Paper

Dynamic characteristics of a simple bursting neuron model

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Abstract: We present a simple neuron model that shows a rich property in spite of the simple structure derived from the 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. The obtained outputs are broadly classified as simple oscillations, spiking, bursting, and chaotic oscillations. The bursting outputs are classified as with spike undershoot and without spike undershoot, and the bursts without spike undershoot are classified as with tapered and without tapered. We show the parameter dependence of these outputs and discuss the connection between these outputs and the potential with active areas.

Key Words: burst, neuron model, spike, chaos, phase diagram, potential, active area

1. Introduction

There have been many researches of various neuron models which typically take the form of ordinary nonlinear differential equations of several dimensions. The neural networks comprising the interconnections of neuron units are actively studied problems in the field of nonlinear dynamics and the brain research. The pattern of neuronal spiking is of great importance, because it is believed that it codifies the information transmitted by neurons. These dynamics have been thoroughly investigated in each individual model based on the bifurcation theory [1, 2] in which we can discuss the characteristics around a critical point and the perturbation in the vicinity of equilibrium points. 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 inputs. 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 in which we can discuss the characteristics around a critical point and the perturbation in its vicinity. These models commonly display two main types of dynamics: firing spikes at regular intervals and bursting of spikes interwoven with periods of quiescence. 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 [4]. However, many important aspects of this situation are poorly understood and lack the satisfying universality of the structural stability discussion among various models because of nonlinearity. We have proposed a concept of potential with active areas to discuss a global landscape for dynamics of various models [5]. In a two-dimensional case, we can discuss the dynamic behavior of models as particle motion on a potential with a damping factor, because the differential equation has a second derivative term. In a more than three-dimensional case, we have to discuss it as quasi-particle motion because of the influence of the higher order derivative term. The shape of the potential function and its modification with parameters are able to indicate the stability conditions. Furthermore, we can also discuss the global stability in connection with active or passive areas [5] on the potential, for example, a negative resistance or damping. The potential functions with globally positive curvature ensure without numerical simulations that an oscillation generated around active areas does not diverge. The concept of potential with active areas is able to provide the new view of the analyses of a nonlinear system in addition to the bifurcation theory.

We already proposed the Burst Inverse-function Delayed (Burst ID) model [5] in which, however, one cannot change the dispositions of plural active areas independently. The outputs of the neuron model depend on the relation among the positions of active areas and equilibrium points of the potential. Therefore, we propose a simple model in which we are able to change the disposition of plural active areas independently. The model consists of three first-order nonlinear differential equations of the Hodgkin-Huxley [6] type, and we explain the parameter dependence of various types of bursting phenomena and firing modes of the model through the concept of potential with active areas and numerical results that may suggest the similar characteristics of the other well-known models. Consequently, we are able to study 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 a modification of the Burst ID model to change dispositions of plural active areas in Section II. The ID model [4] is the slight modification of the BVP model [7, 8], and we have used it to build a network for solving the combinatorial optimization problems and so on [9–11]. The Burst ID model is an extended version of the ID model. The Burst ID model has well-defined parameters to control its firing modes in connection with the disposition of the active areas on the potential. Section III comprises numerical simulations of the Burst ID model and some connected discussions. Section IV concludes this paper with a summary.

2. Burst ID model

Let us consider the following Hodgkin-Huxley type equations with three variables,

$$\tau_x \dot{x} = u + z - g(x), \quad (1)$$

$$\tau_z \dot{z} = z_\infty(x) - z + \theta, \quad (2)$$

$$\tau_u \dot{u} = u_\infty(x) - u, \quad (3)$$

where τ_x , τ_z , τ_u , and θ are time constants of x , z , u , and an external input, respectively, and $g(x)$, $z_\infty(x)$, and $u_\infty(x)$ are arbitrary functions of the variable x . We refer to this system as the Burst ID model. On the analogy of the Burst ID model, we are able to discuss the Hindmarsh-Rose model [12], the Morris-Lecar model [13], the Hodgkin-Huxley system [6], the Lorentz equations [14], the Chua circuit [15], and so on, because each one of these models is transformed into a one-variable differential equation with a potential and active areas [5].

We can obtain the following two-variable (x, u) system from Eqs. (1) and (2),

$$\ddot{x} + \eta(x)\dot{x} = -\frac{\partial U_2(x, u, \theta)}{\partial x}, \quad (4)$$

where
$$\eta(x) = \frac{1}{\tau_x} \frac{dg(x)}{dx} + \frac{1}{\tau_z} = \frac{g'(x)}{\tau_x} + \frac{1}{\tau_z} \quad (5)$$

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

$\eta(x)$ is a damping factor, and $U_2(x, u, \theta)$ can be read as a potential function of the variable x ; however, $U_2(x, u, \theta)$ varies with time because of $u = u(t)$.

We can also obtain the following one-variable (x) system from Eqs. (3) and (4),

$$\ddot{x} + b_2(x)\ddot{x} + b_1(\dot{x}, x)\dot{x} = -\frac{\partial U_3(x, \theta)}{\partial x}, \quad (7)$$

where
$$b_2(x) = \frac{1}{\tau_x} \left\{ g'(x) + \frac{\tau_x}{\tau_z} + \frac{\tau_x}{\tau_u} \right\} = \eta(x) + \frac{1}{\tau_u}, \quad (8)$$

$$b_1(\dot{x}, x) = \frac{g''(x)}{\tau_x} \dot{x} + \frac{1}{\tau_x} \left\{ \frac{g'(x) - z'_\infty(x)}{\tau_z} + \frac{g'(x) - u'_\infty(x)}{\tau_u} + \frac{\tau_x}{\tau_z \tau_u} \right\}, \quad (9)$$

and
$$\frac{\partial U_3(x, \theta)}{\partial x} = \frac{1}{\tau_x \tau_z \tau_u} \{ g(x) - z_\infty(x) - u_\infty(x) - \theta \}. \quad (10)$$

