 Bursting characteristics of a neuron model based on a concept of potential with active areas

著者

doi: 10.1063/1.2908443
Bursting characteristics of a neuron model based on a concept of potential with active areas

Koji Nakajima and Shinya Suenaga
Laboratory for Brainware Systems/Laboratory for Nanoelectronics and Spintronics, Research Institute of Electrical Communication, Tohoku University, Sendai 980-8577, Japan

(Received 19 July 2007; accepted 25 March 2008; published online 22 May 2008)

We present various bursting wave forms that 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 active areas 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. © 2008 American Institute of Physics. [DOI: 10.1063/1.2908443]

There have been many researches of various neuron models that typically take the form of ordinary nonlinear differential equations of several dimensions. The neural networks comprising the interconnection of the neuron units are actively studied problems in the field of nonlinear dynamics and the brain research. It is of great importance to apply various neuron models to the networks that aim at intelligent information processing. One of important aspects of this situation is the lack of universal discussion over the dynamical behaviors of various neuron models. Hence, we reveal that each model has the potential function and the active areas on the potential. This common concept realizes the universal discussion of the dynamical behaviors, for example, bursting, spiking, and so on. A simple model of the Hodgkin–Huxley (HH) type is proposed in this paper as the typical system with a potential function and active areas, and it displays various types of bursting phenomena and the variety of firing modes by the shift of dispositions of the active areas on the potential. We are able to investigate the universal dynamics of the well-known neuron models based on the result obtained for the simple model.

I. 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 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 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 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.

The universality of the dynamic characteristics of these models, which has been discussed mainly through a canonical model, 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 that 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, 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.

The paper is organized as follows. We propose the technique to introduce a concept of potential with active areas for neuron models in Sec. II. We apply the technique to the burst inverse-function delayed (BID) model in Sec. III. The ID model is the extended version of the Bonhoeffer–van der Pol (BVP) model and we have used it to build a network for solving the combinatorial optimization problems and so on. The burst ID model is the extended version of the ID model. We first establish the potential and the active areas for the burst ID model as a test example. The burst ID model has well-defined parameters to control its firing modes in relation to the disposition of the active areas on the potential. Section III also comprises numerical simulations of the burst ID model and some related discussions. In Sec. IV we present the potentials and the active areas for the Hindmarsh–Rose (HR) model, the Morris–Lecar (ML) system, and the Hodgkin–Huxley system. Section V concludes this paper with a summary.

II. 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,

\[ \lambda^3 + b_2 \left( x_0, \frac{dx}{dt} = 0, \frac{d^2x}{dt^2} = 0 \right) \lambda + b_1 \left( x_0, \frac{dx}{dt} = 0, \frac{d^2x}{dt^2} = 0 \right) \lambda + b_0(x_0) = 0, \]

(2)

According to Hurwitz’s theorem the equilibrium point \( x_0 \) is stable, if

\[ b_0(x_0) = -\frac{\partial f(x_0, \theta)}{\partial x} = \frac{\partial^2 U(x_0, \theta)}{\partial x^2} > 0, \]

(3)

\[ b_1(x_0, 0) > 0, \]

(4)

\[ b_2(x_0, 0, 0) > 0, \]

(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. Equation (3) means that the curvature \( b_0 \) of the potential \( U3 \) is positive at \( x_0 \).

If \( b_1(x, 0) > 0 \), \( b_2(x, 0, 0) > 0 \), and \( B_1(x) > 0 \) for \(-\infty < x < \infty\), 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 \( x_1 < x_2 < \cdots < x_{m-1} < x_m \), it is expected that \( x \) always converges on one of the stable equilibrium points without divergence if the curvatures \( b_1(x_m) \) 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 \( x_m < x \) according to Eq. (1). This leads to the negative acceleration and the negative velocity in the long run without resulting in divergence. A similar discussion is available for \( x < x_1 \). 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 \( b_1(x, 0) \equiv 0 \) or \( b_2(x, 0, 0) \equiv 0 \) or \( B_1(x) \equiv 0 \) is satisfied. The disposition of the equilibrium point can be controlled by the external input \( \theta \) 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 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 \( n=2 \). In the BVP model \( b_1(x) \) in Eq. (1) is a function of \( x \) only, and the interval of \( x \) where \( b_1(x) < 0 \) is satisfied represents a negative damping area where energy is injected into the system.
If the global curvature of the potential is positive, each one of those active areas, i.e., $X_{[b1<0]}$, $X_{[b2<0]}$, 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 if 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.

III. BURST ID MODEL

A. Basic equations

The burst ID model is the extended version of inverse function delayed (ID) model, which is the slight modification of the BVP model. In order to compare the BVP model with the conventional network equations, let us rewrite it as

$$\tau_2 \frac{dx}{dt} = -(g(x) - u),$$

(7)

$$\tau_u \frac{du}{dt} = -(u - WX - \theta),$$

(8)

where $x$, $u$, $W$, $\theta (= \sum_j W_j x_j + I_{eq})$, and $W_j$ are the output of the unit, the internal state, the self-connection weight, the external input, and the connection weight from the unit $j$, respectively. We investigated the performance of combinatorial optimization problems with the network constituted of the ID model, which was represented by Eqs. (7) and (8).\textsuperscript{5} The conventional network model has no output delay; that is, $u=g(x)$, which is the inverse function of the conventional output function. However, Eq. (7) includes the delay ($\tau_u \gg \tau_x$), and $g(x)=x^3/3 - ex$ as the BVP model. Since $u$ is a slow variable, Eq. (7) represents a resistive motion on the potential $U_{1D}(x,u)=\int g(x-u)dx=\int g(x)dx-ux$ if we can regard $u$ as a constant parameter.

