Adaptive leaky integrator models of cerebellar Purkinje cells can learn the clustering of temporal patterns

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Abstract

We have shown previously that the metabotropic glutamate receptor signalling network in a cerebellar Purkinje cell can implement adaptive postsynaptic delays. Here we present a leaky integrator version of the Purkinje cell model which uses a simple synaptic delay learning rule. We show that a single leaky integrator can learn a radial basis function-like response to temporal parallel fibre patterns, and that different leaky integrators in a group are able to discover different clusters in a temporal parallel fibre input space. The clustering performance of the model can be improved by desensitization of the input currents. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Ever since Hebb published The Organization of Behavior in 1949 [3], it has been widely accepted that learning in biological and artificial neural networks involves the modification of synaptic efficacies. Here we investigate a different form of learning which is based on adaptive postsynaptic time delays. We have recently shown that a form of synaptic delay adaptation can be implemented by the metabotropic glutamate receptor (mGluR) signalling network in a cerebellar Purkinje cell [6]. Knowing that synaptic delay learning is a biological possibility enables us to develop...
a simplified, leaky integrator version of our model and investigate its computational capabilities in more detail.

2. The leaky integrator

In the basic version of the leaky integrator Purkinje cell model, the effect of the input currents $I_j(t)$ on the membrane potential $V$ is described as in a standard integrate-and-fire neuron [5]:

$$\frac{dV}{dt} = -\frac{V}{\tau_m} + \sum_{j=1}^{N} I_j(t).$$

(1)

However, in contrast to an integrate-and-fire neuron, there is no explicit representation of spikes in our model. Instead, the membrane potential $V$ represents the simple spike frequency of the Purkinje cell which is caused by the continuous background of parallel fibre inputs [1]. Given that Purkinje cells are inhibitory neurons, the magnitude of the effective response corresponds to the extent of the voltage minimum, i.e. the hyperpolarization peak.

Parallel fibre (PF) input to the Purkinje cell leads to stimulation of mGluRs, release of $\text{Ca}^{2+}$ from intracellular stores and activation of $\text{Ca}^{2+}$-dependent $K^+$ channels [2]. For a synapse with a postsynaptic delay $d_j$, the resulting outward current in response to a PF input at $t_j$ is given by

$$I_j(t) = \frac{(t_j + d_j) - t}{\tau_s} \exp \left(1 - \frac{t - (t_j + d_j)}{\tau_a}\right) \text{ for } t > t_j + d_j,$$

$$I_j(t) = 0 \text{ for } t \leq t_j + d_j.$$

(2)

During training, temporal PF patterns $t = \langle t_1, \ldots, t_p, \ldots, t_N \rangle$ are presented together with a climbing fibre (CF) input at $t_{CF}$. Phosphorylation of the mGluRs leads to an adjustment of the vector of postsynaptic delays $d = \langle d_1, \ldots, d_p, \ldots, d_N \rangle$ which is modelled by

$$\Delta d_j = \eta D(t_{CF} - (t_j + d_j)).$$

(3)

where $\eta > 0$ is a constant learning rate and $D(\Delta t)$ is a simple delay learning function:

$$D(\Delta t) = \Delta t \text{ for } -\delta \leq \Delta t \leq \delta,$$

$$D(\Delta t) = 0 \text{ otherwise}$$

(4)

with an effective time window for the delay learning $2\delta$ which is smaller than the intertrial interval (ITI) between two successive CF inputs.

3. RBF learning and temporal pattern clustering

Numerical simulations show that repeated presentations of a single PF pattern $t$ plus a CF input at $t_{CF}$ lead to a stable state where the different delays $d_j$ even out the
Fig. 1. Simulation results for repeated presentations of a 50-dimensional temporal PF input $t$ and a CF input at $t_{CF} = 0.5\, \text{s}$ to a leaky integrator Purkinje cell model with random initial delays $d_j \in [0,0.5\, \text{s}]$. (a) Training transforms the broad hyperpolarization response which is caused by the random initial delays into a narrow peak around $t = 0.7\, \text{s}$. Voltage traces are shown for trials number 1–20. (b) During training, the RBF centre vector $c$ moves towards the PF input vector $t$ until both vectors are identical.

differences between the PF input times $t_j$. In the stable state, all of the $N$ sums $t_j + d_j$ equal the climbing fibre time $t_{CF}$, and all of the input currents $I_j(t)$ peak at $t_{CF} + \tau_e$. Thus, the training transforms the broad hyperpolarization response which is caused by the random initial delays into a narrow hyperpolarization peak shortly after $t_{CF} + \tau_e$ (Fig. 1a).