We obtain the following equation from Eq. (10)

$$\frac{\partial^2 U_3(x, \theta)}{\partial x^2} = \frac{1}{\tau_x \tau_z \tau_u} \{ g'(x) - z'_\infty(x) - u'_\infty(x) \} \equiv b_0(x), \quad (11)$$

where $b_0(x)$ denotes the curvature of the potential $U_3(x, \theta)$ at an equilibrium point $x = x_0$. An equilibrium point x_0 is stable when $b_2(x_0) > 0$, $b_1(\dot{x} = 0, x_0) > 0$, $b_0(x_0) > 0$, and $B_1(x_0) = b_2(x_0)b_1(\dot{x} = 0, x_0) - b_0(x_0) > 0$ according to Hurwitz's theorem. We can define three active areas [5] b_1 -active area, b_2 -active area, and B_1 -active area where $b_1(\dot{x} = 0, x) = b_1(x) < 0$, $b_2(x) < 0$, and $B_1(x) < 0$, respectively. By using Eqs. (8), (9), and (11) we can obtain

$$g'(x) = \tau_x b_2(x) - \delta, \quad (12)$$

$$z'_\infty(x) = \frac{\tau_x \tau_u}{\tau_u - \tau_z} \left[b_2(x) - \tau_z b_1(x) + \tau_z^2 b_0(x) - \frac{1}{\tau_z} \right], \quad (13)$$

$$u'_\infty(x) = -\frac{\tau_x \tau_z}{\tau_u - \tau_z} \left[b_2(x) - \tau_u b_1(x) + \tau_u^2 b_0(x) - \frac{1}{\tau_u} \right], \quad (14)$$

where $\delta = \tau_x(\tau_z^{-1} + \tau_u^{-1})$. In addition, we obtain the following equations from Eqs. (6), (12), (13), and (14),

$$\frac{\partial^2 U_2}{\partial x^2} = b_1(x) - \frac{1}{\tau_u} b_2(x) + \frac{1}{\tau_u^2}, \quad (15)$$

$$\frac{\partial U_2(x, u, \theta)}{\partial x} = \int \left\{ b_1(x) - \frac{1}{\tau_u} b_2(x) + \frac{1}{\tau_u^2} \right\} dx - \frac{1}{\tau_x \tau_z} \left\{ \left(1 - \frac{\tau_z}{\tau_u}\right) u + \theta \right\}. \quad (16)$$

We can rewrite Eq. (1) in the following form,

$$\dot{x} = -\frac{\partial U_1(x, z, u)}{\partial x}, \quad (17)$$

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 $u = u(t)$. We obtain the following equations from Eqs. (12) and (17),

$$\frac{\partial^2 U_1}{\partial x^2} = b_2(x) - \frac{1}{\tau_x} \delta, \quad (18)$$

$$\frac{\partial U_1(x, z, u)}{\partial x} = \int \left\{ b_2(x) - \frac{1}{\tau_x} \delta \right\} dx - \frac{1}{\tau_x} (z + u). \quad (19)$$

By using $b_1(x)$, $b_2(x)$, $U_1(x, z, u)$, $U_2(x, u)$, and $U_3(x)$, we can discuss the global dynamics of the neuron model in connection with the positions of equilibrium points of the potential and the disposition of active areas on the potential.

For simplicity and not to make solutions diverge [5], we assume the potential $U_3(x, \theta)$ has the following form,

$$U_3(x, \theta) = \frac{1}{\tau_x \tau_z \tau_u} (x^4 - 2\gamma x^2 - \theta x), \quad (20)$$

and we obtain

$$\frac{\partial U_3(x, \theta)}{\partial x} = \frac{1}{\tau_x \tau_z \tau_u} \{4x(x^2 - \gamma) - \theta\}, \quad (21)$$

$$\frac{\partial^2 U_3(x, \theta)}{\partial x^2} = b_0(x) = \frac{1}{\tau_x \tau_z \tau_u} (12x^2 - 4\gamma), \quad (22)$$

where the potential $U_3(x, \theta)$ depending on the sign of γ has a single- or double-well shape which has three equilibrium points $x = 0$ with $b_0(0) < 0$ and $x = \pm\sqrt{\gamma}$ with $b_0(\pm\sqrt{\gamma}) > 0$ when $\gamma > 0$ and $\theta = 0$. The position of equilibrium points depends on the external input θ .

The active areas should localize on the potential to avoid the divergence of the output $x(t)$. It means that $b_1(x)$ and $b_2(x)$ should have a positive curvature. For simplicity, we take the lowest degree for the functions of $b_1(x)$ and $b_2(x)$. To have control of a center position and the width of an active area independently each other, we assume

$$b_2(x) = \frac{1}{\tau_x} \left\{ (x - C_2)^2 - \beta_2 \right\}, \quad (23)$$

$$b_1(x) = \frac{1}{\tau_x} \left\{ (x - C_1)^2 - \beta_1 \right\}. \quad (24)$$

The center position and the width of the b_2 -active area are C_2 and $2\sqrt{\beta_2}$, respectively, and those of the b_1 -active area are C_1 and $2\sqrt{\beta_1}$, respectively. Then we obtain the following equations,

$$g'(x) = \tau_x b_2(x) - \delta = (x - C_2)^2 - \beta_2 - \delta, \quad (25)$$

From the integration of Eq. (25), we obtain

$$g(x) = \frac{x^3}{3} - C_2 x^2 + (C_2^2 - \beta_2 - \delta) x, \quad (26)$$

where we set an integral constant equal to zero. From the integrations of Eqs. (13) and (14), we obtain

$$z_\infty(x) = \frac{\tau_z \tau_u}{\tau_u - \tau_z} \left[\left(\frac{4}{\tau_u} + \frac{1 - \tau_z}{3\tau_z} \right) x^3 + \frac{C_1 \tau_z - C_2}{\tau_z} x^2 - \left\{ \frac{4\gamma}{\tau_u} - \frac{C_2^2 - \beta_2}{\tau_z} + C_1^2 - \beta_1 + \frac{\tau_x}{\tau_z^2} \right\} x \right], \quad (27)$$

$$u_\infty(x) = \frac{\tau_z \tau_u}{\tau_z - \tau_u} \left[\left(\frac{4}{\tau_z} + \frac{1 - \tau_u}{3\tau_u} \right) x^3 + \frac{C_1 \tau_u - C_2}{\tau_u} x^2 - \left\{ \frac{4\gamma}{\tau_z} - \frac{C_2^2 - \beta_2}{\tau_u} + C_1^2 - \beta_1 + \frac{\tau_x}{\tau_u^2} \right\} x \right], \quad (28)$$

and

$$z_\infty(x) + u_\infty(x) = -\frac{11}{3} x^3 - C_2 x^2 + (4\gamma + C_2^2 - \beta_2 - \delta) x, \quad (29)$$

where we also set integral constants equal to zero.

