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Rank order decoding of temporal parallel fibre input patterns in a complex Purkinje cell model

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Abstract

The processing speed of many neuronal systems requires temporal coding. Recently, a temporal rank order code has been suggested that uses the temporal order of spikes, disregarding their precise timing. A rank order-coded spike pattern can be decoded by an array of synaptic weights and a postsynaptic desensitization process. We show that a multi-compartmental model of a cerebellar Purkinje cell can implement rank order decoding of temporal parallel fibre input patterns. Basis of the temporal decoding is the activation of K_{Ca} channels in the Purkinje cell dendrites. The model responds preferentially to spatio-temporal patterns which are ordered according to increasing synaptic strengths. © 2002 Published by Elsevier Science B.V.

Keywords: Cerebellum; Purkinje cells; Temporal coding; Pattern recognition

1. Introduction

It is widely believed that the patterns of neuronal firing rates and that of individual spike times are both important for the encoding of information in the brain (e.g. [1,6]). In a simple temporal coding scheme, an analogue input vector is represented using the relative timing of spikes across an array of encoding neurons (e.g. [5], see Fig. 1). Compared to a rate code, such a temporal code allows for the transmission of more information in a shorter time window [9,8].

The decoding of a temporal spike pattern requires a complex system of delay lines and coincidence detection. To simplify the decoding, Thorpe and Gautrais [8] have suggested a coding scheme where the precise timing of the spikes is thrown away and

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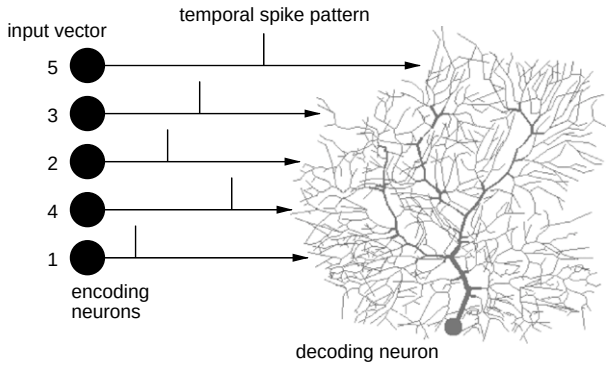

Fig. 1. Encoding of analogue inputs as temporal spike patterns.

the only relevant information is the order in which the spikes arrive. Advantages of this *rank order code* are its invariance to changes in input intensity and contrast, and the existence of a simple decoding algorithm. Without any delay lines, a rank order-coded pattern of input spikes can be decoded by an array of different synaptic weights and a mechanism that desensitizes the decoding neuron depending on how many spikes have already arrived. The activation a of the decoding neuron is given by

$$a = \sum_i \delta^{o_i} w_i, \tag{1}$$

where w_i is the synaptic weight of input i, o_i is the firing order of neuron i in the input sequence, and $0 < \delta < 1$ is a desensitization factor. As a consequence of the desensitization, the activation of the decoding neuron is maximal when the inputs are ordered according to decreasing synaptic weights ($o_i < o_j \Leftrightarrow w_i > w_j$), and minimal for an input sequence with increasing weights ($o_i < o_j \Leftrightarrow w_i < w_j$).

Desensitization of the decoding neuron can be implemented by a number of mechanisms. In cerebellar Purkinje cells, the activation of a sufficient number of parallel fibre (PF) inputs leads to influx of Ca^{2+} into the dendritic tree and to an after-hyperpolarization (AHP) which is mediated by Ca^{2+} dependent K^+ (K_{Ca}) channels (cf. [7]). The AHP is expected to reduce the Purkinje cell responsiveness to subsequent PF inputs and represents a possible desensitization mechanism. Here, we study the recognition of rank order-coded PF input patterns in a multi-compartmental Purkinje cell model with active dendrites. We use the model that has been described in detail in Refs. [3,4]. The model receives excitatory input from 147,400 PFs which activate AMPA receptors on dendritic spines. To increase the computational efficiency, only 1% of the 147,400 spines is represented explicitly. Each of these 1474 spine compartments receives 100 PF inputs. All PFs are activated asynchronously with a frequency between 0.26 and 0.28 Hz, resulting in an asynchronous AMPA receptor activation in each spine compartment with a frequency of 26–28 Hz. The background excitation is balanced by a tonic background inhibition, and the model fires simple spikes with an average frequency between 8 and 50 Hz.