Equations (7) and (8) can be transformed into the one-variable equation

$$\frac{d^2x}{dt^2} + \eta_{1D}(x) \frac{dx}{dt} = -\frac{\partial U_{2ID}(x)}{\partial x},$$

(9)

where

$$\eta_{1D}(x) = \frac{1}{\tau_x} \frac{dg(x)}{dx} + \frac{1}{\tau_u},$$

(10)

$$\frac{\partial U_{2ID}(x)}{\partial x} = \frac{1}{\tau_x \tau_u} \left\{ g(x) - WX - \theta \right\}.$$  

(11)

We can obtain the same Eqs. (9)–(11), even if Eq. (7) has an additional constant term that represents an input variable as the BVP model. Equation (9) corresponds to Eq. (1) with $n=2$, and represents a motion on the potential $U_{2ID}(x)$. $\eta_{1D}(x)$ is a nonlinear viscosity coefficient, and it has a negative part in the BVP model resulting in oscillations. The angular frequency of the oscillation is related to $1/\sqrt{\tau_x \tau_u}$ from Eq. (9). It is expected that since $u$ follows $x$ slowly according to Eq. (8), the oscillation changes $U_{1ID}(x,u)$ with time through the slow variable $u(t)$.

According to the discussion in the previous section and Eqs. (9)–(11), we can obtain

$$b_{0ID}(x) = \frac{1}{\tau_1} \left\{ \frac{\partial g(x)}{\partial x} - W \right\} = \frac{\partial^2 U_{2ID}(x)}{\partial x^2},$$

(12)

$$b_{1ID}(x) = \eta_{1D}(x) = \frac{1}{\tau_u} \left\{ \frac{\partial g(x)}{\partial x} + \frac{1}{\tau_u} \right\},$$

(13)

therefore, $b_{1ID}(x)$ is equal to $\eta_{1D}$, which has a negative part corresponding to a negative resistance. When $\theta$ is constant, Eq. (9) does not show any bursting, which was discussed by using the canonical model.\textsuperscript{2} Many burst models have been presented and analyzed; however, the general relation between bursting dynamics and particle motions on a potential with active areas has not been discussed yet. Let us make the ID model burst to add the third variable $z$ as simple as possible.\textsuperscript{1}

$$\tau_x \frac{dz}{dt} = z - g(x),$$

(14)

$$\tau_u \frac{du}{dt} = WX - u,$$

(16)

where the external input $\theta$ is constant and $\tau_u \gg \tau_x \gg \tau_z$ is assumed. Equations (14) and (15) can be transformed into the equation

$$\frac{d^2x}{dt^2} + \eta_{1BD}(x) \frac{dx}{dt} = -\frac{\partial U_{2ID}(x,u)}{\partial x},$$

(17)

where

$$\eta_{1BD}(x) = \frac{1}{\tau_x} \frac{dg(x)}{dx} + \frac{1}{\tau_z},$$

(18)

$$\frac{\partial U_{2BD}(x,u)}{\partial x} = \frac{1}{\tau_x \tau_z} \left\{ g(x) - \frac{WX - \theta}{\tau_u} - \frac{\tau_u - \tau_z}{\tau_u} u - \theta \right\}.$$  

(19)

$\eta_{1BD}(x)$ in Eq. (17) is a nonlinear function that has negative parts depending on $g(x)$. Therefore, Eq. (17) shows oscillatory outputs even if $u$ is constant. This oscillation whose basic angular frequency is related to $1/\sqrt{\tau_x \tau_u}$ from Eq. (17) is a fast one because of $\tau_u \gg \tau_x \gg \tau_z$, and hence, $\eta_{1BD}(x)$ relates to the fast oscillation. Since $u$ is a slow variable, we might regard it as a parameter in $U_{2BD}(x,u)$. Equation (17) then represents a motion on the potential $U_{2BD}(x,u)$, $u$ follows $x$ slowly according to Eq. (16), and hence, $U_{2BD}(x,u(t))$ 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 $\tau_u \gg \tau_x \gg \tau_z$. The basic angular frequency of
the slow oscillation is related to $1/\sqrt{\tau_I \tau_u}$. A new negative resistance different from $\eta_{\text{BID}}(x)$ is expected for the second oscillation.

Equations (16) and (17) can be transformed into the one-variable equation

$$\frac{d^2x}{dt^2} + \left\{ \eta_{\text{BID}}(x) + \frac{1}{\tau_u} \right\} \frac{d^2x}{dt^2} + \left[ \frac{1}{\tau_I \tau_u} \right] \left\{ \frac{dg(x)}{dx} - \frac{dz_0(x)}{dx} - \frac{\tau_I}{\tau_u} \frac{U_3(x)}{dx} \right\} + \frac{1}{\tau_u} \eta_{\text{BID}}(x) + \frac{dU_{3\text{BID}}(x)}{dx} \frac{dx}{dt} = -\frac{\partial U_{3\text{BID}}(x)}{\partial x},$$

where

$$\frac{\partial U_{3\text{BID}}(x)}{\partial x} = \frac{1}{\tau_I \tau_u} \left[ q(x) - z_0(x) - Wx - \theta \right].$$

The third term of Eq. (20) is related to the new negative resistance. Equation (20) corresponds to Eq. (1) with $n=3$.

