + u_\infty(x)$ is still negative at $x = +\sqrt{\beta_2 + \delta}$, it means that the output x decreases still more and switches toward $x_{2T-} = -2\sqrt{\beta_2 + \delta}$, after that the output x increases toward $x_{2-} = -\sqrt{\beta_2 + \delta}$ because of $z_\infty(x) + u_\infty(x) > 0$. $z_\infty(x) + u_\infty(x)$ is still positive at $x = -\sqrt{\beta_2 + \delta}$, it means that the output x increases still more and switches toward $x_{2T+} = +2\sqrt{\beta_2 + \delta}$, after that the output x decreases toward $x_{2-} = +\sqrt{\beta_2 + \delta}$ because of $z_\infty(x) + u_\infty(x) < 0$. This cycle creates the high frequency

oscillation of the burst, and the frequency mainly depends on τ_z because of $\tau_z \ll \tau_u$.

On the other hand, we can expect the low frequency oscillation of the burst by using Eqs. (6), (18), (21), and (22). $\partial U_2(x, u=0, \theta=0)/\partial x$ is also an N-shaped function and has two equilibrium points which are $x_{1\pm} = (C_1 - C_2 \tau_u^{-1}) / (1 - \tau_u^{-1}) \pm \sqrt{[(C_1 - C_2 \tau_u^{-1}) / (1 - \tau_u^{-1})]^2 + \{\beta_1 - C_1^2 - (\beta_2 - C_2^2) \tau_u^{-1} - \tau_x \tau_u^{-2}\} / (1 - \tau_u^{-1})} \doteq C_1 \pm \sqrt{\beta_1}$ obtained from $\partial^2 U_2 / \partial x^2 = 0$, and hence the number of the roots of $\partial U_2 / \partial x = 0$ ($\tau_x \tau_u \partial U_2(x, u=0, \theta=0) / \partial x = (1 - \tau_z / \tau_u) u \doteq \text{const.}$) is one or two or three.

The only root of $\tau_x \tau_u \partial U_2(x, u=0, \theta=0) / \partial x = (1 - \tau_z / \tau_u) u$ is stable, and the outside and central roots are stable and unstable, respectively, for the three roots that correspond to the two stable equilibrium points and the one unstable equilibrium point of the potential U_2 . The solution sets for the two roots are x_{1+} and $x_{1T-} = (C_1 - C_2 \tau_u^{-1}) / (1 - \tau_u^{-1}) - 2 \sqrt{[(C_1 - C_2 \tau_u^{-1}) / (1 - \tau_u^{-1})]^2 + \{\beta_1 - C_1^2 - (\beta_2 - C_2^2) \tau_u^{-1} - \tau_x \tau_u^{-2}\} / (1 - \tau_u^{-1})} \doteq C_1 - 2 \sqrt{\beta_1}$, or x_{1-} and $x_{1T+} = (C_1 - C_2 \tau_u^{-1}) / (1 - \tau_u^{-1}) + 2 \sqrt{[(C_1 - C_2 \tau_u^{-1}) / (1 - \tau_u^{-1})]^2 + \{\beta_1 - C_1^2 - (\beta_2 - C_2^2) \tau_u^{-1} - \tau_x \tau_u^{-2}\} / (1 - \tau_u^{-1})} \doteq C_1 + 2 \sqrt{\beta_1}$. Through the same process as that for the high frequency oscillation in the preceding discussion, the system creates the low frequency oscillation of the burst, and the low frequency mainly depends on τ_u because of Eqs. (5) and (6). In addition, we are able to explain active areas as an area where a quasi-particle obtains an oscillatory component through a time dependent potential not to receive only one-way acceleration [3], [4].

4. Conclusion

We have discussed the dynamic characteristics of a neuron model through a concept based on a potential with active areas. The obtained outputs are broadly classified as simple oscillations, spiking, bursting, and chaotic oscillations [4]. The bursting outputs are classified as with spike undershoot and without spike undershoot, and the burst without spike undershoot are classified as tapered and without tapered. Burst oscillations with undershoot occur depending on two active areas disposed in substantially overlapping each other on the potential. We showed the parameter dependence of these outputs and discussed the connection between these outputs and the potential with active areas. A potential hill plays a significant role for the chaotic behaviors shown in Fig. 1(c). We can observe similar potential hills in the other chaotic models, for example, the Lorenz model, the Chua circuit, and so on. A potential hill, however, is not always required to realize chaotic behaviors, because we can observe chaotic behaviors in a single well potential [4] where γ is 0. The global positive curvature of the potential ensures these oscillations not to diverge.

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