In the original rank order coding scheme, a temporal pattern consists of a sequence of individual input spikes. In cerebellar Purkinje cells, the effect of a single PF input spike is not strong enough. Thus, the Purkinje cell model is presented with spatio-temporal PF input patterns consisting of the consecutive activation of a sequence of spatial PF patterns. Each of the spatial PF patterns consists of the synchronous activation of 1000 PFs. The PF inputs activate AMPA receptors on the Purkinje cell spines, with maximal conductances that are identical within a spatial pattern and different between the different spatial patterns in the sequence. All simulations are performed using the GENESIS simulator [2].

2. Simulation results

Figs. 2 and 3 show simulation results for a Purkinje cell model that receives 0.27 Hz asynchronous PF background activation, resulting in simple spike firing with an average frequency of 30 Hz. The model is presented with all $3! = 6$ possible permutations of a sequence of three spatial PF input patterns $\{P_1, P_2, P_3\}$ with maximal AMPA receptor conductances $\{\bar{g}_1, \bar{g}_2, \bar{g}_3\} = \{0.56\,\text{nS}, 0.28\,\text{nS}, 0.14\,\text{nS}\}$. For a delay of 15 ms between the three inputs in the sequence, the model fires an average number of 2.9 spikes in 50 ms after the presentation of the first input in the sequence $P_1 \rightarrow P_2 \rightarrow P_3$, and an average number of 5.8 spikes/50 ms in response to the sequence $P_3 \rightarrow P_2 \rightarrow P_1$ (Figs. 2 and 3a).

The ability of the model to discriminate between two spatio-temporal PF patterns can be evaluated by calculating the signal-to-noise ratio (s/n)

$$s/n = \frac{(\mu_a - \mu_b)^2}{0.5(\sigma_a^2 + \sigma_b^2)}, \tag{2}$$

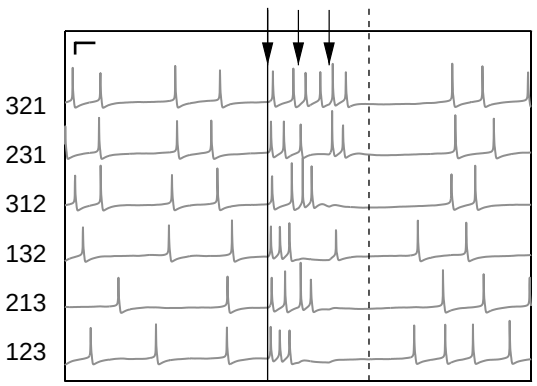

Fig. 2. Response of the Purkinje cell model to the six possible permutations of a sequence of three synchronous activations of 1000 PFs with maximal AMPA receptor conductances $\{\bar{g}_1, \bar{g}_2, \bar{g}_3\} = \{0.56\,\text{nS}, 0.28\,\text{nS}, 0.14\,\text{nS}\}$. The three PF inputs are presented with a delay of 15 ms (times indicated by arrows). 0.27 Hz PF background input results in 30 Hz simple spike firing in the Purkinje cell. Bars indicate 10 ms and 25 mV.

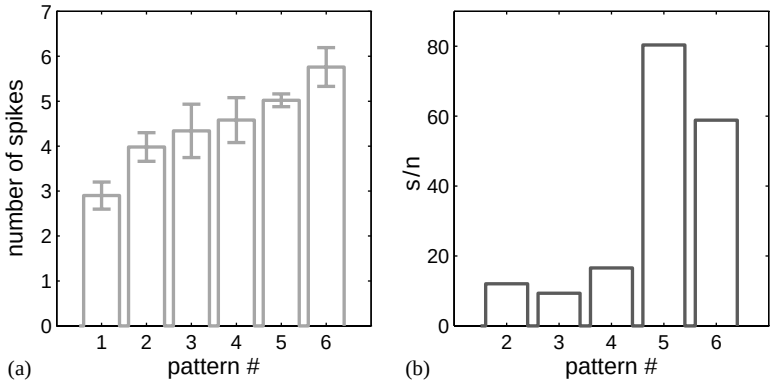

Fig. 3. (a). Average response of the Purkinje cell model to 50 presentations of the six possible permutations of a sequence of three synchronous activations of 1000 random PFs with maximal AMPA receptor conductances $\{\bar{g}_1, \bar{g}_2, \bar{g}_3\} = \{0.56\,\text{nS}, 0.28\,\text{nS}, 0.14\,\text{nS}\}$. The response is given by the number of spikes in the first 50 ms after presentation of the first input in the sequence. Temporal patterns are $1 = P_1P_2P_3$, $2 = P_2P_1P_3$, $3 = P_1P_3P_2$, $4 = P_3P_1P_2$, $5 = P_2P_3P_1$, $6 = P_3P_2P_1$. (b) Signal-to-noise ratio (s/n) for the discrimination between pattern $1 = P_1P_2P_3$ and patterns 2–6. Delay = 15 ms, 0.27 Hz PF background resulting in 30 Hz simple spike firing.