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

$$\eta_{\text{BID}}(x) = 3\{(x - \alpha)^2 - \beta\},$$

where the central position and the width of the negative part of $\eta_{\text{BID}}(x)$ are $x=\alpha$ and $2\sqrt{\beta}$, respectively. Therefore, Eqs. (18) and (22) give

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

$U_{2\text{BID}}(x)$ is not independent of $\eta_{\text{BID}}(x)$ through $g(x)$. However, we can make $U_{2\text{BID}}(x,u)$ and $U_{3\text{BID}}(x)$ independent of $g(x)$, if we choose a suitable function as $z_0(x)$ by using Eq. (19). In order to discuss the characteristics of the model concerning about the position of active areas on the potential, it is appropriate to make $U_{3\text{BID}}(x)$ independent of $g(x)$. The curvature of the potential should be positive at $x \to \pm \infty$ to avoid the divergence of the output $x$. The BVP (ID) model has a double well potential $U_{2\text{BID}}$ if $e + W \neq 0$ because of Eq. (11). Taking it into consideration, we take the function $\partial U_{2\text{BID}}/\partial x \sim p(x) - 2\theta q(x)$, where $p(x)$ and $q(x)$ are odd functions, and the degree of $p(x)$ is higher than that of $q(x)$. Taking account of the lowest degree of $x$, for simplicity, we take the functions $p(x) = x^3$ and $q(x) = x$; accordingly,

$$z_0(x) = g(x) - x^3 + \gamma x - \delta Wx,$$

$$\frac{\partial U_{2\text{BID}}(x,u)}{\partial x} = \frac{1}{\tau_I \tau_u} \left\{ x^3 - \gamma x - (1 - \delta) u - \theta \right\},$$

$$\frac{\partial U_{3\text{BID}}(x)}{\partial x} = \frac{1}{\tau_I \tau_u} \left\{ x^3 - \left( \gamma + (1 - \delta) W \right) x - \theta \right\},$$

where $\delta = \tau_I / \tau_u$, and $U_{2\text{BID}}$ does not depend on $W$, but $U_{3\text{BID}}$ does. Accordingly, we obtain

$$\frac{d^2x}{dt^2} + b_{2\text{BID}}(x) \frac{d^2x}{dt^2} + b_{1\text{BID}}(x) \frac{dx}{dt} = -\frac{\partial U_{3\text{BID}}(x)}{\partial x},$$

where

$$b_{2\text{BID}}(x) = 3\{(x - \alpha)^2 - \beta\} + \frac{1}{\tau_u},$$

$$b_{1\text{BID}}(x) \left( \frac{dx}{dt} \right) = -\frac{1}{\tau_I \tau_u} \left\{ 3(1 + \delta)x^2 - 6\delta ax + 3\delta(a^2 - \beta - \gamma) \right\} + 6(x - \alpha) \left( \frac{dx}{dt} \right)^2.$$

When $U_{3\text{BID}}(x)$ has a double well, that is, $\gamma + W(1 - \delta) > 0$, the equilibrium points obtained from $U_{3\text{BID}}(x)$ with $\theta = 0$ are $x = 0$ and $x^* = \pm \sqrt{\gamma + W(1 - \delta)}$, which is symmetrical about $x = 0$. We discuss the behavior of external input $\theta \neq 0$ in the last of this section. Since $b_{0\text{BID}}(x) = \{3x^2 - \gamma - (1 - \delta) W / \tau_I \tau_u \}$, the point $x = 0$ is unstable because of $b_{0\text{BID}}(0) < 0$; however, $x^*$ have the positive $b_{0\text{BID}}(x^*)$. As $x \to \infty$, $f(x, \theta) = -\partial U_{3\text{BID}}(x) / \partial x < 0$, $b_{3\text{BID}}(x) > 0$, and $b_{1\text{BID}}(x, dx/ dt) > 0$ if $dx/ dt > 0$. Therefore, it is expected not to diverge according to the discussion in Sec. II.

### B. Active areas

The active area $X_{\text{BID}[b_2 < 0]}$, where $b_{2\text{BID}}(x) < 0$ is

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

where $\beta > 1 / 3 \tau_u$. It causes the fast oscillation, because $b_{2\text{BID}}(x)$ is nearly equal to $\eta_{\text{BID}}(x)$ for $\tau_u \gg 1$; however, we should obtain the active area from $b_{2\text{BID}}(x)$ not from $\eta_{\text{BID}}(x)$, according to Hurwitz’s theorem.

If $b_{1\text{BID}}(x, dx/ dt) = 0$, there is a negative part, the active area $X_{\text{BID}[b_1 > 0]}$ is

$$\left[ \frac{\delta}{1 + \delta} \alpha - \sqrt{\frac{1}{1 + \delta}}, \frac{\gamma + \delta \left( \beta - \frac{1}{1 + \delta} \right)}{3} \right],$$

where $\gamma > 3 \delta a^2 / (1 + \delta) - 3 \beta \delta$. If $\delta > 0$, we have

$$X_{\text{BID}[b_1 < 0]} = \left[ -\sqrt{\frac{\gamma}{3}}, \sqrt{\frac{\gamma}{3}} \right].$$

which does not depend on $\alpha$ and $\beta$, and is symmetrical about $x = 0$. $X_{\text{BID}[b_1 < 0]}$ represents the new negative resistance, which causes the slow oscillation. It is confirmed by using the following simulations. The third active area $X_{\text{BID}[b_1 < 0]}$ is obtained from

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

If one of $x_3^+$ is out of the active area, there is a possibility to stop at the point without an oscillation. Therefore, the slow oscillation will occur, if both of the equilibrium points $x_3^+$ are within $X_{\text{BID}[b_1 < 0]}$. It gives
If $\delta \sim 0$, Eq. (34) is $-W < \gamma < -3W/2$, which agrees with the following simulations.

When $\theta=0$ and $U_{3\text{BID}}(x)$ has a single well, that is, $\gamma + W(1-\delta) \leq 0$, the occurrence condition of the slow oscillation is

$$3\delta(\alpha^2 - \beta) < \gamma \leq -(1-\delta)W,$$

which becomes $0 < \gamma \leq -W$ if $\delta \sim 0$.

