

## EXTENSION OF A DIFFERENTIAL EQUATION TO NEURONS WITH COMPLICATED POSTSYNAPTIC POTENTIALS

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### Abstract

A first-order differential equation is obtained for the firing probability of a neuron which receives inputs at synapses with various forms of the post-synaptic potentials. It is shown that in a neuron with a large number of synapses, the relaxation of the membrane potential affecting the neural equation is the average of the relaxation times of the post-synaptic potentials weighted by the activation probabilities of the synapses.

### 1. Introduction

A first order differential equation for the firing probability of a neuron in a neural network was previously obtained (Oonuki, 1976). The properties of firing included were absolute refractoriness and the resetting of the membrane potential due to firing. Concerning the time course of a post-synaptic potential (a psp), it was assumed that the psp produced by the activations of the synapses of a neuron are relaxed with only one time constant. The rising phase (from the foot to the peak of a psp) possessed by a real psp was treated as noise and included in an effective threshold (a high frequency component of a generalized input). When a synapse lies on a dendrite, the rising phase and the time constant of relaxation of a psp produced by activation of the synapse vary with the location on the dendrite. According to the dendrite theory, the psp of the synapses far from a cell body on a dendrite have larger time constants than those close to the cell body (Rall, 1964). If we want to analyse a neural network by including dendrite theory in a neural equation, the neural equation must be extended to contain the various relaxation times of psp. In the present article, the neural equation is extended to a neuron whose membrane potential is affected by psp with a variety of

elaxation times. In order to avoid confusion, previous notations are again described. The extension is useful for researching the excitation pattern of a neural network in development and learning because the relaxation constants of psp's vary with the locations of the synapses on a dendrite and the distribution will change with development and learning.

### Hypothetical potential

When we model a neural element, we must take into account the following phenomena.

1. The excitable membrane of the cell body with an axon as a threshold element.
2. The variation of membrane potential due to the activation of a synapse or a stimulus current is transient and is relaxed with a time constant.
3. After impulse generation, an excitable membrane has a refractory period.
4. After an impulse, the membrane potential is reset to a resting potential.

Since these phenomena are due to changes in the conductances of  $\text{Na}^+$  and  $\text{K}^+$ , the Hodgkin-Huxley equations describing these changes are often used. Another way is to describe the above phenomena mathematically. This expression is called "formal neuron" model and the Caianiello equation is a well-known example. Of course, the latter may be deduced from the former in the approximate treatment where only  $\text{Na}^+$ -conductance in a resting state is considered whereas the variation of  $\text{Na}^+$ -conductance and  $\text{K}^+$ -conductance in depolarized states, which is an important factor for determining the form of an action potential, is not taken into account. For a study of the activity of the elements in a network, it is convenient to start with the latter expression because the form of an action potential is not an important problem.

The present paper develops a formal neuron model because it is more convenient for finding the firing probability when there are random input signals. For this purpose, a refractory parameter and a resetting parameter are introduced with respect to phenomena 3 and 4, respectively.

Number the synapses on the dendrites and cell body of a neuron  $i=1, \dots, N$  (Fig. 1). The firing of preneuron of the  $i$ -th synapse is described as  $\sigma_i=1$ . This paper describes various forms for the time-developments of psp's. A psp is a transient potential variation of about 10 to 40 msec. The decreasing phase is approximated by exponential functions of time. For instance, a psp of the  $i$ -th synapse, denoted by  $p_i(t)$ , is approximated by  $\sum_j p_i^{(j)} \exp(-t/\gamma_j)$ ;  $p_i(t)$  does not always have one relaxation time. In general,  $p_i(t)$  can be written as the inverse of its Laplace transform

$$p_i(t) = \frac{1}{2\pi i} \int_{c-i\infty}^{c+i\infty} p_{i,L}(s) e^{st} ds,$$

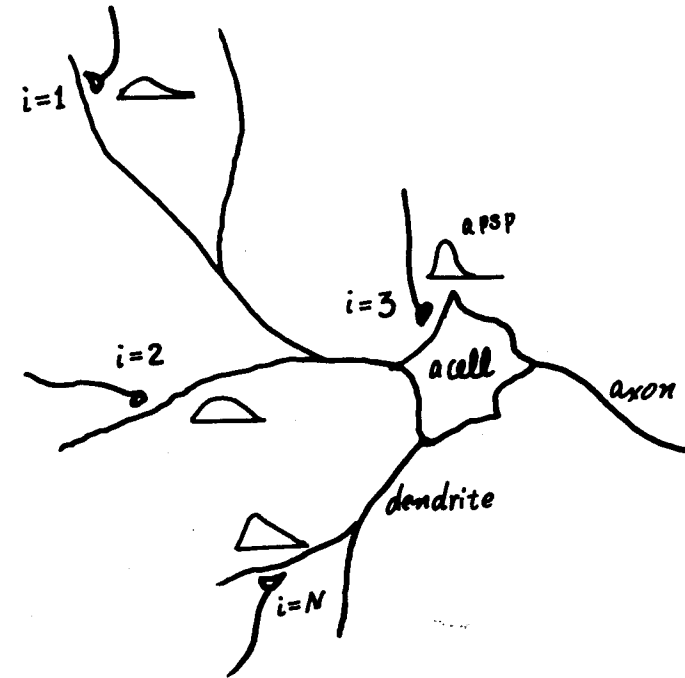


Fig. 1. The present theory is expanded to the system with a various values of relaxation times of psp's on the dendritic junctions.