If we assume the time constants to be $\tau_u \gg \tau_z \gg \tau_x \simeq 1$, 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. (12), (18), and (25), $\partial U_1(x, z=0, u=0)/\partial x$ is an N-shaped function and has two equilibrium points which are $x_{2\pm} = C_2 \pm \sqrt{\beta_2 + \delta} \simeq C_2 \pm \sqrt{\beta_2}$ obtained from $\partial^2 U_1/\partial x^2 = \tau_x^{-1} g'(x) = 0$, and hence the number of the roots of $\partial U_1/\partial x = 0$, namely $g(x) = z + u \simeq \text{const.}$, 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 $g(x) = z + u \simeq \text{const.}$ 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 of the discussion in outline. When $C_2 = 0$ and $\gamma = 0$, for example, we can obtain $z_\infty(x) + u_\infty(x) = \mp 14(\sqrt{\beta_2 + \delta})^3/3$ from Eq. (29) for $x = \pm\sqrt{\beta_2 + \delta}$, and hence $z_\infty(x) + u_\infty(x) < 0$ for $x = +\sqrt{\beta_2 + \delta}$, and $z_\infty(x) + u_\infty(x) > 0$ for $x = -\sqrt{\beta_2 + \delta}$. 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), (15), (23), and (24). $\partial U_2(x, u=0, \theta=0)/\partial x$ is also an N-shaped function and has two equilibrium points which are $x_{1\pm} = (C_1 - C_2\tau_u^{-1})/(1 - \tau_u^{-1})$

$\pm \sqrt{\{(C_1 - C_2\tau_u^{-1})/(1 - \tau_u^{-1})\}^2 + \{\beta_1 - C_1^2 - (\beta_2 - C_2^2)\tau_u^{-1} - \tau_x\tau_u^{-2}\}/(1 - \tau_u^{-1})} \simeq C_1 \pm \sqrt{\beta_1}$ obtained from $\partial^2 U_2/\partial x^2 = 0$, and hence the number of the roots of $\partial U_2/\partial x = 0$, namely $\tau_x\tau_u\partial U_2(x, u=0, \theta=0)/\partial x = (1 - \tau_z/\tau_u)u \simeq \text{const.}$, 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 $x_{1T-} = (C_1 - C_2\tau_u^{-1})/(1 - \tau_u^{-1}) - 2\sqrt{\{(C_1 - C_2\tau_u^{-1})/(1 - \tau_u^{-1})\}^2 + \{\beta_1 - C_1^2 - (\beta_2 - C_2^2)\tau_u^{-1} - \tau_x\tau_u^{-2}\}/(1 - \tau_u^{-1})} \simeq C_1 - 2\sqrt{\beta_1}$, or x_{1-} and $x_{1T+} = (C_1 - C_2\tau_u^{-1})/(1 - \tau_u^{-1}) + 2\sqrt{\{(C_1 - C_2\tau_u^{-1})/(1 - \tau_u^{-1})\}^2 + \{\beta_1 - C_1^2 - (\beta_2 - C_2^2)\tau_u^{-1} - \tau_x\tau_u^{-2}\}/(1 - \tau_u^{-1})} \simeq C_1 + 2\sqrt{\beta_1}$.

Through the same process as that for the preceding high frequency oscillation, the system creates the low frequency oscillation of the burst, and the low frequency mainly depends on τ_u because of Eqs. (4) 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. The b_1 -active area dominates the slow oscillation of the burst because of the large τ_u . On the other hand, the b_2 -active area dominates the fast oscillation of the burst.

3. Result and discussion

The outputs of the Burst ID model depend on the relative positions of the b_1 - and b_2 - active areas and the equilibrium points of the potential [5]. Therefore, we study the phase diagram of the dynamical behaviors of the Burst ID model on the $C_1 - C_2$ plane where C_1 and C_2 are the central positions of the b_1 - and b_2 -active areas, respectively. To obtain the phase diagram, we take $\tau_x = \tau_z = 2$, and $\tau_u = 100$ for the simulation that is carried out by using Eqs. (1)–(3), (26)–(28), and the Runge-Kutta method in which the increment of time is 0.01 with plural arbitrary initial conditions for x , z , and u .

Fig. 1. Phase diagram for the Burst ID model with $\gamma = 0, \beta_1 = 0.7, \beta_2 = 0.5, \tau_x = \tau_z = 2, \tau_u = 100$.

3.1 Single-well potential ($\gamma = 0$)

The Burst ID model with $\gamma = 0$ and $\theta = 0$ has only one equilibrium point at $x = 0$ with $b_0(x = 0) > 0$. The position of the equilibrium point depends on the external input θ because of Eq. (20). Accordingly, the external input can change the state of output from a resting state to an oscillating state to shift the position of the equilibrium point from the outside to the inside of an active area. The oscillating state depends on the relative positions of active areas. We take $\theta = 0$, for simplicity, in the following simulations to study the dynamic behaviors and the basic characteristics of the model.

Figure 1 shows the phase diagram on the $C_1 - C_2$ plane where $\beta_1 = 0.7$ and $\beta_2 = 0.5$. The equilibrium point $x = 0$ is inside the b_1 -active area for $|C_1| < \sqrt{\beta_1} \simeq 0.84$ and inside the b_2 -active area for $|C_2| < \sqrt{\beta_2} \simeq 0.71$. When both active areas do not include the equilibrium point, the output state is able to be quiescent at the equilibrium point as shown in Fig. 1. However, it depends on initial conditions because of inertia of the quasi-particle. We obtained time series of the outputs $x(t)$ after enough time to make the system become a periodic steady state. The phase diagram has roughly four zones that include points denoted by a, b, c, and d each. The outputs at these points show a typical waveform in each zone. The boundaries of these zones slightly shift depending on initial conditions because of the effect of inertia. C_1, C_2, N, s , and E.P. in Fig. 1 denote the center positions of two active areas, the number of spikes per burst, the space between two active areas as shown in Fig. 2, and the equilibrium point, respectively. In Fig. 1 the number of spikes per burst decreases with increasing the value of C_2 in the zones including the point a or d. On the other hand, it increases with increasing the value of C_2 in the zone including the point b as indicated in Fig. 1.

Figures 2(a), (b), (c), and (d) show the time series of the outputs $x(t)$ obtained at the points a, b, c, and d in Fig. 1, respectively. The point e in Fig. 1 shows a disordered burst which we will discuss in

Fig. 2. Time series of the output $x(t)$ for the Burst ID model with $C_1 = -0.4$ and $C_2 = 1.7$ (a), 1.5 (b), 0.9 (c), 0.3 (d).

the third subsection. C_1 is -0.4 for all the points a, b, c, and d, and C_2 is 1.7, 1.5, 0.9, and 0.3 for the points a, b, c, and d, respectively, in Fig. 1. We can find spiking and three kinds of slow-oscillation dominated bursting [5] (SB), which is a burst without spike undershoot, in Fig. 2. The light gray zone, the gray zone, and the dark zone in Fig. 2 denote the b_1 -active area, the b_2 -active area, and the overlap of the two active areas, respectively. The b_1 -active area dominates the slow dynamics of the bursting oscillation because of the large τ_u as discussed in the preceding section. On the other hand, the b_2 -active area dominates the fast dynamics of the bursting oscillation. The equilibrium point $x = 0$ is inside the b_1 -active area in Figs. 2(a), (b), and (c), and it is inside both active areas in Fig. 2(d). The quasi-particle acquires a fast oscillatory component from the b_2 -active area; however, the fast oscillatory component decays passing through the normal damping area denoted by s in Fig. 2(a).