The burst ID model satisfies the necessary condition for bursting, because of the possibility of two oscillations (slow and fast), which relate to the active areas $X_{\text{BID}[b1<0]}$ and $X_{\text{BID}[b2<0]}$, respectively. However, it does not always show bursting. In order to obtain the phase diagram of the dynamical behaviors of the burst ID model on the $\alpha$- $\beta$ plane, where $\alpha, \beta \geq 0$, we take $\tau_e = \tau_s = 1$, and $\tau_u = 100$ for the simulation that is carried out by using Eqs. (14)–(16) and the Runge–Kutta where the increment of time is 0.01. The smallest increment of $\alpha$ or $\beta$ is 0.001 with plural arbitrary initial conditions for $x$, $z$, and $u$. 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 1 shows $U_{2\text{BID}}(x,u=0)$, $U_{3\text{BID}}(x)$, $b_{1\text{BID}}(x)$, $b_{2\text{BID}}(x)$, and $B_{1\text{BID}}(x)$, where $W=-0.35$, $\gamma=0.5$, $\alpha=0.2$, and $\beta=0.5$. The model reveals a bursting, which is shown in Fig. 5(a) for the $x$ component of the solution. The equilibrium points with the positive $b_0$ are $x_2^{+} (\approx \pm 0.71)$ on $U_{2\text{BID}}(x,u= \theta=0)$ and $x_3^{+} (\approx \pm 0.39)$ on $U_{3\text{BID}}(x)$. The active area $X_{\text{BID}[b2<0]} (\approx [0.5,0.9])$ includes $X_{\text{BID}[b1<0]} (\approx [-0.41,0.414])$ in Fig. 1. Besides these, there are also two active areas $X_{\text{BID}[b1<0]}$ and $X_{\text{BID}[b1<0]}^{+}$, where $B_{1\text{BID}}(x)$ is negative. Both $x_3^{+}$ are within both $X_{\text{BID}[b2<0]}$ and $X_{\text{BID}[b1<0]}^{+}$; however, $x_2^{+}$ is without $X_{\text{BID}[b2<0]}$; and both $x_2^{-}$ are without $X_{\text{BID}[b1<0]}$. Such asymmetry seems to cause the bursting.

Figure 2 shows the phase diagram on the $\alpha$- $\beta$ plane. It has roughly six phases which are the fast oscillation “FO,” the slow oscillation “SO,” the spiking “SP,” the fast oscillation dominated bursting “FB,” the slow-oscillation dominated bursting “SB,” and the resting only “RO.” The $x$ components of the solutions FO, SO, SP, FB, and SB are shown in Figs. 3(a), 3(b), 4(a), 5(a), and 5(b), respectively. The solutions FB and SB correspond to the bursting with and without the spike undershoot, respectively. “RO or SP” and “RO or SB” in Fig. 2 denote the coexistence of two states.
and either the resting state or the oscillatory state happens depending on initial conditions. The phase diagram contains various types of bursting and firing modes, which mean the different number of spikes per burst and different frequency oscillations in addition to the above mentioned time series [for example, Figs. 4(b) and 6].

C. Oscillation for α=0

The behavior of the model on the α-β plane is explained mainly by using the relation between the equilibrium points and the active areas. When α = 0, that is, the disposition of active areas is symmetrical, three kinds of oscillations which are characterized by basic frequencies can be observed, however, we cannot find any bursting. The time series of the output x(t) is symmetrical with respect to x = 0 as shown in Fig. 3.

Figure 7 shows the oscillation frequency as a function of β for α = 0, W = −0.35, γ = 0.5, and 0. γ = 0.5 is the same condition as Fig. 2. The model exhibits the slow oscillation for γ = 0.5 and β ≤ 0.45. When β is smaller than about 0.16, both the equilibrium points x_1^± are without X_{BID[β<0]} but within X_{BID[β>0]}. It gives an explanation of the slow oscillation. X_{BID[β>0]} increases with increasing β. The oscillation changes suddenly into the higher frequency at β = 0.46 with increasing β; however, with decreasing β it changes into the low frequency at β = 0.42. There is no such steep transition for γ = 0, where the equilibrium point is x = 0, because X_{BID[β<0]} = 0 and there is no slow oscillation when γ = 0. The frequency decreases with decreasing β; however, it is not zero even for β = γ = 0, which means X_{BID[β<0]} = X_{BID[β>0]} = 0. The oscillation is explained as the equilibrium point is within X_{BID[β>0]} ≈ [−0.14, 0.14]. It is a numerical confirmation to be able to regard X_{BID[β>0]} as an active area.

Figure 8(a) shows the oscillation frequency as a function of W for α = β = 0 and γ = 0 and 0.5. X_{BID[β>0]} = [−x_a, x_a] increases with increasing −W for α = β = γ = 0, because we can obtain

\[ x_a^2 = \frac{1}{6} \left\{ \sqrt{\left(\frac{\delta}{\tau_a + \tau_u}\right)^2 - 4 \frac{1 - \delta}{\tau_a + \tau_u} W - \frac{\delta}{\tau_a + \tau_u}} \right\} \]  

by using Eq. (33). The frequency for γ = 0 is medium; namely, it is larger than the slow-oscillation frequency caused by X_{BID[β>0]}, but smaller than the fast-oscillation frequency caused by X_{BID[β<0]}. When γ = 0.5 in Fig. 8(a), x_a^2 coincide with the edges of X_{BID[β>0]} at the starting point of the oscillation on the W axis. However, the frequency is not medium but slow; that is, the oscillation is controlled by X_{BID[β>0]}, which is almost equal to X_{BID[β<0]} but slightly narrow.

Figure 8(b) shows the frequency as a function of γ for α = β = 0, and W = −0.35 and −1.0. The oscillation changes the frequency from the medium frequency to the slow frequency with increasing γ because of enlargement of X_{BID[β<0]}. When γ > −(3(1−δ^2)W)/(2−3δ), the oscillation

![Fig. 5. Time series of the output x(t) for the burst ID model with W = −0.35, α = 1.0, β = 0.22 (a), β = 0.12 (b), and γ = 0.5.](image)

![Fig. 6. Time series of the output x(t) for the burst ID model with W = −0.35, α = 1.0, β = 0.22 (a), β = 0.12 (b), and γ = 0.5.](image)

![Fig. 7. Frequency as a function of β for W = −0.35, α = 0, and γ = 0 and 0.5.](image)

![Fig. 8. (a) Frequency as a function of −W for α = 0, β = 0, and γ = 0 and 0.5. (b) Frequency as a function of γ for α = 0, β = 0, and W = −0.35 and −1.0.](image)
stops, because $x^+_3$ are out of both the active areas $X_{BID[b1<0]}$ and $X_{BID[b1<0]}$ as shown in Eqs. (34) and (33).