and  $p_{i,L}(s)$  is the Laplace transformation of  $p_i(t)$ :

$$p_{i,L}(s) = \int_0^{\infty} e^{-st} p_i(t) dt.$$

For instance, when  $p_i(t)$  is relaxed as  $\exp(-at)/t$ ,  $p_{i,L}(s)$  is given as  $1/(s-a)$  ( $=1$  for  $s>a$  or  $0$  for  $s<a$ ). When we pull out an arbitrary relaxation,  $\exp(-st)$ , among the various relaxation of  $p_i(t)$  and average with respect to the fluctuation of such a component, the total average of psp is given by the sum for  $i$  and  $s$ . Put  $s = \gamma^{-1}$ , and we introduce an integral operator

$$(1) \quad I_{i*} = \int_0^{\infty} d(1/\gamma) p_{i,L}(1/\gamma) *.$$

Define  $R_i$  as the averaged variation of a membrane potential due to an  $\exp -t/\gamma$  component of the  $i$ -th synapse, and we have the total variation as

$$(2) \quad R = \sum_i I_i R_i.$$

The firing frequency is averaged with respect to the fluctuation of a membrane potential due to the membrane noise and the random arrivals of the input impulses during a time interval. The reason for considering the latter randomness is to take into consideration that a signal does not always arrive at definite discrete time, although such discrete treatment of an occurrence has been frequently used in neural network theories. The removal of the assumption of discrete times is necessary to obtain a differential equation. The first step of the mathematical method in this approach is to describe a difference equation. Although discrete time is used to describe the state of a cell, this does not imply that events occur at just discrete times. The time development of  $R$  is described as follows until the cell fires.

$$R_i(t, nd) = \int_{nd}^t [a_i \exp\{-(t-s)/\gamma\} \sigma_i(s-d_1-d_2) Q(s)] ds,$$

where  $a_i$  is the amplitude of a psp;  $s$ , being the time of generation of a psp;  $d_1$  and  $d_2$ , a synaptic delay and the conduction time on the fiber from the  $i$ -th cell, respectively;  $Q$ , the distribution function of the generation times of psp; a cell is observed every discrete time,  $nd$ ;  $d$  equals an absolute refractory period. This is an expression of an input averaged with respect to random arrival times of stimuli. This average is limited within an interval  $d$ , i.e.  $nd \leq t \leq nd+d$ . Let's call it time-average. Hereafter the following expressions are used:

$$\bar{R}(t) = R(t, t-d),$$

$$\bar{R}_i(t) = R_i(t, t-d).$$

When the time-averaged psp by the activation of the  $i$ -th synapse ( $v_i$ ) is developed with the other psp; if a cell is not excited between  $nd$  and  $nd+d$  (Fig. 2a), the membrane potential due to the  $i$ -th synapse is simply

$$\begin{aligned} v(nd+d) &= \sum v_i(nd+d) \\ &= \sum I_i [bv_i(nd) + \bar{R}_i(nd+d)], \end{aligned}$$

where

$$b = \exp(-d/\gamma).$$

If the sum of the psp; reaches a threshold value ( $\theta$ ), a cell is fired and, immediately the membrane potential is reset to a resting potential as all of the psp; are liquidated. A