When the normal damping area has an enough width, the output shows a “tapered” bursting [3]. The quasi-particle slips down into the b_1 -active area along the potential curve after the decay of the fast oscillatory component as shown in Fig. 2(a). Then the quasi-particle goes up the opposite slope of the potential curve passing by the equilibrium point with the acquisition of a slow oscillatory component from the b_1 -active area, and it slips down again into the b_1 -active area along the slope as shown in Fig. 2(a) where the number of spikes per burst is $N = 6$. With decreasing s , the quasi-particle goes up the opposite slope before the decay of the fast oscillatory component as shown in Fig. 2(b) where the number of spikes per burst is $N = 3$ that is also indicated in Fig. 1. The overlap of the active areas causes a spiking oscillation ($N = 1$) as shown in Fig. 2(c). With decreasing C_2 , the fast oscillatory component becomes to slightly decay passing through the normal damping area above the b_2 -active area and is amplified again after the slight decay as shown in Fig. 2(d) where $N = 4$.

This amplification becomes clearer with increasing the time constant τ_u . Figure 3(b) shows the time series of the output of the model with the same parameter values as Fig. 2(d) except for $\tau_u = 400$. Figure 3(a) shows the time series of the output of the model with the same parameter values as Fig. 2(a) except for $\tau_u = 400$, and the time series of the output has the longer decay part of the fast oscillatory component than that shown in Fig. 2(a). We can observe the similar output to Fig. 3(a) for the model with the same parameter values as Fig. 2(b) except for $\tau_u = 400$. Therefore, not only C_2 and C_1 but also τ_u cause the qualitative change of output. The increase of τ_u relaxes the inclination of the potential slope because of Eq. (20), accordingly, these behaviors are expected.

When the equilibrium point is not inside the b_1 -active area, but inside the b_2 -active area, we obtain the output shown in Fig. 4. The quasi-particle acquires a fast oscillatory component from the b_2 -active area near the equilibrium point. The amplitude of the fast oscillation increases with time, and the quasi-particle consequently enters the b_1 -active area. The quasi-particle, as a result, acquires a slow oscillatory component from the b_1 -active area, after that it goes up the opposite slope (the negative x region) of the potential curve passing through the b_2 -active area. Then the quasi-particle slips down along the potential slope toward the equilibrium point with reducing the fast oscillatory component, which was obtained from the b_2 -active area, in the normal damping area. The waveform corresponds

Fig. 3. Time series of the two outputs (a) and (b) for the model with the same parameter values as Fig. 2(a) and (d), respectively, except for $\tau_u = 400$.

Fig. 4. Time series of the output for the model with the same parameter values as Fig. 1 except for the fixed values of $C_1 = 1.2$ and $C_2 = 0.4$.

Fig. 5. (a) and (b): Time series of the output $x(t)$ for the Burst ID model with $C_1 = 0.15$, $C_2 = 0.275$, $\beta_1 = 0.5$, $\beta_2 = 1.2$, and $\tau_x = \tau_z = 2$. (c): Phase diagram for FB on the $\beta_1 - \beta_2$ plane. FB denotes a fast-oscillation dominated bursting (a burst with spike undershoot).

to the upside-down pattern of the waveform shown in Fig. 3(b) because of the symmetrical potential shape. Thus, we always set the b_2 -active area on the upside of the b_1 -active area in the following simulations. We can expect the result through the consideration of the peculiarity of the active areas.

When the b_1 -active area is covered with the b_2 -active area, the model shows the fast-oscillation dominated bursting [5] (FB) which is a burst with spike undershoot as shown in Figs. 5(a) and (b). Figures 5(a) and (b) have the same values for the parameters except for $\tau_u = 100$ or 400. The number of spikes per burst is three ($N = 3$) in Fig. 5(a) and two ($N = 2$) in Fig. 5(b). Figures 5(c) and 6 show phase diagrams for FB on the $\beta_1 - \beta_2$ plane where τ_u is 100 or 400 and on the $C_1 - C_2$ plane where τ_u is 100, respectively. The time series of the output shown in Fig. 5(b) is obtained at the point b ($C_1 = 0.15$, $C_2 = 0.275$) in Fig. 6 where we use the notation (2.2) to denote the pattern of Fig. 5(b). The notations (2.2), (3.3), (2_2), and (2_1_2), in which the number and ‘_’ denote the number of the spikes and the spike vacancy, respectively, refer to observed different patterns of FB. We think that the slow oscillation makes a spike vacancy in the spike train generated by the fast oscillation depending on the phase relation between the two oscillations. The zone where we can observe a burst with spike undershoot is narrower than that for a burst without spike undershoot.

3.2 Double-well potential ($\gamma = 0.5$)

The Burst ID model with $\gamma = 0.5$ and $\theta = 0$ has three equilibrium points at $x = 0$ with $b_0(x = 0) < 0$ and $x = \pm\sqrt{\gamma} = \pm\sqrt{0.5} \simeq \pm 0.71$ with $b_0(x = \pm\sqrt{0.5}) > 0$. Figure 7 shows the phase diagram on the $C_1 - C_2$ plane where $\beta_1 = 0.5$ and $\beta_2 = 0.2$. N , s , and E.P. in Fig. 7 denote the number of spikes per

Fig. 6. Phase diagram for the model with $\gamma = 0$, $\beta_1 = 0.5$, $\beta_2 = 1.2$, $\tau_x = \tau_z = 2$, $\tau_u = 100$. The point b indicates the position of Fig. 5(b) observed.

Fig. 7. Phase diagram for the model with $\gamma = 0.5, \beta_1 = 0.5, \beta_2 = 0.2, \tau_x = \tau_z = 2, \tau_u = 100$.

burst, the space between two active areas, and an equilibrium point, respectively. The equilibrium point $x \simeq -0.71$ is inside the b_1 -active area for $-\sqrt{\gamma} - \sqrt{\beta_1} < C_1 < -\sqrt{\gamma} + \sqrt{\beta_1}$ ($-1.41 \lesssim C_1 < 0$) and inside the b_2 -active area for $-\sqrt{\gamma} - \sqrt{\beta_2} < C_2 < -\sqrt{\gamma} + \sqrt{\beta_2}$ ($-1.15 \lesssim C_2 \lesssim -0.25$). The equilibrium point $x \simeq 0.71$ is inside the b_1 -active area for $\sqrt{\gamma} - \sqrt{\beta_1} < C_1 < \sqrt{\gamma} + \sqrt{\beta_1}$ ($0 < C_1 \lesssim 1.41$), and inside the b_2 -active area for $\sqrt{\gamma} - \sqrt{\beta_2} < C_2 < \sqrt{\gamma} + \sqrt{\beta_2}$ ($0.25 \lesssim C_2 \lesssim 1.15$). When both active areas do not include an equilibrium point, the output state is able to be quiescent at the equilibrium point as shown in Fig. 7. The phase diagram has zones of resting states, spiking ($N = 1$) oscillations, bursting ($N > 1$) oscillations, and oscillations without burst. “Oscillation” in Fig. 7 denotes that its amplitude is at opposite sides of its neutral path of oscillation in a nearly symmetrical manner different from spiking oscillation in an asymmetric manner. The boundaries of these zones slightly shift depending on initial conditions because of the effect of inertia as well as the single-well potential.