If there is only one active area, the oscillation frequency is determined by the characteristics of the active area; however, the frequency depends on the interrelation among active areas in case of the coexistence of plural active areas as shown in the above numerical results.

D. Oscillation for $\alpha \neq 0$

In order to explain the boundaries of the phase diagram in Fig. 2, we inquire into the lines that show the coincidence of the equilibrium point $x^+_3$ and the edges of the active areas on the $\alpha-\beta$ plane where both $\alpha$ and $\beta$ are positive. The equilibrium point $x^+_3$ is always unstable, because $x^+_3$ is within $X_{BID[b1<0]}$ regardless of $\alpha$ and $\beta$ on the plane, and also within $X_{BID[b2<0]}$ in the area where $\beta > \alpha^2 - 2\alpha \sqrt{\gamma + (1 - \delta)W} + \gamma + (1 - \delta)W + 1/3 \tau_a$, which is almost all area of the plane because of $\alpha > 0$. Accordingly, the behavior of the model on this $\alpha-\beta$ plane depends mainly on the relation between $x^+_3$ and the active areas.

$x^+_3$ is within $X_{BID[b2<0]}$ above the line (L1 in Fig. 2),

$$\beta = \alpha^2 + 2\alpha \sqrt{\gamma + (1 - \delta)W} + \gamma + (1 - \delta)W + \frac{1}{3 \tau_a}, \tag{37}$$

it is within $X_{BID[b1<0]}$ above the line (L2 in Fig. 2),

$$\beta = \alpha^2 + 2\alpha \sqrt{\gamma + (1 - \delta)W} + \frac{2 + 3 \delta}{3 \delta} \gamma + \left(\frac{1}{\delta} - 1\right)W, \tag{38}$$

and it is within $X_{BID[b1<0]}$ above the line (L3 in Fig. 2),

$$\beta = \alpha^2 + 2\alpha \sqrt{\gamma + (1 - \delta)W} + \left(\frac{1}{\delta} - \frac{1}{2 \tau_a \delta}\right) \gamma + \left(\frac{1}{2 \tau_a \delta} + \frac{1}{6 \tau_a}\right) (1 - \delta)W + \frac{1}{6 \tau_a} - \sqrt{A + B}, \tag{39}$$

where

$$A = \left(\frac{\gamma}{\tau_a \delta} + \frac{1}{\delta} - 1\right) W - \frac{1}{6 \tau_a},$$

$$B = \frac{2}{9 \tau_a \tau_c} \left(\gamma + (1 - \delta)W\right).$$

These lines L1, L2, and L3 are obtained by using Eqs. (30), (31), and (33), respectively. The bottom line on the $\alpha-\beta$ plane is Eq. (39), and hence, the model is able to be a resting state without any oscillation under Eq. (39). It agrees with numerical simulations shown in Fig. 2. The equilibrium point $x^+_3$ is within any active areas in the RO-or-SP and RO-or-SB regions of Fig. 2, however an oscillation occurs depending on the initial condition. The occurrence of the oscillatory state seems to be due to the second and third time-derivative terms in Eq. (27), and to be explained by the inertia and the existence of the active areas in the vicinity of $x^+_3$.

The dynamical behavior between L1 and L2 is considered to be controlled by $X_{BID[b1<0]}$, because $x^+_3$ is within $X_{BID[b1<0]}$ and the influence of $X_{BID[b1<0]}$ is small as shown in Fig. 8; however, there are two phases (SP and SB) as shown in Fig. 2. It may relate to the positions of $x^+_3$, which are always without $X_{BID[b1<0]}$. However, $x^+_3$ are within $X_{BID[b2<0]}$ above the line (L4 in Fig. 2),

$$\beta = \alpha^2 + 2\alpha \sqrt{\gamma + \gamma + \frac{1}{3 \tau_a}}, \tag{40}$$

The boundary between SP and SB qualitatively closes Eq. (40). The qualitative agreement seems to be due to the fact that $x^+_3$ are obtained on the assumption $\alpha=0$. The boundary between FB and SP agrees with Eq. (37), because the dynamical behavior above L1 is considered to be controlled by $X_{BID[b2<0]}$, which promotes the fast oscillation. The slight difference seems to be due to the fact that the active areas are obtained by using the linear stability theory where $b_{1BID}(x, dx/dt=0)$ is used.

Figure 9(a) shows the number ($N$) of spikes per burst, which is with spike undershoot (FB in Fig. 2), as a function of $\alpha$ for $\beta=0.5$, $\gamma=0.5$, and $W=-0.35$. When $N=1$, it corresponds to spiking (SP in Fig. 2) whose waveform is shown in Fig. 4(a). In SP region $x^+_3$ is without $X_{BID[b2<0]}$, but within $X_{BID[b1<0]}$ which promotes the slow oscillation. The waveform shown in Fig. 5(a) is the burst of $N=7$ with spike undershoot. (5+4) in Fig. 9 denotes the sequential appearance of the burst with five spikes and four spikes. Figure 9(b) shows the number of spikes per burst, which is without spike undershoot (SB in Fig. 2), as a function of $\beta$ for $\alpha=0.5$, $\gamma=0.5$, and $W=-0.35$. The waveforms shown in Figs. 4(b) and 5(b) are the bursts of $N=2$ and $N=11$ without spike undershoot, respectively. It can be seen from Fig. 9 that the number of spikes per burst is determined through the disposition of the active areas on the potential, because the disposition of the active areas depends on the system parameters $\alpha$ and $\beta$. The result shown in Fig. 9 may be relevant to the block structured dynamics,10,11 and hence, the neural code.
In order to investigate the behavior of the external input \( \theta \), we put \( \lambda_0 \) on the outside of the active areas for \( \theta = 0 \) by adjusting parameters. Figure 10 shows the frequency as a function of the external input \( \theta \) for (a): \( \alpha=0.2, \beta=0.6, \gamma=0.5 \), and \( W=-0.1 \); and (b): \( \alpha=0.2, \beta=0.6, \gamma=0.5, \) and \( W=-0.32 \). The model behaves like the Class 2 neuron in Fig. 10(a), where the fast oscillation is dominant because of the relatively large \( \beta=0.6 \), and the Class 1 neuron in Fig. 10(b), where the slow oscillation is dominant for small \( \theta = 0 \). The model behaves like the Class 2 neuron because of the small overlap of the two active areas with relatively large \( \alpha \). Figure 11 shows the three series of the outputs which correspond to the results shown in Fig. 10.