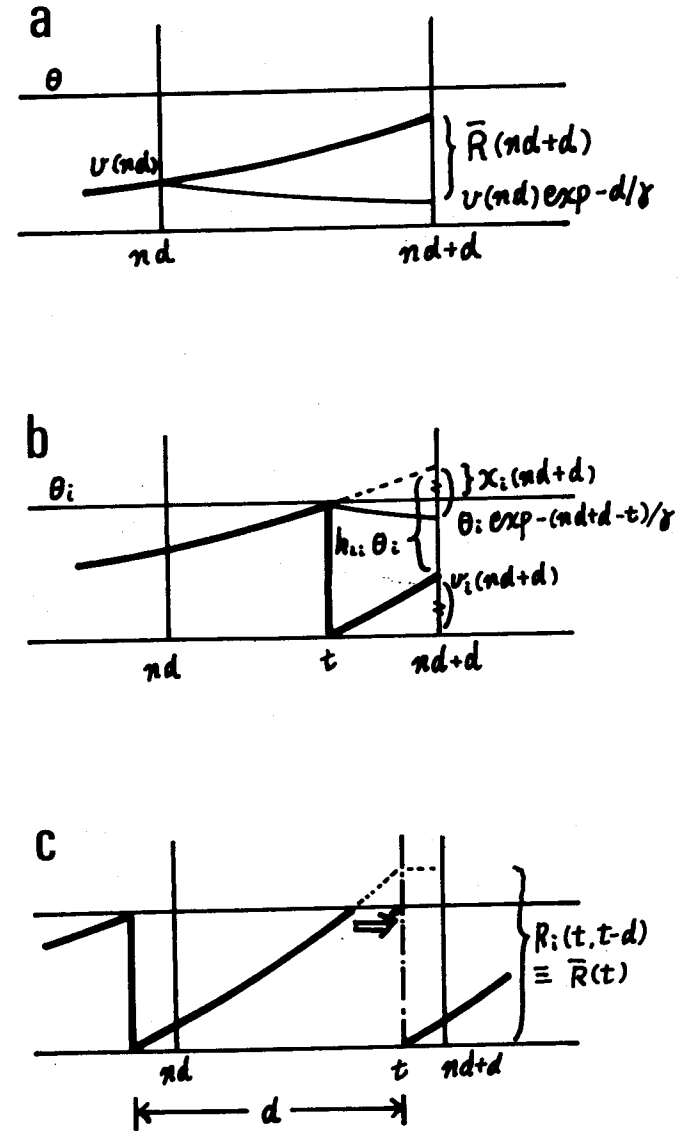


Fig. 2. The actual time development of a membrane potential is illustrated in the thick real line. The dotted line is a hypothetical potential introduced here. a, An input is small and a cell is not excited between time  $nd$  and  $nd+d$ . b, An input is larger than in the case a and a cell is excited. c, An input is so large that a membrane potential reaches a threshold twice an interval  $d$ .

hypothetical potential is introduced as the modification of an actual membrane potential to define a cell firing or no-firing. The hypothetical potential at time  $t$  is defined as the sum of the liquidated value ( $k_{Li}(nd+d)\theta_i$ ) and the psp growing until  $t$  after liquidation. A liquidation parameter works when a cell fires between the present observation time,  $nd+d$  and the last observation time,  $nd$ , i.e.,  $\sigma(nd+d)=1$ ;

$$(3) \quad x_i(nd+d) = v_i(nd+d) - [1 - \sigma(nd+d) k_{Li}(nd+d)] \theta_i,$$

where the level of  $x_i$  is transferred by  $\theta_i$  because a cell is judged to be excited if and only if the sum of  $x_i$ s is positive,

$$(4) \quad \begin{aligned} \sigma(t) &= 1 [ \sum I_i x_i(t) ], \\ &= \begin{cases} 1, & \text{for } \sum I_i x_i \geq 0, \\ 0, & \text{for } \sum I_i x_i < 0, \end{cases} \\ \theta &= \sum I_i \theta_i. \end{aligned}$$

The individual  $\theta_i$ s introduced here are the hypothetical thresholds. It is permitted to set them arbitrarily under the condition that the sum and integral of them is a threshold of a membrane ( $\theta$ ). It is noticed that the firing of a cell is judged by  $X (= \sum I_i x_i)$  exceeding  $\theta$  and not by an individual  $x_i$ . The time development of  $x_i$  will be obtained from that of the membrane potential ( $v_i$ ). The value of  $v_i$  at  $nd+d$  is the sum of relaxed  $v_i(nd)$ , a psp of  $\bar{R}_i(nd+d)$  and a liquidated value if a cell fires between  $nd$  and  $nd+d$ : the value is changed whether an absolute refractoriness works or not. When an input reaches a threshold only once during  $d$  ( $\sigma=1$ ), the liquidation value is a threshold value relaxed after firing ( $b$  in Fig. 2), because, if the cell fires at  $t'$  and  $t$ ,

$$\begin{aligned} \sum v_i(nd+d) &= \sum I_i R_i(nd+d, t) \\ &= \sum I_i [ R_i(nd+d, t) - b(nd+d-t) R_i(t, t') \sigma(nd+d) ] \\ &= \sum I_i [ b v_i(nd) + R_i(nd+d, nd) - k_{Li}(nd+d) \theta_i \sigma(nd+d) ], \end{aligned}$$

and, here,  $R(t, t') = \theta_i$  and

$$k_{Li} = b(nd+d-t).$$

If an input is so large that a potential faces a threshold within  $d$  after the last firing time ( $c$  in Fig. 2), the firing is prolonged until an absolute refractory period passes (an arrow in the figure) and, in this case, the liquidation value is the potential at the time of firing being allowed;

$$\begin{aligned} \sum v_i(nd+d) &= \sum I_i R_i(nd+d, t) \\ &= \sum I_i [ R_i(nd+d, t-d) - b(nd+d-t) R_i(t, t-d) ] \\ &= \sum I_i [ b v_i(nd) + \bar{R}_i(nd+d) - k_{Li}(nd+d) k_r \bar{R}_i(nd+d) ] \end{aligned}$$

and, in the last equation, it is assumed that  $\bar{R}$  varies slowly during  $d$  and  $\bar{R}(t)$  is approximated by  $\bar{R}(nd+d)$ . A refractory parameter is defined as

$$(5) \quad k_r(nd+d) = 1 [ \bar{R}(nd+d) - \theta ] \sigma(nd)$$

In the three cases stated above, the time development of  $v_i$  is finally described by

$$(6) \quad \begin{aligned} v_i(nd+d) &= b v_i(nd) + \bar{R}_i(nd+d) + [ k_r(nd+d) - \sigma(nd+d) ] k_{Li}(nd+d) \theta_i - \\ &\quad - k_r(nd+d) k_{Li}(nd+d) \bar{R}(nd+d). \end{aligned}$$

Substituting this into Eq. (3), we obtain

$$(7) \quad \begin{aligned} x_i(nd+d) &= b x_i(nd) - b \sigma(nd) k_{Li}(nd) \theta_i + [ 1 - k_r(nd+d) k_{Li}(nd+d) ] \times \\ &\quad \times H_i(nd+d) + b k_r(nd+d) k_{Li}(nd+d) \theta_i, \end{aligned}$$

where

$$(8) \quad H_i(t) = \bar{R}_i(t) - (1-b) \theta_i.$$

Using Eq. (5), the sum of  $x_i$ s, i.e., the hypocritical potential of a cell is

$$(9) \quad \begin{aligned} X &= \sum I_i b x_i(nd) - \sigma(nd) \sum I_i b k_{Li}(nd) \theta_i + \sum I_i [ 1 - k_r(nd+d) \times \\ &\quad \times k_{Li}(nd+d) ] H_i(nd+d) + k_r(nd+d) \sum I_i k_{Li}(nd+d) b \theta_i, \end{aligned}$$

where  $X = \sum I_i x_i$ .