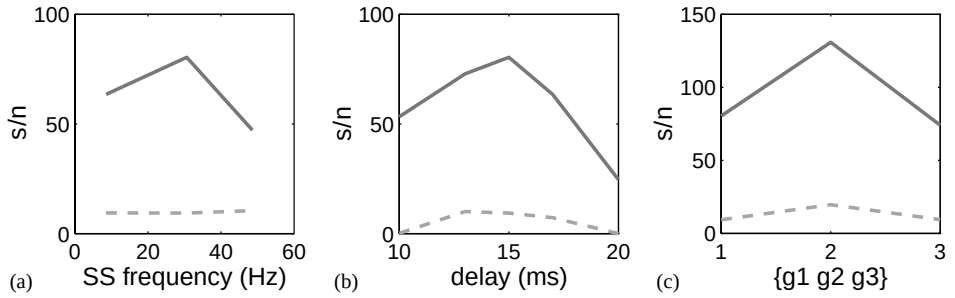

Fig. 4. Parameter sensitivity of the rank order decoding. The signal-to-noise ratio is shown for the easiest and hardest discrimination task (easiest task: $P_1P_2P_3$ vs. $P_3P_2P_1$ or $P_2P_3P_1$, depending on the parameters, solid line; hardest task: $P_1P_2P_3$ vs. $P_2P_1P_3$ or $P_1P_3P_2$, broken line). The AMPA receptor conductance vectors $\{\bar{g}_1, \bar{g}_2, \bar{g}_3\}$ in (c) are $1 = \{0.56, 0.28, 0.14\}$ nS, $2 = \{0.56, 0.35, 0.14\}$ nS, $3 = \{0.63, 0.35, 0.14\}$ nS.

where μ_a and μ_b are the mean values and σ_a^2 and σ_b^2 the variances of the response to two patterns a and b, respectively. As shown in Fig. 3b, the pattern $P_1 \to P_2 \to P_3$ that results in the weakest Purkinje cell response can be distinguished from all other patterns with a signal-to-noise ratio between 9.4 and 80.

Fig. 4 shows that the temporal pattern recognition performance is fairly insensitive to parameter variations. Rank order decoding of PF input patterns is possible in Purkinje cell models that fire simple spikes with rates between 8 and 50 Hz, and for different combinations of AMPA receptor conductances. The delay between the PF inputs in the

sequence can be varied between 13 and 17 ms before the model becomes unable to discriminate the pattern $P_1 \rightarrow P_2 \rightarrow P_3$ that gives the weakest response from all other patterns. All parameters tested enabled the model to distinguish patterns $P_1 \rightarrow P_2 \rightarrow P_3$ and $P_3 \rightarrow P_2 \rightarrow P_1$ without any error.

3. Conclusions

We have shown that a multi-compartmental model of a cerebellar Purkinje cell can implement rank order decoding of temporal parallel fibre (PF) input patterns, similar to the algorithm that was suggested by Thorpe and Gautrais [8] for simple integrate-and-fire neurons. Basis of the rank order decoding in the Purkinje cell model is the afterhyperpolarisation (AHP) that is caused by activation of K_{Ca} channels after PF input. Stronger PF inputs lead to a stronger AHP and to a weaker response to subsequent PF inputs. As a consequence, strong PF inputs shadow following weaker PF inputs, but not vice versa. Thus, in contrast to Thorpe's and Gautrais' algorithm where input sequences with decreasing synaptic weights elicit the strongest activation, the response of the Purkinje cell model is maximal when the inputs are ordered in the opposite way so that the inputs with the lowest AMPA receptor conductances are presented first. We are currently extending our parameter sensitivity study to longer sequences of PF inputs, and working on a learning algorithm that could establish such a temporal decoding mechanism in the cerebellum.

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Volker Steuber studied biochemistry at the University of Tübingen and the ETH Zürich. After graduating in 1993, he joined David Willshaw's group at the University of Edinburgh. In 1998, he received a Ph.D. for his work on "Computational Theories of Intracellular Signalling in Cerebellar Purkinje Cells". He is currently a postdoctoral fellow in Erik De Schutter's group at the University of Antwerp, using computer simulations and in vivo recordings to study the function of cerebellar Purkinje cells.

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