The Differential Operation by Neural Assembly

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1. Introduction

A great number of studies have been conducted on the way how information is expressed in brain. Among these, synfire chain hypothesis, which was proposed by Abeles [1], is a well-known study. According to the hypothesis, information is expressed by a spike packet, which is composed by coincident spikes that synchronously propagate through the neural network. The stability of this propagation was discussed by a numerical simulation [2] and theoretical analysis of the Fokker-Planck equation [3].

However, little is known about the mechanism of encoding external information into spike packets and that of decoding spike packets. Since it is difficult for brain to deal completely with external information, it is natural that some efficient processes such as information reduction or principal component extraction are done in the encoding and decoding processes. Our quick perception suggests that these efficient processes must be carried out very quickly. There has been no study that tries to explain such rapid and efficient processes with a realistic neural model.

The above-mentioned processes are based on information transmission among single neurons. However, cortical neurons have several characteristics that seem to be inappropriate for efficient information transmission. The first is feedback inhibition due to interneurons [4] that are electrically connected with each other through gap junctions [5, 6]. It is likely that in this firm inhibitory feedback network the activation of an excitatory neuron inhibits not only itself but also the other excitatory neurons to a large extent. Then, the feedback inhibition may suppress the propagation of spike packets. The second is the existence of chemical connections among excitatory neurons. Unreliable transmission via chemical connections causes synaptic depression phenomena [7]; namely, only the first few spikes in sequential spikes generated by a presynaptic neuron are transmitted to postsynaptic neurons. This depression may interrupt plural spike packets to be transmitted within a short interval, hence it is hard for neurons to express information by combining plural packets. Moreover, it is shown by experiments and numerical simulations that a neuron is sensitive to stimulus change more than stimulus amplitude [8–11]. It is also suggested that excitatory stimulus decreases the membrane decay time constant [12]. Neurons thus modulate its way to process information.

This article discusses the hypothesis of differential code realized by a neural assembly. This hypothesis includes and supports the synfire chain hypothesis and is implied by possible functions of the firm and wide feedback inhibition, the synaptic depression, and the sensitivity to stimulus change. It is shown that the differential code fails to work if one of these functions is absent. It is also discussed that the differential code has many advantages in the information processing in brain.

2. Models

In this study, an excitatory neuron is modeled by a Hodgkin-Huxley type ionic conductance model composed of a single compartment [13]. The model of an inhibitory neuron is described in the caption of Figure 1. The membrane potential V(mV) is expressed as the following differential equation:

$$C_m \frac{dV}{dt} = -I_{Na} - I_K - I_l - I_{syn}, \tag{1}$$

where coefficient C_m is the membrane capacitance (1.0μF/cm^2). Currents (μA/cm^2) in the right hand side are a fast sodium current I_{Na}, a delayed rectifier potassium current I_K, a leak current I_l, and a synaptic current I_{syn}. Parameters for these currents are described in Table 1.

Synaptic current I_{syn} is the sum of excitatory (reversal potential $E_{exc} = 0$mV) and inhibitory ($E_{inh} = -70$mV) synaptic currents. Synaptic conductance induced by the ith synaptic event is defined by an α function [14, 15]:

$$g_{syn}(i) = \frac{g_{peak} \cdot (t - t(i))}{t_{peak} \cdot S} exp\left(1 - \frac{t - t(i)}{t_{peak}}\right) \cdot r(i), \tag{2}$$