### 3. A flux-gradient law

The neural event has discontinuous features in its time development such as arrival of signals and the reset of the membrane potential. Since the membrane potential already lost its discontinuous feature by being averaged with respect to the fluctuations of the arrival of the signals, it will satisfy a flux-gradient relationship like a hydrodynamic phenomenon in a continuous flow during a limited time interval  $d$ . In this section, a general flux-gradient law is given to a quantity as the function of a hypothetical potential. If the variation of the probability of stimulus coming is small during  $d$  (in other words, inputs are in a stationary state), a brief time interval, the firing times are distributed uniformly during  $d$ . This is called *d-range uniformity*. Let's denote a function of  $x_i$  ( $i=1, \dots, N$ ) by  $Y(x)$ . The velocities of  $Y$ 's at the maximum  $Y$  and the minimum of it are obtained from the equation of the time development of  $x_i$ 's in the states of the maximum  $X$  and zero of  $X$ . When  $X$  takes the maximum value, a cell does not encounter liquidation except at the beginning of a new period (Fig. 3), and the development of  $v_i$  during  $d$  is given by

$$v_i(t) = v_i(nd) \exp - (t - nd) / \gamma + R_i(t, nd).$$

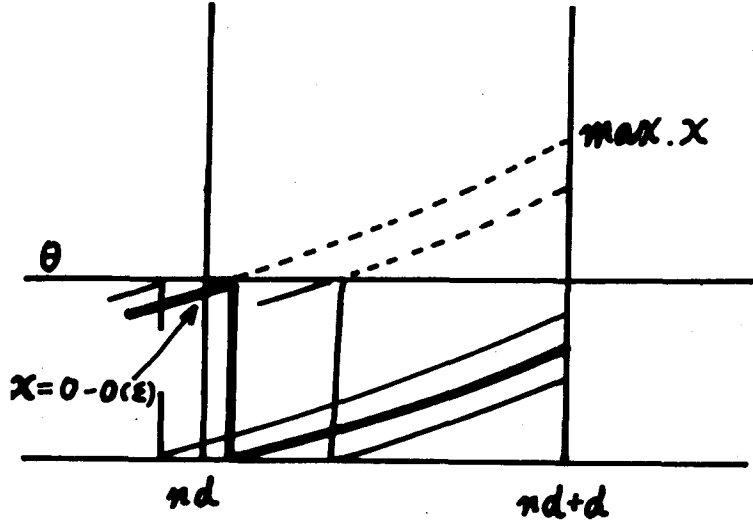


Fig. 3. The maximum  $X$  at  $nd+d$  comes from  $v=0-0(\epsilon)$  at  $nd$ . In other cases (narrow real lines),  $X(nd+d)$ s are smaller than  $\max(X)$ .

From Eq. (2) with  $d$ -range uniformity, and with  $Q(s)=1/d$ ,  $\bar{R}_i = H_i - (1-b)\theta_i = a_i(1-b)/d$ . We have

$$(10) \quad v_i(t) = v_i(nd) \exp-(t-nd)/\gamma + [H_i + (1-b)\theta_i]d / [(1-b)\gamma] \times \\ \times \int_{nd}^t \exp-(t-s)/\gamma ds \text{ for } nd \leq t \leq nd+d.$$

The velocity is given by

$$v_i(t) = [-v_i(nd)/\gamma + \theta_i d/\gamma + H_i d/(1-b)\gamma] \exp-(t-nd)/\gamma.$$

The velocity of  $v_i$  at the maximum  $X (= \sum I_i H_i)$  is given by putting  $v_i(nd) = \theta_i$ ; see Fig. 3), while the point  $X(=0)$  at  $nd+d$  comes from the point  $v_i(nd) (= -\sum I_i H_i/b)$  because  $\sigma(nd) = 0, k_r = 0$  in Eq. (9). The velocity at  $X(=0)$  is, therefore, given by putting  $v_i(nd) = -H_i/b + \theta_i$ . Since the velocity of  $x_i (= H_i$  or  $0$ ) at  $t (= nd+d)$  is equal to that of  $v_i (= \theta_i$  or  $-H_i/b + \theta_i)$ , the velocity of  $Y$  is obtained

$$\dot{Y}_1 = \sum I_i \delta Y / \delta x_i \xi_i, \text{ at } Y(U), \\ \dot{Y}_2 = \sum I_i \delta Y / \delta x_i (\xi_i/b), \text{ at } Y(0),$$

where  $\xi_i = bH_i/(1-b)\gamma$ .

