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The cerebellum as a liquid state machine

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Abstract

We examined closely the cerebellar circuit model that we have proposed previously. The model granular layer generates a finite but very long sequence of active neuron populations without recurrence, which is able to represent the passage of time. For all the possible binary patterns fed into mossy fibres, the circuit generates the same number of different sequences of active neuron populations. Model Purkinje cells that receive parallel fiber inputs from neurons in the granular layer learn to stop eliciting spikes at the timing instructed by the arrival of signals from the inferior olive. These functional roles of the granular layer and Purkinje cells are regarded as a liquid state generator and readout neurons, respectively. Thus, the cerebellum that has been considered to date as a biological counterpart of a perceptron is reinterpreted to be a liquid state machine that possesses powerful information processing capability more than a perceptron.

Keywords: Cerebellum; Perceptron; Liquid state machine; Spatiotemporal activity patterns; Sparse coding; Recurrent inhibitory network; Long-term depression; Hybrid network

1. Introduction

In the Marr–Albus–Ito theory of cerebellar computation (Albus, 1971; Ito, 1984; Marr, 1969), the cerebellum is considered as a biological counterpart of a simple perceptron, which is a two-layer neural network with learning capability (Rosenblatt, 1958). Specifically, granule cells and Purkinje cells in the cerebellar cortex constitute the input and output layers, respectively, and connections between them by granule cell axons called parallel fibres are modifiable by an instruction signal coming from the inferior olive to Purkinje cells through climbing fibres, which is well known as long-term depression (LTD) (Ito, 1989, 2002b). While a simple perceptron is able to compute a function that describes only linear separation of input signals (Haykin, 1999), the cerebellum plays an essential role in motor control for coordinating movements of different body parts into a harmoniously integrated body movement, in which an enormous number of muscles must be activated precisely in a correct order and timing. Moreover, recent studies have suggested that the cerebellum is involved in higher cognitive functions including time perception and language processing (Ito (2002a) for review). How does the cerebellum as a simple perceptron perform such a complex task?

The granule cell layer comprises granule cells in a recurrent inhibitory network with Golgi cells (Ito, 1984), the major granule cell layer interneuron, suggesting that the input layer of the cerebellum represents a recurrent circuit. According to this observation, several groups have proposed cerebellar models in which the input layer is a recurrent network (Buonomano & Mauk, 1994; Hofstötter, Mitz, & Verschure, 2002; Medina, Garcia, Nores, Taylor, & Mauk, 2000; Yamazaki & Tanaka, 2005a). Yet, the computational power of the entire network has not been clarified. We have studied the dynamics of the recurrent circuit theoretically with a simplified rate-coding model (Yamazaki & Tanaka, 2005a) and a realistic model composed of spiking neuron units (Yamazaki & Tanaka, 2005b). These studies have shown that model granule cells exhibit a random repetition of transitions between active and inactive states. The sparse population of active cells changes with time, and there is no recurrence of active cell populations. Therefore, one population in a sequence of active cell populations is able to represent exclusively a specific time interval. Namely, the model cerebellum represents the passage of time in a sparse-population coding scheme. We have also demonstrated (1) resetability of activity pattern generation,

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(2) robust generation of an activity pattern against noise, (3) representation of different time passages associated with different input signals.

In the present study, we examined in more detail the information representation capability of the recurrent circuit in the model granular layer and the ability of model Purkinje cells to read out information. We considered to learn and represent a Boolean function, which has K bit inputs and M bit outputs. Model neurons in the recurrent circuit were able to distinguish all combinations of 2^K binary input signal patterns by a sparse-population coding, suggesting spatial discrimination capability of the network. Furthermore, the neurons could distinguish elapsed time from the onset of an input signal, indicating temporal discrimination capability as well. Taken together, the recurrent circuit was a spatiotemporal discriminator of input signals. On the other hand, we verified that our model cerebellar circuit is able to learn and represent any given Boolean function.

The spatiotemporal activity patterns of neurons generated by the recurrent circuit in the model granular layer have no fixed point attractors, because the same pattern does not appear more than once. On the other hand, model Purkinje cells, which receive the activity patterns and instruction signals, learn to generate desired output signals. In terms of the liquid state machine (Maass, Natschläger, & Markram, 2002), the granular layer in the cerebellum corresponds to a liquid state generator, and Purkinje cells work as readout neurons. Such functional resemblance of the cerebellum to a liquid state machine explains the huge computational power of the previous cerebellar models having a recurrent network as an input layer (Buonomano & Mauk, 1994; Hofstötter et al., 2002; Medina et al., 2000; Yamazaki & Tanaka, 2005a). Moreover, our liquid state machine hypothesis will supersede the classical perceptron hypothesis of the cerebellum.