Figure 12, which corresponds to Fig. 10(b) shows \( U_{3BID}(x, \theta=0) \), \( U_{3BID}(x, \theta=0.1) \), \( dU_{3BID}(x, \theta=0)/dx \), \( dU_{3BID}(x, \theta=0.1)/dx \), \( B_{1BID}(x) \), \( B_{2BID}(x) \), and \( B_{1BID}(x) \) where \( W=-0.32, \alpha=0.6, \beta=0.2, \gamma=0.5, \) and \( \theta=0 \) and 0.1. The stable equilibrium point is without the active areas for \( \theta = 0 \), and it goes into the active areas with increasing \( \theta \).

### IV. THE OTHER MODELS

In order to investigate the general relation between the active areas and potential structures, we pick up a few typical models in this section.

![Figure 10](image1.png)

**FIG. 10.** Spiking frequency as a function of \( \theta \) for (a) \( W=-0.1, \alpha=0.2, \beta=0.6, \gamma=0.5 \), and \( \theta=0.1 \); and (b) \( W=-0.32, \alpha=0.2, \beta=0.2, \gamma=0.5 \).

![Figure 11](image2.png)

**FIG. 11.** Time series of the output \( x(t) \) for the burst ID model. (a): \( W=-0.1, \alpha=0.2, \beta=0.6, \gamma=0.5, \) and \( \theta=0.1 \), where the spiking frequency is shown in Fig. 10(a). (b) and (c): \( W=-0.32, \alpha=0.6, \beta=0.2, \gamma=0.5, \) and \( \theta=0.1 \) (b), and \( \theta=0.2 \) (c) where the spiking frequencies are shown in Fig. 10(b).

![Figure 12](image3.png)

**FIG. 12.** Potentials and active areas of the burst ID model whose dynamics are shown in Figs. 11(b) and 11(c). U30, U31, dU30, dU31, b1, b2, and B1 denote 8000U3BID(x, \( \theta=0 \)+4, 8000U3BID(x, \( \theta=0.1 \)+2.5, 1000U3BID(x, \( \theta=0 \))/dx, 1000U3BID(x, \( \theta=0.1 \))/dx, \( b_{3BID}(x) \), \( b_{2BID}(x) \), and \( B_{1BID}(x) \), respectively.

#### A. Hindmarsh–Rose model

The Hindmarsh–Rose equations define a recognized model for the bursting-spiking dynamics of the membrane potential \( x(t) \). The equations of the model written in dimensionless form reads

\[
\dot{x} = y + 3x^2 - x^3 - z + I, \\
\dot{y} = 1 - 5x^2 - y, \\
\dot{z} = -r(z - 4(y + \frac{8}{3}) - \frac{1}{3}z^2 - 27/5). 
\]

The equations can be transformed into the one-variable equation

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

Hence, we can obtain

\[
U_{3HR}(x) = r \left( \frac{x^4}{4} + 2\frac{x^3}{3} + 2x^2 + \left( \frac{27}{5} - I \right) \right), \\
b_{0HR}(x) = r(3x^2 + 4x + 4) = r \left( 3 \left( x + \frac{2}{3} \right)^2 + \frac{8}{3} \right), \\
b_{1HR}(x) = 3(1 + r)x^2 + 2(2 - 3r)x + 5r \\
= 3(1 + r) \left( x + \frac{2 - 3r}{3(1 + r)} \right)^2 + \frac{6r^2 + 27r - 4}{3(1 + r)}, \\
b_{2HR}(x) = 3(x - 1)^2 + r - 2, \\
B_{1HR}(x) = b_{1HR}(x) - b_{0HR}(x). 
\]

The burst ID model is equal to the Hindmarsh–Rose model, if we carry out the following replacements: \( g(x) = x^3 - 3x^2 \), \( z_\infty(x) = -5x^2 + 1, \), \( \tau_r = \tau_e = 1/r, \), \( x = x_{HR}, \) \( z = y_{HR}, \) \( u = -z_{HR} + 32/5, \) \( \alpha = -1, \) and \( \beta = 2/3 \). \( b_{0HR}(x) \) has no negative area for...
r > 0, \( b_{1_{HR}}(x) \) has a negative area if \( r < 0.143 \). The active area obtained from \( b_{1_{HR}}(x) \) controls the slow oscillation because of \( r \ll 1 \). \( b_{2_{HR}}(x) \) has a negative area if \( r < 2 \). The active area obtained from \( b_{2_{HR}}(x) \) controls the fast oscillation. The equilibrium points are obtained from \( dU_{3_{HR}}(x) / dx = 0 \).