For  $\delta t \ll 1$ , we obtain

$$\langle \sigma(nd+d+\delta t) \rangle = \int_{Y(0)}^{Y(U)} g(Y, H; nd+d+\delta t) dY \\ = \int_{Y(0)-\dot{Y}_2 \delta t}^{Y(U)-\dot{Y}_1 \delta t} g(Y, H; nd+d) dY \\ = \int_{Y(0)-\dot{Y}_1 \delta t}^{Y(U)-\dot{Y}_1 \delta t} g dY + \int_{Y(0)-\dot{Y}_2 \delta t}^{Y(0)-\dot{Y}_1 \delta t} g dY.$$

From series expansion of  $\langle \sigma(nd+d+\delta t) \rangle$ , we have

$$(11) \quad d^m \langle \sigma(t) \rangle / dt^m = (-1)^{m+1} [g^{(m-1)}(Y(0), H; nd+d) - \\ - g^{(m-1)}(Y(U), H; nd+d)] (\sum I_i \delta Y / \delta x_i \xi_i)^m + \\ + (-1)^{m+1} g^{(m-1)}(Y(0), H; nd+d) (\dot{Y}_1^m - \dot{Y}_2^m).$$

#### 4. A continuous approach

A membrane has a noise called *membrane noise*. The origin of the noise is thought of as Johnson noise, the fluctuation of the activation of the ion channel on a membrane and the fluctuated emission of chemical transmitters from the presynaptic membrane. The noise of the fluctuated channels, the largest one of the above noises, is evaluated as about 4% of a threshold value (Lecar and Nossal, 1971). The noise will make the firing random and the curve of firing rate versus averaged membrane potential, therefore, become rather smooth than a concrete step function. For this reason, we adopt the following mathematical approach in which a step function of firing is given by the limit or the approximation of a continuous function.

A continuous-differentiable function which approaches a unit step function at the limit of  $\epsilon \rightarrow 0$  is denoted by  $k(Y)$ , where  $Y$  is a linear combination of  $x_i$ s ( $i=1, \dots, N$ ). The function  $k$  is usually a sigmoidal function. Wherever  $k$  is any

function having the property of approaching zero or unit as  $Y$  approaches  $-0$  or  $0$ , respectively, it can be approximated as a linear function of  $Y$  for small  $\varepsilon$  such as

$$(12) \quad k(Y) = \varepsilon Y/Y(0) + q(1 - \varepsilon) + (1 - q)\varepsilon,$$

where

$$q(Y) = \begin{cases} 0 & \text{for } Y < -\Delta\varepsilon + Y(0) \\ 1 & \text{for } Y > \Delta\varepsilon + Y(0), \end{cases}$$

$$Y(\theta) = Y(\theta_1, \theta_2, \dots, \theta_N),$$

and it is supposed that  $k$  on both sides of  $Y=0$  are connected with each other smoothly between  $-\Delta\varepsilon$  and  $+\Delta\varepsilon$  ( $\Delta\varepsilon \ll \varepsilon \ll 1$ ). In the following calculation, the condition that  $Y=0$  if  $X=0$  is introduced. This is referred to as *zero-linearization*, for simplicity. Denoting the upper value and the lower value of  $Y$  by  $Y(U)$  and  $Y(L)$ , respectively, the average of  $k$  is calculated as

$$(13) \quad \langle k(t) \rangle = \int_{-\infty}^{\infty} k(Y(X))g(X, H; t)dX \\ = [\varepsilon/Y(0)] \int_0^{Y(U)} (Y - Y(0))g(Y, H; t)dY + \int_0^{Y(U)} g(Y, H; t)dY + \\ + [\varepsilon/Y(0)] \int_{Y(L)}^0 (Y + Y(0))g(Y, H; t)dY.$$

For an arbitrary value of  $A$  and  $B$ , an Euler-Maclaurin expansion gives

$$(14) \quad \int_0^A (Y+B)g(Y, H; t)dY = \sum_{j=0}^{\infty} [(-Y(U))^{j-1}/j!] [g^{(j-1)}(Y(0), H; t) - \\ - g^{(j-1)}(Y(U), H; t)] \int_0^A (Y+B)B_j((Y-Y(U))/-Y(U))dY,$$

where

$$g^{(-1)}(x, H; t) = \int_0^x g(y, H; t)dy,$$

and  $B_j$  is a Bernoulli polynomial. Denoting the angular velocity of  $\langle \sigma \rangle$  by  $\omega$  and substituting the flux-gradient equation of (11) under the approximation of  $\dot{Y}_1 \approx \dot{Y}_2$ , we have

$$(15) \quad \int_0^A (Y+B)g(Y, H; t)dY = \int_0^A (Y+B) \sum_j [(-Y(U))^{j-1}/j!] (-1)^{j+1} \dot{Y}_1^{-j} \times \\ \times d^j \langle \sigma \rangle / dt^j B_j((Y-Y(U))/-Y(U))dY \\ = \langle \sigma \rangle \int_0^A (Y/Y(U) + B/Y(U)) \sum (Y(U)\omega/\dot{Y}_1)^j B_j(1 - Y/Y(U))/j! dY \\ = \langle \sigma \rangle Y(U) \int_1^{1-A/Y(U)} (y-1-B/Y(U)) \sum z^j B_j(y)/j! dy \\ = \langle \sigma \rangle Y(U) z \int_1^{1-A/Y(U)} (y-1-B/Y(U)) \exp(zy) dy / (\exp(z) - 1) \\ = \langle \sigma \rangle B \exp(z) [Bz + Y(U) - ((B+A)z + Y(U)) \exp(-Az/Y(U))] / z(\exp(z) - 1) \\ = \langle \sigma \rangle [6BY(U)A + 3Y(U)A^2 + \{6BY(U)A + 3(Y(U) - B)A^2 - \\ - 2A^3\}Z + \dots] / 6Y(U)^2,$$

where  $z = Y(U)\omega/\dot{Y}_1$ .