Fig. 8. Time series of the output $x(t)$ for the Burst ID model with $C_1 = -0.25$ and $C_2 = 1.25$ (a), 1.05 (b), 0.8 (c), 0.5 (d), 0.45 (e), 0.3 (f).

Fig. 9. Number of spikes per burst as a function of C_2 . The points denoted by D, E, and F correspond to D, E, and F in Fig. 7, respectively.

For example, the top boundary of the zone denoted by “Oscillation around the E.P. $x=0.71$ ” shifts from the solid line to the broken line as shown by using a vertical arrow in Fig. 7, and we can also see the zone overlaps at the upper right part and the lower left part of Fig. 7. Both boundaries of “Resting at the E.P. $x=0.71$ ” are almost symmetrical about the line of $C_2 \simeq (0.25 + 1.15)/2$. It is consistent with the aforementioned analysis that the equilibrium point $x \simeq 0.71$ is inside the b_2 -active area for $0.25 \lesssim C_2 \lesssim 1.15$. The zone denoted by “ $N>3$ ” wedges into the left resting zone and they overlap each other. The left part of the zone denoted by “Oscillation or $N=1$ ”, which is located at the lower left of the zone “ $N>3$ ”, and the left resting zone also overlap each other. Consequently, the left resting zone is divided into four parts. The top part is a resting state without overlap, the wedge-shaped second part is an overlap of “ $N>3$ ” and the resting state, the third part is an overlap of “Oscillation or $N=1$ ” and the resting state, the fourth part is an overlap of “ $N>1$ ” and the resting state. The right part of “Oscillation or $N=1$ ”, which includes the point d, has no overlap.

Figures 8(a), (b), (c), (d), (e), and (f) show the time series of the outputs obtained at points A, B, C, D, E, and F in Fig. 7, respectively. C_1 is -0.25 for all the points A, B, C, D, E, and F, and C_2 is 1.25, 1.05, 0.8, 0.5, 0.45, and 0.3 for the points A, B, C, D, E, and F, respectively. The waveforms shown in Figs. 8(a), (c), and (f) are similar to the waveforms shown in Fig. 2(b), (c), and (d), respectively. However, the zone denoted by “ $N = 1$ ” does not divide the zone denoted by “ $N = 2$ ” into two separate parts different from Fig. 1. The number of spikes per burst is three ($N = 3$) in Fig. 8(a), two ($N = 2$) in Fig. 8(b), one ($N = 1$) in Fig. 8(c), two ($N = 2$) in Fig. 8(d), three ($N = 3$) in Fig. 8(e), and eight ($N = 8$) in Fig. 8(f). The number of spikes per burst steeply increases with decreasing C_2 as shown in Fig. 9 where $C_1 = -0.25$ and $C_2 < 0.8$. As shown in the inset of Fig. 9 where the top edge of the b_2 -active area is $x = 0.64$ and $C_2 = 0.19$, the output $x(t)$ comes down to the equilibrium point ($x = 0.71$) decreasing the amplitude of the spikes (fast oscillation) outside the top edge of the b_2 -active area. After the decrease of the amplitude, the fast oscillation is amplified again because of contact with the b_2 -active area and with the b_1 -active area at last. The contact with the b_1 -active area causes an overshoot beyond the potential hill in the vicinity of $x = 0$.

Figures 10(a), (b), (c), (d), (e), (f), (g), and (h) show the time series of the outputs obtained at the points a, b, c, d, e, f, g, and h in Fig. 7, respectively. C_1 is $-0.05, -0.5, -0.7, -0.8, -0.9, -0.91, -1.35$, and -1.4 in decreasing order for the points a, b, c, d, e, f, g, and h, respectively, and C_2 is 0.41 for all the points a, b, c, d, e, f, g, and h. We classify Fig. 10(a) and Fig. 8(d) into the same group with $N = 2$ as indicated in Fig. 7. Figure 10(b) shows a periodic burst with $N = 4$; on the other hand,

Fig. 10. Time series of the output $x(t)$ for the Burst ID model with $C_1 = -0.05$ (a), -0.5 (b), -0.7 (c), -0.8 (d), -0.9 (e), -0.91 (f), -1.35 (g), -1.4 (h) and $C_2 = 0.41$.

Fig. 10(c) is a disordered burst. Figure 10(d) shows the time series of the output which belongs to the zone denoted by “Oscillation or $N = 1$ ” in Fig. 7. Figure 10(e) that belongs to the small zone including the point e in Fig. 7 shows a beat-like output. The fast oscillation takes place around the equilibrium point $x = 0$ with $b_0(x = 0) < 0$ in Fig. 10(e). The output changes from the beat-like waveform shown in Fig. 10(e) to the burst shown in Fig. 10(f) with a slight decrease of the value of C_1 . The quasi-particle goes down toward the equilibrium point $x = -0.71$ after the reduction of the fast oscillatory component in Fig. 10(f), and the burst thus occurs. The quasi-particle, as the result, enters the b_1 -active area. With further decrease of C_1 value, the output changes from Fig. 10(f) to Fig. 10(g), and the fast oscillation disappears at last as shown in Fig. 10(h).

Figure 11 shows the period T of the burst as a function of C_1 , if we define T as shown in the inset of Fig. 11. The points denoted by f, g, and h in Fig. 11 correspond to the points f, g, and h in Fig. 7, respectively. With decreasing C_1 , the period T has a peak at about $C_1 = -1.26$, after that T steeply decreases. For $C_1 > -1.26$, the minimum amplitude of the fast oscillation overlaps the b_1 -active area

Fig. 11. Period T of the burst as a function of C_1 for $C_2 = 0.41$.

Fig. 12. Phase diagram for the model with $\gamma = 0.5, \beta_1 = 1.0, \beta_2 = 0.5, \tau_x = \tau_z = 2, \tau_u = 100$.