2. Model description

Fig. 1 shows a schematic diagram of cell types and synaptic connections in the cerebellum (Eccles, Ito, & Szentágothai, 1967; Ito, 1984). The entire network computes a function $f : (\mathcal{B}^K, \mathcal{N}) \rightarrow \mathcal{B}^M$, where $\mathcal{B}$ and $\mathcal{N}$ denote the Boolean and natural integers, respectively. That is,

$$\mathbf{o} = f(\mathbf{x}, t), \tag{1}$$

where $\mathbf{x}$ and $\mathbf{o}$ denote $(x_1, x_2, \ldots, x_K)$ and $(o_1(t), o_2(t), \ldots, o_M(t))$, respectively, and t represents the discrete elapsed time from the onset of an input signal.

The model granular layer transforms static K inputs $(x_1, x_2, \ldots, x_K)$ into N spatiotemporal activity patterns $(z_1(t), z_2(t), \ldots, z_N(t))$ as shown below. Model Purkinje cells receive the spatiotemporal activity patterns and generate M outputs $(r_1(t), r_2(t), \ldots, r_M(t))$. For any i and t, $r_i(t)$ is given by

$$r_i(t) = \sum_j J_{ij} z_j(t), \tag{2}$$

where J_{ij} is the synaptic weight of the connection from neuron j in the granular layer to Purkinje cell i. The final output of the

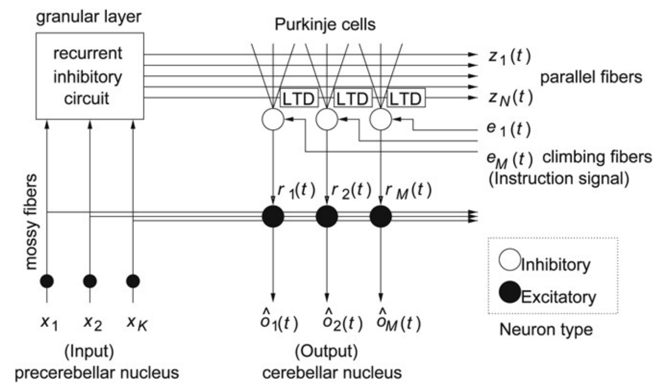

Fig. 1. Schematic diagram of cell types and synaptic connections in cerebellum.

network $(\hat{o}_1(t), \hat{o}_2(t), \ldots, \hat{o}_M(t))$ is calculated as

$$\hat{o}_i(t) = \Theta[1 - r_i(t) - \theta], \quad \text{for } i = 1, \ldots, M, \tag{3}$$

where 1 in the argument of Θ represents the normalized amplitude of excitatory input signals through mossy fibres, $\Theta[x] = 1$ for $x \geq 0$ and 0 otherwise, and θ is a threshold constant. The weights of J_{ij} of parallel fibre inputs to Purkinje cells, are modified via a climbing fibre dependent LTD rule (Ito, 1989). That is, the conjunctive stimulation of parallel fibres (i.e. $z_j(t) > 0$) and the climbing fibre (i.e. $e_i(t) = 1$) depresses synapses of the parallel fiber terminals on the Purkinje cell dendrites. The instruction signal pattern is set at a desired output pattern as

$$e_i(t) = o_i(t), \quad \text{for } i = 1, \ldots, M. \tag{4}$$

Accordingly, J_{ij} is set as follows:

$$J_{ij} = \begin{cases} 0 & z_j(t) > 0 \text{ and } e_i(t) = 1, \\ 1 & \text{otherwise.} \end{cases} \tag{5}$$

Next, the model granular layer consists of N neurons (model granule cells). Let $z_i(t)$ be the activity of neuron i at time t, which is given by

$$z_i(t) = [u_i(t)]^+, \tag{6}$$

Here $[x]^+ = x$ for $x > 0$ and 0 otherwise. $u_i(t)$ is the internal state of neuron i at time t. $u_i(t)$ is defined by

$$u_i(t) = I_i - \sum_j w_{ij} \sum_{s=1}^{t} \exp(-(t-s)/\tau) z_j(s-1), \tag{7}$$

where I_i and w_{ij} denote the afferent input signal to neuron i through mossy fibres and the synaptic weight of recurrent inhibition from neuron j to neuron i. The summation with respect to s in the second term on the right-hand side represents the temporal integration of activities over a long time. This indicates that the activity of neuron j is integrated through time by the convolution with an exponential decay factor, and τ determines the integration range. Derivation of Eq. (7) is found in our previous paper (Yamazaki & Tanaka, 2005a).

We determine the value of w_{ij} randomly, indicating that the model granular layer is a random recurrent inhibitory network.