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Review

Regulation of information passing by synaptic transmission: A short review

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ABSTRACT

The largest part of information passed among neurons in the brain occurs by the means of chemical synapses connecting the axons of presynaptic neurons to the dendritic tree of the postsynaptic ones. In the present paper, the most relevant open problems related to the mechanisms of control of the information passing among neurons by synaptic transmission will be shortly reviewed. The "cross talking" between synapses, their mutual interactions and the control of the information flow between different areas of the dendritic tree will be also considered. The threshold mechanism based on the "reversal potential" will be considered for its role in the control of information transfer among neurons and also for its contribution to the information flow among different areas of the dendritic tree and to the computational ability of the single neuron. The concept of "competition for plasticity" will be proposed as a mechanism of competition based on the synaptic activation time.

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1. Introduction

The basic activities of the brain are devoted to relate the individuals with the physical world and for this task it collects environmental information (stimuli) by the means of specialized neurons (sensory receptors). The input information, collected outside the brain by the sensory receptors, is transferred into the brain and compared with memory traces to correctly elaborate the appropriate outputs (behaviour) and to create new memory traces (update of the system). Activities much more complex than the collection of stimuli can occur internally to the brain (for example cognitive processes) the results of which can be either output directed to the external world (behaviour) and/or to other systems of the brain. In general, all these operations can be defined as "*Information Processing*" that, probably, is the most important activity of the brain since all the others belong to it. To perform information processing, a relevant computational ability is needed and it is still a matter of debate if this ability is proper of neural networks, as proposed earlier by McCulloch and Pitts (1943), or if a key contribution can be already given at the level of the single neuron. To understand both the role in information processing and the computational ability of the single neuron, it is important to analyze the way it receives and manages information.

In the single neuron, information seems to be coded in sequences of spikes, which can be considered the basic elements of the neuronal language, and is transferred to the other neurons by the means of synaptic contacts. Concerning the input of external stimuli, the first step of their elaboration is the conversion of their properties (amplitude, duration, etc.) in the appropriate sequence of spikes. Sensory pathways usually are made of a sequence of three neurons, located outside the brain, the first of which is modified to receive the appropriate stimulus (sensory receptor) and the last has the role to carry the information into the brain. Although the coded stimulus is passed along the chain from one neuron to the other, the information is not represented in all the neurons as a copy of the same sequence of spikes. Usually, each neuron receives inputs from several different neurons and its outputs are the results of complex processes of integration (but also of compression and/or re-coding). In the retinal system of light (image) perception, for example, in some cases, a single ganglion cell (the last cells of this sensory pathway the axons of which form the optical nerve) on the average receives inputs from about 10 bipolar cells (the second neuron of the chain) each of which receives inputs from about 10 photoreceptors (cones and/or rods). The information collected by 100 photoreceptors is integrated (compressed) onto a single ganglion cell with a ratio of 100:1 before entering the brain. In addition, the process of integration of the visual information is further "contaminated" by the activity of both the amacrine and horizontal cells that contribute to modify the signals generated by the photoreceptors into the retina. Similar integration and compression systems are common to all the types of sensory transduction. The most common point of view in this respect is that the sensory systems remove (filtering) the part of information that is irrelevant to the identification and to the elaboration of the stimuli by the brain although, probably, these processes produce a relocation of the information in a compressed code more than a simple filtering.

The successive integrations and re-codifications along the sensory pathways modify the structure of the original code so dramatically that, once passed the receptor level (sensory perception), the identification of particular information by the spike sequence of a single neuron (decoding) becomes very hard, if not impossible and, very likely, this is one of the most important reasons why the structure of the neural code still remains a mystery.

At the brain level the situation is even more dramatic because a classical pyramidal neuron, in the hippocampus or in the cortex, receives tens of thousands of synaptic contacts and some of them can be active simultaneously. In these neurons, the largest part of the synaptic contacts is located on the dendritic tree and only a minority rests on the soma and on the axon. The location of the synaptic inputs plays an important role because the weight they can have on the spiking activity of the neuron is a function of their distance from the hillock (but see section 4.4).

The complex structures and dynamics of pyramidal neurons rarely permit that the spiking activity of one of them is determined by the stimulation of another single neuron connected on the far dendritic districts. Usually a pyramidal neuron requires the simultaneous activation of several dendritic synaptic contacts (but see section 4.4) to reach the threshold level for the spike generation. This evidence suggests that normally the information carried by the single neuron to the dendritic tree is irrelevant to the activity of the postsynaptic neuron if not transferred "*in coincidence*" with the information carried by other neurons (coincidence detection). When the "*coincidence*" of several inputs occurs and the threshold level is reached, the resulting sequence of spikes represents, in the coded form, the integration of the information carried by all the stimulating neurons. The identification of the information carried by the single neuron becomes almost an impossible task since it is mixed into the information carried by all the other simultaneously active neurons. The information expressed alone by a neuron (not in coincidence) is apparently lost because it does not contribute to the output of the postsynaptic neuron. However, these "isolated activities" (subthreshold stimulations) produce postsynaptic responses able to modify the synaptic properties with long lasting effects (see later). Several parameters of the synaptic transmission, involved in the regulation of the synaptic efficacy, in fact, change as a function of the synaptic activity (see later) and this can be independent from the output of the postsynaptic neuron. An immediate consideration in this respect is that the passage of information from the pre- to the postsynaptic neuron is more complex than a simple mechanism attempting to induce the postsynaptic neuron to produce spikes.

The large number of synaptic contacts, their intrinsic variability, their position relative to the hillock, the complex geometry and the variability of the dendritic properties, make difficult the definition of a simple general model of the relationships between the synaptic inputs, the spiking activity and the information processing tasks performed by the single neuron. Presently, the clear identification of how and what