When the variation of  $\langle \sigma \rangle$  is so slow that higher orders of  $z$  can be neglected, i.e., if the above series expansion is approximated only by the zero-th order of  $z$ , we put  $A = Y(U)$  or  $Y(L)$  and  $B = -Y(\theta)$  or  $Y(\theta)$  in Eq. (14) and have

$$\langle k \rangle = [1 + \varepsilon(Y(U)^2 - 2Y(\theta)Y(U) - Y(L)^2 - 3Y(\theta)Y(L))/2Y(\theta)Y(U)]$$

$$\langle \sigma \rangle + 0(\varepsilon).$$

Equation (12) gives

$$(16) \quad \varepsilon Y/Y(0) = k - (1 - 2\varepsilon)q - \varepsilon$$

and the average of  $Y$  is obtained as

$$(17) \quad \langle Y \rangle = \langle \sigma \rangle [Y(U)^2 + 2Y(\theta)Y(U) - Y(L)^2 - 2Y(\theta)Y(L)] / 2Y(U) - Y(\theta) + 0(\varepsilon) + 0(\Delta\varepsilon),$$

where  $\langle q \rangle$  is calculated as

$$\begin{aligned} \langle q \rangle &= \left( \int_{\Delta\varepsilon}^{\infty} + \int_{-\infty}^{-\Delta\varepsilon} \right) q(Y)g(Y, H; nd+d)dY \\ &= \int_{\Delta\varepsilon}^{\infty} g dY + 0(\Delta\varepsilon) \\ &= \langle \sigma \rangle + 0(\Delta\varepsilon). \end{aligned}$$

### 5. Difference equation

In order to obtain the average of Eq. (7), the averages of  $\sum I_i x_i (= \sum x_i)$  and  $\sum I_i b x_i$  must be calculated. When  $Y(X) = \sum I_i x_i$ ,  $Y(U) = U (= \sum I_i u_i)$  and  $Y(L) = L (= \sum I_i l_i)$ ,  $Y(\theta) = \theta$ , we have from Eq. (17),

$$(18) \quad \langle \sum I_i x_i \rangle = \langle \sigma \rangle (U^2 + 2\theta U - L^2 - 2\theta L) / 2U - \theta.$$

When  $Y(X) = \sum I_i b x_i$ ,  $Y(U) = \sum I_i b u_i$  and  $Y(L) = \sum I_i b l_i$ ,  $Y(\theta) = \sum I_i b \theta_i = b_0 \theta$  in Eq. (17),

$$(19) \quad \langle \sum I_i b x_i \rangle = \langle \sigma \rangle [(b_1 U)^2 + 2b_0 \theta (b_1 U) - (b_2 L)^2 - 2b_0 \theta (b_2 L)] / 2b_1 U - b_0 \theta,$$

where

$$(20) \quad b_0 = \sum I_i b \theta_i / \theta,$$

$$(21) \quad b_1 = \sum I_i b H_i / \sum I_i H_i,$$

$$(22) \quad b_2 = \sum I_i b (H_i - b \theta_i) / \sum I_i (H_i - b \theta_i).$$

Next the liquidation parameter is calculated. When a cell fires at  $t$  between  $nd$  and  $nd+d$ , i.e.,  $\sigma(nd+d) = 1$ , from its definition,

$$(23) \quad \begin{aligned} k_{Li} &= \exp -(nd+d-t) / \gamma \\ &= b \exp -(nd-t) / \gamma \\ &= b [(1-b)v_i(nd) - H_i - (1-b)\theta_i] / [(1-b)v_i(t) - H_i - (1-b)\theta_i]. \end{aligned}$$

Since  $v_i(t) = \theta_i$ ,

$$(24) \quad k_{Li} = b [H_i - (1-b)(v_i(nd) - \theta_i)] / H_i.$$

In the case that  $\sum I_i H_i \leq \sum I_i b \theta_i$ ,  $k_r = 0$  and we have from putting  $x_i(nd) = v_i(nd) - \theta_i$  in Eq. (7) with  $\sigma(nd) = 0$ ,

$$v_i(nd) = [x_i - (H_i - b\theta_i)] / b,$$

then,

$$(25) \quad k_{Li} = 1 - (1-b)x_i / H_i.$$

The average of  $b k_{Li} \sigma \theta_i$  is given by

$$(26) \quad \begin{aligned} \langle b k_{Li} \sigma \theta_i \rangle &= \int_{-\infty}^{\infty} b [1 - (1-b)x_i / H_i] \sigma \theta_i g(x_i, H_i; nd+d) dx \\ &= \int_0^{u_i} b \theta_i [1 - (1-b)x_i / H_i] g dx_i \\ &= b \theta_i \langle \sigma \rangle - [b \theta_i (1-b)] / H_i \int_0^{u_i} x_i g dx_i \\ &= b \theta_i \langle \sigma \rangle - [b \theta_i (1-b)] / H_i \int_0^{u_i} x \langle \sigma \rangle dx_i / u_i \\ &= b \theta_i \langle \sigma \rangle - [b \theta_i (1-b)] / H_i \cdot u \langle \sigma \rangle / 2 \\ &= b \theta_i \langle \sigma \rangle (1+b) / 2, \end{aligned}$$