Figure 13 shows \( U_{3_{HR}}(x, I = 0) \), \( dU_{3_{HR}}(x, I = 0) / dx \), \( dU_{3_{HR}}(x, I = 3.28) / dx \), \( b_{1_{HR}}(x) \), \( b_{2_{HR}}(x) \), and \( B_{1_{HR}}(x) \), where \( r = 0.0021 \). The potential \( U_{3_{HR}}(x) \) has a single well the stable equilibrium point of which is without the active areas for \( I = 0 \), and hence, we cannot observe any oscillation. The stable equilibrium point goes into the active areas with increasing \( I \) as shown in Fig. 13, and hence, we can observe a bursting, because the active areas are disposed asymmetrically. The corresponding dynamical solution of the \( x \) component for \( I = 3.28 \) can be seen in Fig. 1 of Ref. 12.

**B. Morris–Lecar system**

According to Terman,\(^{13}\) the equations of the Morris–Lecar system are given by

\[
\dot{v} = y - 0.5(v + 0.5) - 2w(v + 0.7) - m_w(v)(v - 1),
\]

\[
\dot{w} = 1.15(w_w(v) - w)\tau(v),
\]

\[
\dot{y} = \varepsilon(k - v),
\]

where

\[
w_w(v) = \frac{1}{2}
\left[
\frac{v - 0.1}{0.145}
\right],
\]

\[
m_w(v) = \frac{1}{2}
\left[
\frac{v + 0.01}{0.15}
\right],
\]

\[
\tau(v) = \cosh\left(\frac{v - 0.1}{0.29}\right).
\]

The equations can be transformed into the one-variable equation

\[
\dot{v} + \frac{2}{f(v, \dot{v})} \dot{v}^2 + \dot{v} \left[ 0.5 + m'_w(v)(v - 1) + m_w(v) + 1.15 \tau(v) + \frac{\dot{v}}{f(v, \dot{v})} \right] \left[ 1 + 2m'_w(v)(v - 1) + 2m_w(v) - 2.3' v(v + 0.7) - 2.3 \tau(v) \right]
\]

\[= \frac{1}{f(v, \dot{v})} (4.6w_w(v)\tau(v)(v + 0.7) - 2\varepsilon(k - v)) \]

\[+ \dot{v} \left[ m'_w(v)(v - 1) + 2m'_w(v) - \frac{2.3}{f(v, \dot{v})} (0.5 + m'_w(v)(v - 1) + m_w(v)) \right]
\]

\[\times \{ \tau'(v)(v + 0.7) + \tau(v) \} \]

\[+ \dot{v} \left[ e + 2.3(v + 0.7)w_w(v)\tau(v) + w_w(v)\tau'(v) \right] + 4.6w_w(v)\tau(v) + 1.15\tau(v)
\]

\[= \{ 0.5 + m'_w(v)(v - 1) + m_w(v) \} + \frac{2.3}{f(v, \dot{v})} \left[ 2.3w_w(v)\tau(v)(v + 0.7) - e(k - v) \right] \tau'(v)(v + 0.7) + \tau(v) \} = -1.15 \tau(v)e(v - k),
\]

(53)

where

\[
f(v, \dot{v}) = 2.3 \tau(v)(v + 0.7) - 2\dot{v}.
\]

We can obtain \( dU_{3_{ML}}(v) / dv \), \( b_{0_{ML}}(v) \), \( b_{1_{ML}}(v) \), \( b_{2_{ML}}(v) \), and \( B_{1_{ML}}(v) \) from Eq. (53) to require the linearity for the time derivative terms. The requirement is consistent with the characteristics equation obtained from the linear stability theory. \( U_{3_{ML}}(v) \) does not depend on \( w_w(v) \) and \( m_w(v) \). On the other hand \( b_{2_{ML}}(v) \) and \( b_{2_{ML}}(v) \) depend on both \( w_w(v) \) and \( m_w(v) \).

Figure 14 shows \( U_{3_{ML}}(v) \), \( dU_{3_{ML}}(v) / dv \), \( b_{1_{ML}}(v) \), \( b_{2_{ML}}(v) \), and \( B_{1_{ML}}(v) \), where \( \varepsilon = 0.004 \) and \( k = -0.22 \). The potential \( U_{3_{ML}}(v) \) has the single well like a wide basin, and the equilibrium point, which has a positive curvature, is within the active areas that are disposed asymmetrically. The corresponding dynamical solution of the \( x \) component that shows a bursting can be seen in Ref. 13.

**C. Hodgkin–Huxley system**

The equations of the Hodgkin–Huxley system\(^{14}\) read

\[
C\dot{V} = G(V, m, n, h) + I_{ext}
\]

\[= g_{Na}m^3h(V_{Na} - V) + g_kn^4(V_N - V) + g_L(V_L - V) + I_{ext},
\]

(54)
Unfortunately, it is hard to transform the equations into a single equation with one variable without any approximation. Hence, we take the nullcline approximation, where we use $\dot{v} = \dot{m} = \dot{n} = \dot{h} = 0$; namely, instead of Eq. (54) we use

$$C_v = m + n + h - g_H(v),$$

where

$$g_H(v) = m(v) + n(v) + h(v),$$

$$m(v) = \frac{g_K n_K(v)^4 (v - V_K)}{g_N a_H(v)(V_{Na} - v)} + \frac{g_L (v - V_L) - I_{ext}}{g_N a_H(v)(V_{Na} - v)}$$

and

$$n(v) = \frac{g_N a_H(v)^3 n_a(v)(v - V_Na)}{g_K (V_K - v)} + \frac{g_L (v - V_L) - I_{ext}}{g_K (V_K - v)},$$

$$h(v) = \frac{g_K n_K(v)^4 (v - V_K)}{g_N a_H(v)^3 (V_{Na} - v)} + \frac{g_L (v - V_L) - I_{ext}}{g_N a_H(v)^3 (V_{Na} - v)}.$$
\[ \frac{dU_{4HH}(v)}{dv} = \frac{g_H(v) - m_x(v) - n_x(v) - h_x(v)}{\tau_H}, \]

\[ b_{0HH}(v) = \frac{g_H'(v) - m_x'(v) - n_x'(v) - h_x'(v)}{\tau_H}, \]