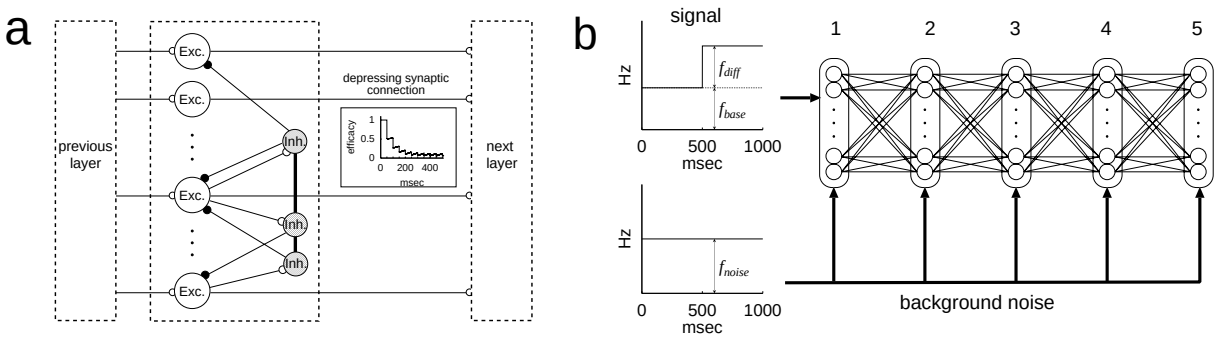

Figure 1: **a**. Network architecture of a single layer. N_e excitatory neurons have no connection with each other, but inhibitory feedback connections via inhibitory interneurons. When an excitatory neuron provokes a spike, instead of the actual calculation of inhibitory neurons, it sends inhibitory input to N_r excitatory neurons that are randomly selected in advance (allows itself and overlaps). This inhibitory feedback input has delay time d chosen from an uniform distribution $U(5.0, d_r)$ (msec). The inset shows the transmission efficacy with $\delta = 0.5$, when synaptic events are provided periodically with 50 msec period. **b**. The whole network is composed of layers described in **a**. There are depressing synaptic connections between every neuron pairs from a presynaptic layer to a postsynaptic one. A signal is input into only the leftmost layer and a background noise is input into all layers. The input frequency (Hz) of the signal changes as a step function (from f_{base} to f_{diff}), while the background noise has a constant frequency f_{noise}. Each input is an independently stochastic event simulated by a Poisson process.

Table 1: Parameters of ionic currents

current (μA/cm^2)	conductance (mS/cm^2)	reversal potential(mV)
I_{Na}	$120.0m^3h$	$50.0 - E_r$
I_K	$36.0n^4$	$-77.0 - E_r$
I_k	0.3	$-54.4 - E_r$

Variables in the conductance, m, h, and n, obey the differential equation $dx/dt = \alpha_x(1-x) - \beta_x x$, where $x = m, h, n$. Voltage-dependent functions α_x and β_x are referred to [13]. The resting potential $E_r = -65.0$ mV.

where $t(i)$ is the time of the ith synaptic event and t_{peak} is the interval between $t(i)$ and the time at which the conductance reaches its peak value g_{peak} (nS); $t_{peak} = 2.0$ and $g_{peak} = 0.3$ for excitatory synapses, and $t_{peak} = 5.0$ and $g_{peak} = 5.0$ for inhibitory synapses. S denotes the surface area of a soma that is regarded as a sphere with radius 20μm. $r(i)$ is the efficacy of synaptic transmission; $r(i)$ is constant $r(i) = 1.0$ for inhibitory synapses and varies for excitatory ones. In order to simulate the synaptic depression, excitatory $r(i)$ is multiplied by δ $(0 < \delta \leq 1)$ after the ith synaptic event; without synaptic events, it exponentially recovers toward 1.0 with time constant τ_e. The inset in Figure 1**a** shows the behavior of the transmission efficacy $r(i)$ when synaptic events occur periodically.

The network consists of cortical areas, each of which is represented by a single layer consisting of excitatory and inhibitory neurons (Figure 1**a**). Figure 1**b** shows synaptic connections between presynaptic and postsynaptic layers. All the connections have the depressing effect ($\delta < 1$).

Two kinds of external inputs are provided to the network. One kind is visual stimuli, which are assumed to be provided from the outside of brain through brain parts like thalamus. Visual information or contrast is represented by the frequency. The other is background noise, which is assumed to be produced in the other brain areas.