Fig. 13. Time series of the output $x(t)$ for the Burst ID model with $C_1 = -0.6$ and $C_2 = 1.4$ (a), 0.9 (b), 0.6 (c).

as shown in Fig. 10(f). On the other hand, for $C_1 < -1.26$, the minimum amplitude does not overlap the b_1 -active area as shown in the inset of Fig. 11. We think it is the reason to have the peak of T as a function of C_1 . The almost vertical line where $C_2 \simeq 0.45$ from the point e to h in Fig. 7 corresponds to the line where the bottom edge of the b_2 -active area and the equilibrium point $x = 0$ overlap each other. The almost horizontal line that is $C_1 \simeq -1.3$ on the right side of the point g in Fig. 7 corresponds to the line where the peak height of the output $x(t)$ reaches the bottom edge of the b_2 -active area as shown in Fig. 10(g).

To investigate the effect of the width of the active areas, we carried out simulations for two cases with the different widths. The first model has $\beta_1 = 1.0$ and $\beta_2 = 0.5$, namely, wider active areas. The phase diagram on the $C_1 - C_2$ plane has zones similar to Fig. 7. However, the zones of the upper part of the phase diagram spread; on the other hand, those of the lower part shrink. Figure 12 shows the only upper part of the phase diagram. The equilibrium point $x \simeq -0.71$ is inside the b_1 -active area for $-1.71 \lesssim C_1 \lesssim 0.29$ and inside the b_2 -active area for $-1.41 \lesssim C_2 < 0$. The equilibrium point $x \simeq 0.71$ is inside the b_1 -active area for $-0.29 \lesssim C_1 \lesssim 1.71$ and inside the b_2 -active area for $0 < C_2 \lesssim 1.41$. Both active areas do not include the equilibrium point $x \simeq 0.71$ in the right lower zone, the output state is able to be quiescent at the equilibrium point. The boundaries of these zones slightly shift depending on initial conditions as well as Fig. 7. For example, the top boundary of the zone denoted by “Oscillation” shifts from the solid line to the broken line as shown by a vertical arrow in Fig. 12,

Fig. 14. Phase diagram for the model with $\gamma = 0.5, \beta_1 = 0.1, \beta_2 = 0.2, \tau_x = \tau_z = 2, \tau_u = 100$.

Fig. 15. Time series of the output $x(t)$ for the Burst ID model with $C_1 = -0.5$ and $C_2 = 0.4$ (a), 0.385(b), 0.38(c), 0.36(d), 0.31(e), 0.27(f).

and we can also see the zone overlaps at the right part of Fig. 12.

Figures 13(a), (b), and (c) show the time series of the outputs obtained at the points a, b, and c in Fig. 12, respectively. C_1 is -0.6 for all the points a, b, and c, and C_2 is 1.4, 0.9, and 0.6 for the points a, b, and c, respectively. Though the number of spikes per burst is different, the waveforms shown in Figs. 13(a) and (c) show waveforms similar to Figs. 8(a) and (e), respectively. The waveforms shown in Figs. 13(a) and (c) are different each other, though they have the same number $N = 5$ of spikes per burst. The difference corresponds to that of Figs. 8(a) and (e) in connection with the relative positions of the b_1 - and b_2 -active areas. The number of spikes per burst increases with increasing the space s between the two active areas as it is indicated at the part between $s = 0$ and $s = 0.5$ in Fig. 12; on the other hand, it increases with shifting the two active areas toward the negative direction of x keeping on the space s fixed as it is indicated at the left part in Fig. 12. The point d in Fig. 12 shows a disordered burst which we will discuss in the third subsection.

The second model to investigate the effect of the width of the active area has $\beta_1 = 0.1$ and $\beta_2 = 0.2$, namely, narrower active areas. Figure 14 shows the phase diagram on the $C_1 - C_2$ plane. The equilibrium point $x \simeq -0.71$ is inside the b_1 -active area for $-1.02 \lesssim C_1 \lesssim -0.39$ and inside the b_2 -active area for $-1.15 \lesssim C_2 \lesssim -0.26$. The equilibrium point $x \simeq 0.71$ is inside the b_1 -active area for

Fig. 16. Time series of the output $x(t)$ for the Burst ID model with $C_1 = -0.4$ (a), -0.6 (b), -0.9 (c), -1.0 (d) and $C_2 = 0.385$.

Fig. 17. Number of spikes per burst as a function of C_1 for $C_2 = 0.385$. The points denoted by b, c, and d correspond to b, c, and d in Fig. 14, respectively.

Fig. 18. Number of spikes per burst as a function of C_2 for $C_1 = -0.5$. The points denoted by D and E correspond to D and E in Fig. 14, respectively.

Fig. 19. Number of spikes per burst as a function of C_2 for $C_1 = -0.7$.

$0.39 \lesssim C_1 \lesssim 1.02$ and inside the b_2 -active area for $0.26 \lesssim C_2 \lesssim 1.15$. Both active areas do not include the equilibrium point $x \simeq -0.71$ in the top part of Fig. 14, and consequently, the output state is able to be quiescent at the equilibrium point.

Figures 15(a), (b), (c), (d), (e), and (f) show the time series of the outputs obtained at the points A, B, C, D, E, and F in Fig. 14, respectively. C_1 is -0.5 for all the points A, B, C, D, E, and F, and C_2 is $0.4, 0.385, 0.38, 0.36, 0.31$, and 0.27 for the points A, B, C, D, E, and F, respectively. Figures 15(b) and (c) show waveforms similar to Figs. 10(e) and 10(f), respectively, and Fig. 15(e) shows a disordered burst. Figures 16(a), (b), (c), and (d) show the time series of the outputs obtained at the points a, b, c, and d in Fig. 14, respectively. C_1 is $-0.4, -0.6, -0.9$, and -1.0 for the points a, b, c, and d, respectively, and C_2 is 0.385 for all the points a, b, c, and d. Figure 16(a) shows a disordered burst, and Figs. 16(c) and (d) show waveforms similar to Figs. 10(g) and 10(h), respectively. These results suggest similarity between Fig. 14 and the lower left part of Fig. 7.

Figure 17 shows the number of spikes per burst as a function of C_1 for $C_2 = 0.385$. The points denoted by b, c, and d in Fig. 17 correspond to the points b, c, and d in Fig. 14, respectively. The

Fig. 20. Phase diagram for the model with $\gamma = 0.5, \beta_1 = 0.5, \beta_2 = 1.0, \tau_x = \tau_z = 2, \tau_u = 100$.

Fig. 21. Phase diagram for FB on the $\beta_1 - \beta_2$ plane.