\[ b_{1HH}(v) = \frac{1}{\tau_H} \left( g_H(v) \left( \frac{1}{\tau_m} + \frac{1}{\tau_n} + \frac{1}{\tau_h} \right) - \frac{m_x'(v)}{\tau_m} - \frac{n_x'(v)}{\tau_n} - \frac{h_x'(v)}{\tau_h} \right), \]

\[ b_{2HH}(v) = \frac{1}{\tau_H} \left( g_H(v) \left( \frac{1}{\tau_m} + \frac{1}{\tau_n} + \frac{1}{\tau_v} \right) - \frac{m_x'(v)}{\tau_m} - \frac{n_x'(v)}{\tau_n} - \frac{h_x'(v)}{\tau_v} \right), \]

\[ b_{3HH}(v) = \frac{1}{\tau_H} \left( g_H(v) \left( \frac{1}{\tau_m} + \frac{1}{\tau_n} + \frac{1}{\tau_h} \right) - \frac{m_x'(v)}{\tau_m} - \frac{n_x'(v)}{\tau_n} - \frac{h_x'(v)}{\tau_h} \right), \]

\[ B_{1HH}(v) = b_{3HH}(v) - b_{1HH}(v), \]

\[ B_{2HH}(v) = b_{1HH}(v)B_{1HH}(v) - b_{0HH}(v)(b_{3HH}(v))^2. \]

\[ h_x(v) \rightarrow 1.6h_x(v). \]

This modification does not bring a qualitative change of the global structure of the potential and the active area for \( I_{ext} = 0 \), but a slight shift of the stable point. Figure 15 shows \( g_H(v), m(v), n(v), \) and \( h(v) \) of the modified system that correspond to Eqs. (65)–(68).

Figure 16 shows \( dU_{4HH}(v)/dv, b_{0HH}(v), b_{1HH}(v), \)

\[ h_x(v) \rightarrow 1.6h_x(v). \]

This modification does not bring a qualitative change of the global structure of the potential and the active area for \( I_{ext} = 0 \), but a slight shift of the stable point. Figure 15 shows \( g_H(v), m(v), n(v), \) and \( h(v) \) of the modified system that correspond to Eqs. (65)–(68).

Figure 16 shows \( dU_{4HH}(v)/dv, b_{0HH}(v), b_{1HH}(v), \)

FIG. 16. Derivative of the potential and the active areas of the modified Hodgkin–Huxley system with \( I_{ext} = 0 \). (a) \( dU/4 \), b1, b2, and b3 denote \( 5dU_{4HH}(v)/dv, b_{1HH}(v), b_{2HH}(v), \) and \( b_{0HH}(v) \), respectively. (b) \( dU_{4HH}(v)/dv, B_{1HH}(v)/200, B_{2HH}(v)/1000, \) and \( 50b_{0HH}(v) \), respectively.

FIG. 17. Derivative of the potential and the active areas of the modified Hodgkin–Huxley system with \( I_{ext} = 10 \). (a) \( dU/4 \), b1, b2, and b3 denote \( 20dU_{4HH}(v)/dv, b_{1HH}(v), b_{2HH}(v), \) and \( b_{0HH}(v) \), respectively. (b) \( dU_{4HH}(v)/dv, B_{1HH}(v)/5, B_{2HH}(v)/30, \) and \( 50b_{0HH}(v) \), respectively.
$b_{2HH}(v), b_{3HH}(v), B_{1HH}(v),$ and $B_{2HH}(v)$ for $I_{ext}=0$. The potential has a single well. The active areas are disposed asymmetrically; however, the overlap of the areas is large. The stable point of $U_{HH}(v)$ goes into the active areas with increasing $I_{ext}>8.6$ as shown in Fig. 17, where the overlap of the active areas is still large, and hence, it seems to be the cause of making this model display Class 2 neural excitability.

We also carried out the nullcline approximation for the previous Morris–Lecar system to compare its original potential structure with active areas. The result shows that the difference is small in the vicinity of the stable point.

V. 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 that 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 spiking behavior different from the fast and slow oscillations appears in the case of the different dispositions between the two active areas of the model as shown in Fig. 2. The result as the number of spikes per burst depends on the system parameters $\alpha$ and $\beta$ may be relevant to the block structured dynamics and hence the neural code. The detailed analysis of the relation is a subsequent subject. These results of the burst ID model seem to be common properties for the models characterized by a potential with active areas.

Similar to the derivation of the potential function and the active areas of the burst ID model, we obtained the potential functions and the active areas for the Hindmarsh–Rose model, the Morris–Lecar system, and the Hodgkin–Huxley system. All potential functions of these models have a positive curvature in the range of large enough absolute value of their variable. Moreover, all active areas localize on the potential of each model. Therefore, it is clear that these models with localized active areas display no divergence.

If outputs of the other units in an 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 by using the presented technique.

There are models which are presented for the other fields different from neural systems, and show the typical chaotic behaviors, for example, Lorenz equations, Chua circuit, and so on. The two models also have the potential and the active areas, because the models can be transformed into one-variable equations. Therefore, the presented technique is expected to be applicable to these cases.

It is not easy to obtain the full comprehension of the higher order properties such as the higher order dimensions, but it is a useful concept the part of which is indicated through the Hurwitz’s theorem. The concept of potential with active areas is expected to be helpful for the real time applications or the basic models of the functional brain study.

ACKNOWLEDGMENTS

This research has been supported by Japan Society for the Promotion of Science, Grant-in-Aid for Scientific Research (B), 18360159, 2006. We acknowledge the many conversations we have had with Yoshihiro Hayakawa on the dynamics of neurons.

2J. Guckenheimer and P. Holmes, Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields (Springer, New York, 2002).
14S. Doi and S. Kumagai, Biophysical Neural Networks (Mary Ann Liebert, New York, 2001), Chap. 10, p. 261.