3. Results

This article examines the internal coding scheme within a neural network. Since information from the outside of brain is not constant but variable, we examine the network's response to stepwise changes in the frequency. A step is assumed to signify the difference in the visual contrast. Sample responses are shown in Figure 2. Each layer is insensitive to the amplitude of the input frequency, while it responds well to the differential of the input frequency. The first layer encodes the frequency change into a spike packet, and each of the higher layers transmit the spike packet into the next layer. In particular, the second layer amplifies the differential information detected in the first layer. If the inhibition is weak, erroneous spike packets appear before the step change (Figure 3). If the depressing effect is removed, in contrast, higher layers generate spike packets even after the step change (Figure 4). These results show that depressing synapses prevent continuous spikes from propa-

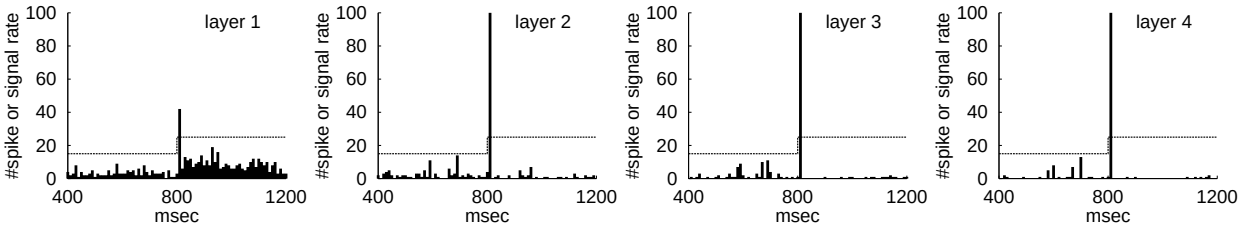

Figure 2: Sample responses of the network consisting of four layers (10 msec bin). Parameters are $\delta = 0.5$, $\tau_e = 800$, $N_e = 200$, $N_r = 100$, $d_r = 1000$, $f_{base} = 500$, $f_{diff} = 1000$, and $f_{noise} = 1000$. The input frequency increases stepwise by f_{diff} at $t = 800$ msec (dotted line, 1/100 scale).

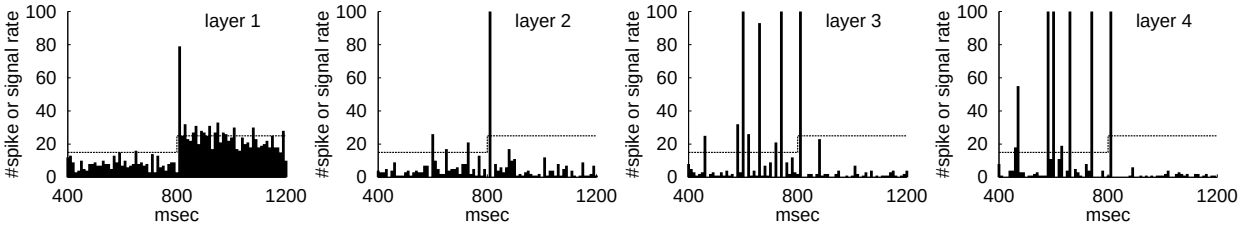

Figure 3: Same as Fig. 2 but the inhibition is weak (inhibitory $g_{peak} = 0.5$).

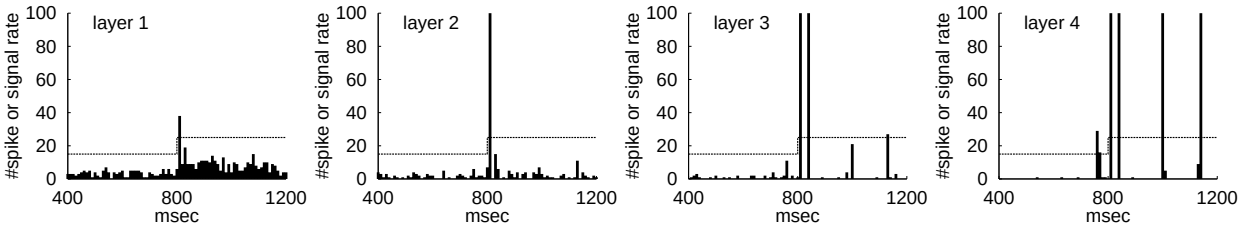

Figure 4: Same as Fig. 2 but the depressing effect is removed ($\delta = 1.0$).

gating to the next layer and that the feedback inhibition works to suppress erroneous activities before the input change and make layers prepare to detect the next input change. Consequently, the depressing synapses and the feedback inhibition work to transmit stably and accurately a spike packet that represents input change.