The leaky integrator can be represented by a radial basis function (RBF) centre vector $c = \langle c_1, \ldots, c_j, \ldots, c_N \rangle$ with components $c_j$ which are given by the difference between the CF input time and the synaptic delays $t_{CF} - d_j$. Thus, if a single leaky integrator is trained with a CF signal and a single PF pattern, its centre vector $c$ moves towards the PF input vector $t$ until both vectors are identical (Fig. 1b).

To illustrate the analogy with RBF units in artificial neural networks (ANNs), the leaky integrator was presented with random temporal PF inputs, and the extent of the hyperpolarization response was measured as a function of the distance between its centre $c$ and the PF input vector $t$. As shown in Fig. 2, the hyperpolarization response is maximal for a template input pattern $t$ and decreases with an increasing distance between the two vectors $\|c-t\|$.

Thus, a single leaky integrator can learn a response which is very similar to RBF units in ANNs and to the RBF-like temporal decoding neurons which were postulated by Hopfield [4].

As a consequence of the RBF-like response of a single leaky integrator to temporal input patterns, it is possible to use a group of leaky integrators in a temporal pattern clustering task. By assuming that the leaky integrator Purkinje cell with the strongest hyperpolarization response inhibits the delay adaptation in all the other cells in the group, we can create a winner-take-all situation so that the modification of synaptic delays is restricted to the Purkinje cell whose centre is the closest match to the current input vector.
Thus, if a group of leaky integrator Purkinje cell models is presented with temporal PF patterns from a number of input clusters, the RBF centre vectors of the different integrators move towards the centres of different clusters in the PF input space.

4. Adaptive input currents

Similar to Natschläger and Ruf’s results for RBF learning by a network of spiking neurons [5], it was found that the clustering performance of the basic leaky integrators varies depending on their initial RBF centres and the positions of the input clusters. For equal numbers of integrators and clusters, it is quite common that some of the integrators are not used at all, while others are activated by two clusters and oscillate between them.

We can solve this problem by assuming that the mGluR mediated response undergoes a form of use-dependent desensitization. In the adaptive leaky integrator version of the Purkinje cell model, the mGluR evoked outward currents are downregulated every time the response is strong enough to result in modification of the synaptic delays, and the change of the membrane potential $V$ is given by

$$\frac{dV}{dt} = -\frac{V}{\tau_m} + z^W \sum_{j=1}^{N} I_j(t),$$

where $z$ is an adaptation factor between zero and one, and $W$ is the number of past delay updates or “wins”. In simulations with an equal number of adaptive leaky integrators and clusters, all of the integrators manage to discover their personal input clusters and specialise on the recognition of different subsets of temporal PF input patterns (Fig. 3).
5. Conclusions

We have shown previously that the intracellular signalling network in a cerebellar Purkinje cell can implement an adaptive postsynaptic delay between mGluR stimulation and voltage response. Here, we have presented a simple leaky integrator version of the Purkinje cell model with a delta-like synaptic delay learning rule. We have demonstrated how a single leaky integrator Purkinje cell model can learn an RBF-like response to temporal parallel fibre patterns, and how a group of leaky integrators can discover different clusters in a temporal PF input space. The clustering performance can be improved by desensitization of the mGluRs.

References


Volker Steuber studied biochemistry at the University of Tübingen, Germany and the ETH Zürich, Switzerland where he worked in Melitta Schachner’s developmental neurobiology lab. After graduating in 1993, he joined David Willshaw’s group at the University of Edinburgh. He received a Ph.D. in computational neuroscience in 1998 and is currently a postdoc in Erik De Schutter’s theoretical neurobiology laboratory at the University of Antwerp.

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