Fig. 22. Periods T and T^* of the burst with spike undershoot as a function of τ_u for three values of $N = 2, 4, 6$.

result shown in Fig. 17 corresponds to the result about the period T shown in Fig. 11. The number of spikes per burst shows a peak with decreasing C_1 as well as the result shown in Fig. 11. The characteristics shown in Fig. 17 connect the amplitude of the fast oscillation with the space s between the two active areas as well as the discussion for the result shown in Fig. 11.

Figures 18 and 19 show the number of spikes per burst as a function of C_2 for $C_1 = -0.5$ and $C_1 = -0.7$, respectively. The number of spikes decreases with decreasing C_2 ; however, for smaller value of C_2 we can observe disordered bursts. The results shown in Figs. 18 and 19 show no peak different from Fig. 17. The decrease of the number of spikes per burst is expected in this range of the space s which decreases with decreasing C_2 . The scatter of the number of spikes in Fig. 18 and 19 means that the time series of the output contains bursts with variable number of spikes as shown in Fig. 15(e).

When the b_1 -active area is almost covered with the b_2 -active area, the model even with a double-well potential shows the fast-oscillation dominated bursting (FB) with spike undershoot as well as the model with a single-well potential.

Figures 20 and 21, where τ_u is 100 or 400, show phase diagrams for FB on the $C_1 - C_2$ plane and on the $\beta_1 - \beta_2$ plane, respectively. The phase diagram for the double-well potential shown in Fig. 20 corresponds to that for the single-well potential shown in Fig. 6, and the two diagrams have similar figures. Consequently, it seems not to be affected by potential shape, if β_1 and β_2 are larger than γ . In Fig. 20 we use the same notations (2_2), (3_3), (4_4), (2_2_2), and (2_1_2) as in Fig. 6. The phase diagram shown in Fig. 21 corresponds to Fig. 5(c), and it seems to be affected by potential shape in the range $\beta_1 \lesssim 0.5$. In Fig. 21 the appearance area of FB for $\tau_u = 400$ is wider than that for $\tau_u = 100$. This result is similar to Fig. 5(c).

Figure 22 shows the period of the burst with spike undershoot as a function of τ_u and the time series of the output $x(t)$ which is obtained for $\gamma = 0.5, \beta_1 = 0.4, \beta_2 = 1.0, C_1 = 0$, and $C_2 = 0.24$. T and T^* in Fig. 22 denote the spiking and the quiescent periods, respectively. T^* increases with

Fig. 23. Time series of the output $x(t)$ obtained at the point e in Fig. 1 and its phase portrait on the $x - u$ plane.

Fig. 24. Time series of the output $x(t)$ obtained at the point d in Fig. 1 and its phase portrait on the $x - u$ plane.

increasing τ_u ; on the other hand, T is nearly constant for a fixed N . It is not easy to obtain a large N for a small τ_u and to obtain a small N for a large τ_u . It means that T^* and N are connected with the slow oscillation through τ_u , on the other hand, T has a weak connection with the slow oscillation.

3.3 Chaotic outputs

We observed disordered bursts at the points e in Fig. 1, c in Fig. 7, d in Fig. 12, E and a in Fig. 14. Figures 10(c), 15(e), and 16(a) show the time series of the outputs obtained at the points c in Fig. 7, E and a in Fig. 14, respectively. Figure 23 shows the time series of the disordered burst obtained at the point e in Fig. 1 and its phase portrait on the $x - u$ plane where we thinned out the obtained data at the plotting as well as in the following phase portraits. To compare the phase portrait of the disordered burst with that of a periodic burst, Fig. 24 shows the time series of the output $x(t)$ obtained at the point d in Fig. 1 and its phase portrait on the $x - u$ plane. The time series shown in Fig. 24 is the same data as shown in Fig. 2(d) except for the observing time limit.

The phase portraits of the time series of the output obtained at the points c in Fig. 7 and d in Fig. 12 resemble the phase portrait shown in Fig. 23 where we can see the confused orbit changed

Fig. 25. Phase diagram for the model with $\gamma = 0.5$, $\beta_1 = 0.154$, $\beta_2 = 0.27$, $\tau_x = \tau_z = 2$, and $\tau_u = 30$.

Fig. 26. Time series of the output $x(t)$ obtained at the point d in Fig. 25 and its phase portrait on the $x - u$ plane.

Fig. 27. Phase diagram for chaotic outputs on the $\tau_x - \tau_u$ plane where $\gamma = 0.5$, $\beta_1 = 0.154$, $\beta_2 = 0.27$, $C_1 = -0.27$, and $C_2 = 0.93$.

from the orderly phase portrait shown in Fig. 24. On the other hand, the phase portraits of the time series of the output obtained at the points E and a in Fig. 14 do not resemble the phase portrait shown in Fig. 23, but that shown in Fig. 26 having a horn like figure. It can be expected from Figs. 3, 5, 21, and 22 that the large difference between time constants leads stable periodic bursts. Therefore, to study the chaotic behaviors we use the model with the smaller value for the time constant τ_u .

Figure 25 shows the phase diagram on the $C_1 - C_2$ plane for the model with $\tau_u = 30$. The equilibrium point $x \simeq -0.71$ is inside the b_1 -active area for $-1.10 \lesssim C_1 \lesssim -0.31$ and inside the b_2 -active area for $-1.23 \lesssim C_2 \lesssim -0.19$. The equilibrium point $x \simeq 0.71$ is inside the b_1 -active area for $0.31 \lesssim C_1 \lesssim 1.10$ and inside the b_2 -active area for $0.19 \lesssim C_2 \lesssim 1.23$. Both active areas do not include the equilibrium point $x \simeq -0.71$ in the top part of Fig. 25, and consequently, the output state is able to be quiescent at the equilibrium point. The model shows chaotic behaviors in the zones that include the point a ($C_1 = -0.27, C_2 = 0.93$) or d ($C_1 = -0.91, C_2 = 0.4$) in Fig. 25. The three points a in Fig. 25, c in Fig. 27, and a in Fig. 30 are the same point in the different figures. The time series of the outputs obtained at points a and d in Fig. 25 are shown in Figs. 28(c) and 26, respectively. Figure 26 also shows the phase portrait of the time series of the output obtained at point d in Fig. 25. The time series of the output $x(t)$ in the zone indicated by b in Fig. 25 is similar to Fig. 28(b). “Oscillation (small amplitude)” and “Oscillation (large amplitude)” in Fig. 25 denote the waveforms similar to the time series shown in Figs. 28(a) and (j), respectively. The time series of the output $x(t)$ in the zone indicated by c in Fig. 25 is similar to Fig. 10(e) or Fig. 15(b). The outline of the phase diagram shown in Fig. 25 resembles that shown in Figs. 7 and 14. It means that the periodic bursts observed in Figs. 7 and 14 change into chaotic oscillations or oscillations without burst by reduction of τ_u .