Stochastic resonance is a phenomenon in which background noise enhances sensitivity of a nonlinear system so to detect a weak signal [11, 16–19]. The effect of the background noise is shown in Figure 5. The layers exhibit stochastic resonance phenomena; when noise of a certain intensity exists, the differential detection realized in the layers is optimized.

4. Discussion

In this article, the differential code hypothesis is examined. The differential code is based on the feedback inhibition, the synaptic depression, and the neural sensitivity to input change. Although only responses to a positive change are examined in this article, those to a negative change can be examined by preparing "off type" neurons. Durstewitz et al. gave a good account of the way to decode differential information [20]. According to their model, dopamine prolongs the activity of a cortical network after an instant stimulus (e.g. a spike packet). From their work, we consider that differential information can be primitive information in brain.

The differential code has many advantages. First, the coding scheme is equivalent to detecting edges in the visual system. Then, neurons are allowed to ignore irrelevant information except for edges so that efficient and economical processes can be done. Second, weak differential information can be ignored by controlling noise intensity. This enables brain to extract principal components depending on the level of attention. Third, the differential code does not significantly depend on the number of neurons or connections in a layer, because the differential information is represented as a spike packet (see Figure 2, [2, 3]). If there are no feedback inhibition nor depressing synapses, the spike rate will be the major information transmitted by the layers. However, the spike rate is dependent on the number of neurons and connections in the layers.

Brain deals with dynamical stimuli input from the external environment. Actually, neurons are prone to re-

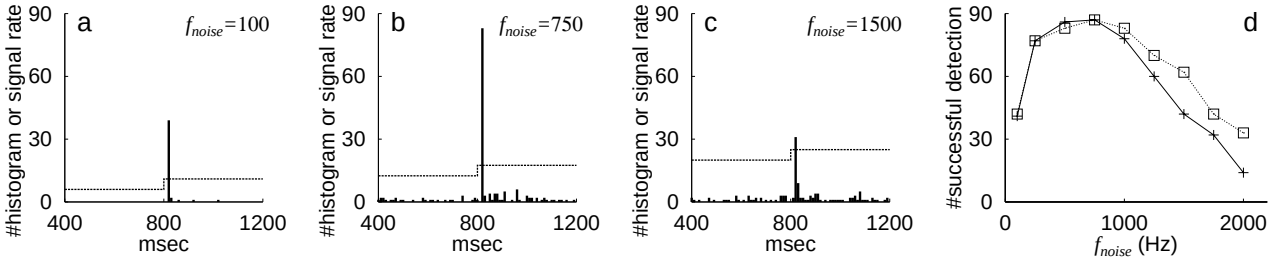

Figure 5: Noise dependent detection for a weak signal ($f_{base} = f_{diff} = 500$, dotted line). **a**–**c**. The *distribution of large spike histogram* (≥ 100 spikes $= N_e/2$) in the 5th layer over 100 trials ($f_{noise} = 100, 750, 1500$). For example, the leftmost figure shows that 41% trials succeed in detecting a step signal occurring at 800 msec for $f_{noise} = 100$. **d**. The differential detection rate for each f_{noise} is shown. For example, the value for $f_{noise} = 750$ is the sum of the peak height and two neighboring heights in **b**. The solid (dotted) curve is obtained from the 5th (10th) layer. The detection rate becomes maximum with a certain frequency of noise (stochastic resonance).

spond to dynamical stimuli more than to static stimuli [8, 21]. In order to process dynamical stimuli, neural system should detect the dynamic change and transmit correctly and robustly using neural assemblies. We consider that the differential code satisfies such demand.

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