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Complementary action of chemical and electrical synapses to perception

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ABSTRACT

We study the dynamic range of a cellular automaton model for a neuronal network with electrical and chemical synapses. The neural network is separated into two layers, where one layer corresponds to inhibitory, and the other corresponds to excitatory neurons. We randomly distribute electrical synapses in the network, in order to analyse the effects on the dynamic range. We verify that electrical synapses have a complementary effect on the enhancement of the dynamic range. The enhancement depends on the proportion of electrical synapses as compare to the chemical ones, and also on the layer that they appear. © 2015 Elsevier B.V. All rights reserved.

1. Introduction

The cerebral cortex contains neurons and their fibres [1]. These neurons are grouped together into functional or morphological units, called cortical areas [2], each of them playing a well-defined role in the processing of information in the brain [3]. Hence the theoretical understanding of the principles of organisation and functioning of the cerebral cortex can shed light on the knowledge of many distinct and important subjects in neuroscience [4]. One relevant subject is psychophysics, that analyses the perceptions due to external stimuli [5].

Studies about the relation between sensation and stimulus by measuring the quantity of both factors were realised by Weber and Fechner [6]. They proposed that the relation was logarithmic [7]. However, Stevens proposed a theory based on a power-law relation between stimulus and response, where the exponent depends on the type of stimulation [8].

The capacity of a biological system to discriminate the intensity of an external stimulus is characterised by the dynamic range (DR) [9]. DR is a range of intensities for which receptors can encode stimuli [8,10,11]. It is the logarithm of the difference between the smallest and the largest stimulus value for which the responses are not too weak to be distinguished or too close to saturation, respectively. The lower and upper bounds are arbitrarily chosen due to the fact that the scaling region is well fit by a power law. In other words, small changes do not affect our results. The visual and the auditory perception have high dynamic range. The human sense of sight can perceive changes in about ten decades of luminosity, and the hearing covers twelve decades in a range of intensities of sound pressures [7]. The DR of the human visual is important in the design of high dynamic range display devices [12]. Whereas the DR of the hearing is used for cochlear implants [13].

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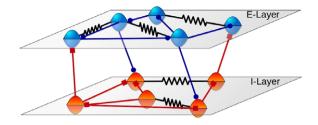


Fig. 1. Scheme of the E–I layered network with one excitatory layer (E-layer), and one inhibitory layer (I-layer). The lines with blue filled circles represent the excitatory connections, the lines with red filled squares represent the inhibitory connections, and the other links represented by black saw lines are the electrical connections. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In this work we study the dynamic range of a cellular automaton modelling a neural network whose neurons are connected with electrical and chemical synapses [14]. We consider that the chemical synapses can be excitatory or inhibitory, and a layered model [15], where one layer consists of excitatory neurons, and the other layer consists of inhibitory neurons. Network consisting of excitatory and inhibitory neurons was considered to describe the primary visual cortex [16]. Pei and collaborators [17] investigated the behaviour of excitatory–inhibitory excitable networks with an external stimuli. They suggested that the dynamic range may be enhanced if high inhibitory factors are cut out from the inhibitory layer. In our work, we consider a neural network in which neurons interact by chemical and electrical synapses in an excitatory–inhibitory layered model. Our main results are: the derivation of an equation for the dynamic range for a random neural network with chemical and electrical synapses, and to show a result that allows us to demonstrate that the electrical synapses in the excitatory layer have an influence on the dynamic range more significative than in the inhibitory layer, due to the fact that the electrical synapses in the excitatory layer are responsible for the complementary effect of dynamic range enhancement.

This paper is organised as follows: in Section 2 we introduce the cellular automaton rule, and the random network. Section 3 shows our analytical and numerical results obtained for the dynamic range. The last section presents the conclusions.

2. Neuronal network model of spiking neurons

We consider a cellular automaton model in that a node can spike, $x_i = 1$, when stimulated in its resting state, $x_i = 0$ (i = 1, ..., N). When a spike occurs there is a refractory period until the node returns to its resting state, $x_i = 2, ..., \mu - 1$. During the refractory period no spikes occur. There are excitatory and inhibitory connections linking nodes unidirectionally. The pre-synaptic node whose out chemical synapses are excitatory (inhibitory) is called an excitatory (inhibitory) node. Excitatory nodes increase the probability of excitation of their connected nodes, while inhibitory nodes decrease this probability. The network presents also electrical connections, that are bidirectional links.

The dynamics of the cellular automaton is given by:

- 1. if $x_i(t) = 0$, then
 - a node can be inhibited by an excited inhibitory node $j(x_j(t) = 1)$ with probability B_{ij} , remaining equal to zero in the next time step;
 - a node can be excited by an excited excitatory node $j'(x_{j'}(t) = 1)$ with probability $B_{ij'}$;
 - a node with electrical connection can be excited by an excited node j'' with probability $A_{ij''}$;
 - a node can be excited by an external stimulus with probability *r*;
- 2. if $x_i \neq 0$, then $x_i(t+1) = x_i(t) + 1 \pmod{\mu}$, where $x_i(t) \in \{0, 1, \dots, \mu 1\}$ is the state of the *i*th node at time *t*. In other words, the node spikes ($x_i = 1$) and after that remains insensitive during $\mu 2$ time steps.

The weighted adjacency matrices A_{ij} and B_{ij} describe the strength of interactions between the nodes. The matrix A_{ij} contains information about the electrical connections, and the matrix B_{ij} about the excitatory and inhibitory connections. The connection architecture is described by a random graph, in that the connections are randomly chosen [18]. We separate the neurons by layers. Fig. 1 shows the scheme of the E–I layered network, where the E layer contains N_e excitatory nodes, and the I layer contains N_i inhibitory nodes. Then, the layered network has a total of $N_e + N_i = N$ nodes. The excitatory connections (blue lines) go from excitatory nodes (blue circles) to other nodes, the inhibitory connections (red lines) go from inhibitory nodes (red circles) to other nodes, and the electrical connections are bidirectional (black sawed lines). Each layer can have nodes interacting by both excitatory and inhibitory connections.

The neuron responses are obtained through the density of spiking neuron

$$p(t) = \frac{1}{N} \sum_{i=1}^{N} \delta(x_i(t), 1),$$
(1)

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