Coding by Neural Population Oscillations?

Francesco Ventriglia

Istituto di Cibernetica "E. Caianiello",
CNR Via Campi Flegrei,
34, 80078 - Pozzuli (NA), Italy
franco@ulisse.cib.na.cnr.it

Abstract. The search of the code underlying the transmission of information through the different stages of integration of the brain is a very active investigation field. Here, the possible involvement in the neural code of global population oscillatory activities has been discussed. The behaviorally important rhythmic activities of the hippocampal CA3 field have been analyzed to this aim. The genesis and the features of such activities have been studied by the computer simulation of a model of the entire CA3. The simulation demonstrated the ability of the network of inhibitory interneurons to control nicely the transmission of activity through the pyramidal population. The results suggested that the hippocampal formation and the CA3 field—in particular—could be organized in a way to allow the passing of excitatory activities only during specific and narrow time windows, confined by inhibitory barrages possibly linked to attentional processes.

1 Introduction

The neural information flows in brain along the multiple stages of the neural circuitry, starting from the primary (sensorial) cortices, till the Hippocampus and superior areas and back. The problem of the modalities according which the information is coded within the neural populations of brain, is very elusive and yet there are no clear indications about its nature. The most common hypotheses about such code, the "rate code" and the "temporal code", received contrasting evidence and the issue remains controversial. The rate code hypothesis assumes that the neurons, basically noisy, can transmit information only via the mean rate of spiking. This hypothesis is based on the common observation that recorded sequences of spike intervals in cortical pyramidal neurons are so highly irregular to support the existence of important random influences on its genesis [13,14,15,24]. The more recent temporal-code view, partially based on the assumption that the rate code proposal produces a too poor code, retains that the information is conveyed by the precise order of the inter-spike time intervals, or in a weaker form, it is related to the precise time of the first spike after an event [1,2,16,17].

The base of a new hypothesis on the rules governing the transmission of information in brain is discussed here. This hypothesis considers the global oscillatory

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activities in neural populations as the possible base of a temporal code, very different from that outlined above. Synchronous oscillatory activities constitute one of the most characteristic aspects of the brain activity and are associated closely to behavioral states. Rhythmic oscillations in the gamma (20-80 Hz) and theta (4-15 Hz) ranges are among the most prominent patterns of activity in Hippocampus [3] and both rhythms are believed to be essential products of the hippocampal machinery. The theta rhythm is commonly supposed to be produced in the hippocampus by activity coming from medial septum and entorhinal cortex. Recent experimental and theoretical articles support the hypothesis that the network of inhibitory interneurons in the Hippocampus generates intrinsically the gamma rhythm. Both rhythms are present during the exploratory activity in awake animals and are related to learning, memory processes and to cognitive functions [19,4]. Some fast (80-200 Hz) [6] and ultra-fast (200-500 Hz) [10] oscillations have been also recorded in the hippocampus (and cortex) of several animals and in man.

The CA3 field of the Hippocampus, one of the most significant components of the limbic system, has been used here as a case study to evaluate the new hypothesis. In particular, the global reactions of CA3 to its inputs and the precise spatio-temporal behavior of excitatory and inhibitory waves invading the CA3 field have been closely investigated. The results suggested that this field is organized as an inhibitory filter which allows the passing of excitatory activities only during narrow time windows. They are strictly confined by inhibitory barrages possibly linked to attentional processes.

2 The Kinetic Model

Based on a kinetic theory of neural systems, formulated several years ago [20,22], a set of differential equations was constructed for the description of the activity of the CA3 neural field. This theory translates the action potentials traveling within the neural fields along the axonic branches in massless particles. They move freely within the neural systems until they collide with a neuron. The collision can result in the absorption of the impulse by the neuron and in this case the subthreshold excitation of the neuron increases or decreases according to the quality, excitatory or inhibitory, of the absorbed impulse. When the subthreshold excitation reaches the threshold value (here assumed equal to 1 for simplicity) the firing occurs and a stream of new impulses is emitted within the neural field. After the firing the neurons go in refractoriness state, for a period of time τ. The functions $f_s(\mathbf{r}, \mathbf{v}, t)$ and $g_{s'}(\mathbf{r}, e, t)$ describe, respectively, the impulse velocity distribution and the distribution of the subthreshold neuronal excitation within the neural field. Whereas, $\psi_{s'}(\mathbf{r})$ denotes the local density of neurons. The variables $\mathbf{r}, \mathbf{v}, e$ and t are associated to the position, the velocity, the subthreshold excitation and the time, respectively. The index s refers to the different action potentials traveling within the neural field (CA3 pyramidal short range, CA3 pyramidal long range, CA3 inhibitory fast and CA3 inhibitory slow, Enthorinal Cortex pyramidal, Mossy Fibers from Dentate Gyrus,