where the fourth column is the 0-th order approximation of the calculation by the flux-gradient law. Then the sum is obtained as

$$(27) \quad \begin{aligned} \sum I_i (b k_{Li} \sigma \theta_i) &= \sum I_i b (1+b) \theta_i \langle \sigma \rangle / 2 \\ &= b_1 k_L \theta \langle \sigma \rangle, \end{aligned}$$

where

$$(28) \quad k_L = \sum I_i b(1+b) \theta_i / 2b_1 \theta$$

In the case  $H > \sum I_i b \theta_i$ , a cell does not miss firing. If an input  $\bar{R}$  varies slowly, a cell fires every discrete time and

$$k_{L_i}(nd+d) = k_{L_i}(nd) = k_{L_i}(nd-d) = \dots = k_{L_i} \text{ at } H_i = b\theta_i$$

Therefore, using the equality that  $k_r \sigma = k_r$ , we have

$$\begin{aligned} \langle k_r k_{L_i} H_i \rangle &= \langle k_r k_{L_i} \sigma H_i \rangle \\ &= k_r \langle k_{L_i} \sigma H_i \rangle \\ &= k_r \int_0^{u_i} [1 - (1-b)x_i/H_i] H_i g dx_i \\ &= k_r H_i (1+b) / 2. \end{aligned}$$

The sum is given by

$$(29) \quad \begin{aligned} \sum I_i \langle k_r k_{L_i} H_i \rangle &= k_r \sum I_i (1+b) H_i / 2 \\ &= \langle k_r k_L \rangle H_i, \end{aligned}$$

where

$$\langle k_r k_L \rangle = k_r \sum I_i (1+b) H_i / 2H.$$

Substituting Eqs (18), (19), (27), (29) into Eq. (9), we have

$$(30) \quad \begin{aligned} \langle \sigma(nd+d) \rangle &= \langle \sigma(nd) \rangle [ (b_1 \beta U)^2 + 2(b_1 \beta U)(b_0 - b_1 k_L) - (b_2 \beta L)^2 - \\ &\quad - 2b_0(b_2 \beta L) ] / b_1 [ (\beta U)^2 + 2\beta U - (\beta L)^2 - 2(\beta L) ] + \\ &\quad + 2\beta U [ (1 - \langle k_r k_L \rangle)(\beta H - b_0) + \beta ] / \\ &\quad [ (\beta U)^2 + 2(\beta U) - (\beta L)^2 - 2(\beta L) ], \end{aligned}$$

where

$$\beta = 1/\theta.$$

Comparing Eq. (30) with the solution of a differential equation

$$(31) \quad (\tau/d) \times d\langle \sigma \rangle / dt = -\langle \sigma \rangle + h$$

we can find that

$$(32) \quad \begin{aligned} \tau/d &= \ln [ (\beta U)^2 + 2(\beta U) - (\beta L)^2 - 2(\beta L) ] - \ln [ (b_1 \beta U)^2 + \\ &\quad + 2(b_1 \beta U)(b_0 - b_1 k_L) - (b_2 \beta L)^2 - 2b_0(b_2 \beta L) ] + \ln b_1, \\ (33) \quad h &= 2b_1(\beta U) [ (1 - \langle k_r k_L \rangle)(\beta H - b_0) + \beta ] / [ b_1(1 - b_1)(\beta U)^2 + \\ &\quad + 2(1 - b_0 + b_1 k_L)(b_1 \beta U) - (b_1 - b_2^2)(\beta L)^2 - 2(b_1 - b_0 b_2)(\beta L) ]. \end{aligned}$$

$X$  takes the upper value at time  $nd+d$  when an input is not so large as  $k_r=1$  and  $X$  encounters liquidation immediately after a new unit period begins (see Fig. 3), i.e.,  $X(nd) = 0 - 0(\epsilon)$ ,  $\sigma(nd) = 0$  and  $k_r(nd+d) = 0$ . From Eq. (9), the upper bound is given as

$$U = H.$$

Then we can put the upper bound of individual  $x_i$  as

$$u_i = H_i.$$

The lower bound of  $X(nd+d)$  comes from  $X(nd) (= 0 + 0(\epsilon))$ . In this case, the liquidation occurred slightly before time  $nd$  and, therefore,  $k_{L_i}(nd) = 1$  and  $\sigma(nd) = 1$ . The lower bound takes two values according as  $k_r = 1$  or 0. If an input is too large to make a cell fire every discrete time, i.e.,  $\sigma(nd) = 1$ ,  $k_r = 1$ ,  $k_{L_i} = 1$ ,  $\sum I_i b x_i = 0$  in Eq. (9), the lower bound is zero. An input yielding this situation is  $\bar{R} \geq \theta$ , i.e.,  $H \geq \sum I_i b \theta_i$ . If an input is not so large,  $\sigma(nd) = 1$ ,  $k_r = 0$ ,  $k_{L_i} = 1$  and  $\sum I_i b x_i = 0$  in Eq. (9), and the lower bound is  $H - \sum I_i b \theta_i$ :

$$L = \begin{cases} H - \sum I_i b \theta_i & \text{for } H \leq \sum I_i b \theta_i \\ 0 & \text{for the others.} \end{cases}$$