Figure 27 shows the phase diagram on the $\tau_x - \tau_u$ plane for the model with $\gamma = 0.5$, $\beta_1 = 0.154$, $\beta_2 = 0.27$, $C_1 = -0.27$, and $C_2 = 0.93$. Figures 28(a), (b), (c), (d), (e), (f), (g), (h), (i), and (j) show the time series of the outputs obtained at the points a, b, c, d, e, f, g, h, i, and j in Fig. 27, respectively. The point c in Fig. 27 is the same point as the point a in Fig. 25. Figure 29 shows the phase portrait

Fig. 28. Time series of the output $x(t)$ obtained at the points a, b, c, d, e, f, g, h, i, and j in Fig. 27.

of the time series of the output $x(t)$ shown in Fig. 28(c) on the $x - u$ plane. Figures 28(c), (e), (g), and (i) show chaotic oscillations. The chaotic area in Fig. 27 decreases with increasing τ_x and τ_z . The phase diagram shown in Fig. 27 shows the existence of band like zones for periodic bursts and spiking oscillations as shown in Figs. 28(b), (d), (f), and (h). In Fig. 27 the zones where stable periodic solutions are observed are not overlapped with the accuracy of the present numerical simulation.

To study the γ dependence on behaviors of the model, Fig. 30 shows the phase diagram on the $\gamma - C_1$ plane where $C_2 = 0.93$. The model has the same values of the parameters as those of the model studied in Fig. 25 for $\beta_1, \beta_2, \tau_x, \tau_z$, and τ_u . The point denoted by a ($c_1 = -0.27, \gamma = 0.5$) in Fig. 30 is the same point as the point c in Fig. 27, namely the point a in Fig. 25. The model shows chaotic behaviors in the zone that includes the point a in Fig. 30. “Oscillation (small amplitude)” and “Oscillation (large amplitude)” in Fig. 30 denote the waveforms similar to the time series shown in Figs. 28(a) and (j), respectively. It can be seen that chaotic behaviors occur in the limited region of the γ value, accordingly a potential hill plays a significant role for the chaotic behaviors shown in Figs. 26 and 29. We can observe similar potential hills in the other chaotic models, for example, the Lorenz model, the Chua circuit, and so on. However, a potential hill is not always required to realize chaotic behaviors as shown in Fig. 23 where γ is 0. The phase portraits shown in Figs. 26 and 29 have

Fig. 29. Phase portrait of the time series of the output shown in Fig. 28(c) on the $x - u$ plane.

Fig. 30. Phase diagram for chaotic outputs on the $\gamma - C_1$ plane.

more structured patterns than that shown in Fig. 23. The phase portraits obtained from Figs. 15(e) and 16(a) are like Figs. 26 and 29; on the other hand, those obtained at the points c in Fig. 7 and d in Fig. 12 are like Fig. 23. The models with the former phase portrait have a positive s ; on the other hand, the models with the latter phase portrait have a negative s . Consequently, we can connect the complex structures of phase portrait with the potential with active areas.

4. Conclusions

We have discussed the dynamic characteristics of a neuron model by using the concept based on a potential with active areas. Without numerical simulations, the potential functions with globally positive curvature ensure that an oscillation generated around active areas does not diverge. The outputs of the neuron model depends on the relative positions of active areas and equilibrium points of the potential. We therefore proposed a modification of the Burst ID model in which we are able to change the disposition of plural active areas. The model consists of three first-order nonlinear differential equations of the Hodgkin-Huxley type, and we explained the parameter dependence of various types of bursting phenomena and firing modes of the model through the concept of potential with active areas and numerical results that might suggest the similar characteristics of the other well-known models that were transformed into one-variable differential equations with a potential and active areas [5]. Consequently, we are able to study both the correlation among the models and the characteristics of each individual model in a systematic manner.

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. The obtained outputs are broadly classified as simple oscillations, spiking, bursting, and chaotic oscillations. 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.

We showed the parameter dependence of these outputs and discussed the relation between these outputs and the single- or double-well potential with active areas. The Burst ID model with $\gamma \leq 0$ has only one equilibrium point, and hence its potential has a single-well, and it with $\gamma > 0$ has three equilibrium points, and hence its potential has a double-well. We always set the b_2 -active area on the upside of the b_1 -active area not losing the generalization because of the assumption of the symmetrical potential shape.

When the normal damping area between two active areas has an enough width, the output shows a “tapered” bursting [3] which is a kind of burst without spike undershoot. The number of spikes per burst without spike undershoot increases with decreasing the space between the two active areas, and it decreases after taking a maximum number. In the region where the number of spikes per burst increases, the minimum amplitude of the fast oscillation does not overlap the b_1 -active area; on the other hand, the minimum amplitude overlaps the b_1 -active area in the region where the number of spikes per burst decreases. For a relatively narrow space between two active areas and for a overlap of the two active areas, the output shows a “square” bursting [3] which is also a kind of burst without spike undershoot. With increasing the overlap of the two active areas to keep up the width of the b_2 -active area, the fast oscillatory component becomes to slightly decay passing through the normal damping area above the b_2 -active area and is amplified again after the slight decay, after that the output goes to a resting state. When the b_1 -active area is covered with the b_2 -active area which is wider than the b_1 -active area, the model shows a burst with spike undershoot. The number of spike per burst with spike undershoot depends on the time constants and the relative position between the two active areas. To investigate the effect of the width of the active area, we carried out simulations for the model with wider and narrower active areas. Both models showed qualitatively similar phase diagrams.

We observed disordered bursts and obtained their phase portraits on the $x - u$ plane. To study the chaotic behaviors we used the model with the smaller value for the time constant τ_u , because the large difference between time constants led stable periodic bursts. The simulations for the model show that the periodic bursts change into chaotic oscillations or oscillations without burst by reduction of τ_u . The phase portraits of the model with the double-well potential has a more structured pattern than

that of the model with the single-well potential, and hence we think that complex structures of phase portrait depend on the potential structures and the relative position between two active areas.

These results of the Burst ID model seem to be common properties for the models characterized by a potential with active areas. According to the same way as the derivation of the potential function and the active areas of the Burst ID model, we can obtain 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 over 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 show no divergence.

The concept of potential with active areas is expected to be helpful for the real time comprehension of basic models for the functional brain study. It is possible but not easy to obtain the full comprehension of models with higher order dimensions more than four, because the higher order dimensions bring many active areas and complex potential functions, and hence, we have to examine the reciprocal relation among the active areas, the amplitude of oscillations, and the equilibrium points of the potential. However, we believe the concept is useful on the basis of Hurwitz's theorem in addition to the conventional bifurcation theory.

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