## 7. Conclusion

It is widely observed in a spinal cord and a brain that the excitation times of sensory organs and neurons are fluctuated. Those distributions of fluctuated response to a stimulus are spread over 40 msec at the lowest. The distribution in a short range of  $d$  ( $\approx 1$  msec), therefore, can be thought of being approximately uniform. Under the  $d$ -range uniformity, the time averaged amplitude of a psp due to the activation of the  $i$ -th synapse is given as

$$(34) \quad \bar{R}_i = a_i c_i \sigma_i.$$

where

$$(35) \quad c_i = \int_0^\infty d(1/\gamma) P_{i,L}(1/\gamma) (1 - \exp - d/\gamma) \gamma / d.$$

Here, the average of  $b (= \exp - d/\gamma)$  with respect to the input is defined as

$$(36) \quad \begin{aligned} \bar{b} &= \exp - d/\bar{\gamma} \\ &= \Sigma I_i b \bar{R}_i / \Sigma I_i \bar{R}_i \\ &= \Sigma a_i b_i \sigma_i / \Sigma a_i c_i \sigma_i, \end{aligned}$$

where

$$(37) \quad b_i = \int_0^\infty d(1/\gamma) P_{i,L}(1/\gamma) \exp - d/\gamma (1 - \exp - d/\gamma) \gamma / d.$$

When one of the synapses has the relaxation coefficient very close to  $\bar{\gamma}$  defined above, Eqs (32), (33) have the easily calculable form by setting the hypothetical threshold of the synapse as  $\theta$  and the others as zero. This set makes all of  $b_0$  in Eq. (20),  $b_1$  in Eq. (21),  $b_2$  in Eq. (22) equal to  $\bar{b}$ , and Eqs (32), (33) become

$$(38) \quad \tau/d = \ln[x^2 + 2x - y^2 - 2y] - \ln[x^2 + (1 - \bar{b})x - y^2 - 2y] - \ln \bar{b}$$

$$(39) \quad h = 2x[(1 - k_r k_L)(x - \bar{b}) + \beta] / [(1 - \bar{b})x^2 + 2(k_L + (1 - \bar{b})(1 - k_L))x - (1 - \bar{b})y^2 - 2(1 - \bar{b})y]$$

$$(40) \quad x = \beta \{ \bar{R} - (1 - \bar{b}) \}$$

$$(41) \quad k_L = (1 + \bar{b})/2$$

$$\beta = 1/\theta$$

$$k_r = \begin{cases} 1 & \text{for } x > \bar{b}, \text{ i.e., } \bar{R} > \theta \\ 0 & \text{for } x < \bar{b}, \text{ i.e., } \bar{R} < \theta \end{cases}$$

$$y = \begin{cases} x - \bar{b} & \text{for } x < \bar{b}, \text{ i.e., } \bar{R} < \theta \\ 0 & \text{for } x > \bar{b}, \text{ i.e., } \bar{R} > \theta. \end{cases}$$

$$\bar{R} = \Sigma_i \bar{R}_i.$$

Equations (38), (39) are different from the equation obtained in the previous paper (1976), which treated the neuron having only one value of a psp's relaxation, in the point that the average  $\bar{b}$  varies with the distribution of the inputs  $\bar{R}_i (i = 1, \dots, N)$ .

In a neural system, the input  $R$  in Eq. (2) is fluctuated due to the fluctuations of the excitations of the neurons or the sensory organs contributing to  $R$ . The final equations are, therefore, given by the averaging Eqs (38), (39) with respect to the firing probabilities of those inputs;

$$\begin{aligned} \langle\langle \tau/d \rangle\rangle &= \sum_{\substack{\sigma_1=0 \\ \text{or } 1}} \sum_{\substack{\sigma_2=0 \\ \text{or } 1}} \dots \sum_{\substack{\sigma_N=0 \\ \text{or } 1}} \tau/d f(\sigma_1, \sigma_2, \dots, \sigma_N) \\ \langle\langle h \rangle\rangle &= \sum_{\substack{\sigma_1=0 \\ \text{or } 1}} \sum_{\substack{\sigma_2=0 \\ \text{or } 1}} \dots \sum_{\substack{\sigma_N=0 \\ \text{or } 1}} h f(\sigma_1, \sigma_2, \dots, \sigma_N), \end{aligned}$$

where the sum is taken over all of the cases  $\sigma_i = 1$  or  $0 (i = 1, \dots, N)$  and  $f(\dots)$  is the probability of it.

Finally, the conditions are summarized, partially the same as in the case of a single value of  $\gamma$ .

1. The input fluctuation is uniformly distributed in a brief interval of an absolute refractory period. This condition is able to be satisfied because the interval in the condition is extremely small.

2. The firing probability varies so slowly that the angular velocity is smaller than  $b/((1 - b)\gamma)$ .

3. A system has a synapse of which psp has the relaxation time close to the average of the relaxation times with respect to the activated synapses. This condition is easily satisfied when a neuron has a large number of synapses.

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