Propagation of Synfire Activity in Cortical Networks: a Statistical Approach

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1 Introduction

Recently it was demonstrated that the activity of frontal cortical neurons in the awake behaving monkey comprises excessive occurrences of highly accurate (~1-3 ms) spatio-temporal firing patterns. Moreover, these patterns can be related to the behavioral state of the animal [1, 10]. On the basis of the characteristic anatomy and physiology of the cortex, it was proposed that synfire activity, propagating through the sparsely firing cortical neural network, presents a natural explanation for this phenomenon [2, 1]. In order to test this hypothesis, we investigated the dependence of reliable synfire propagation on the structural and the dynamical properties of a model cortical network, using the newly developed simulation tool SYNOD [6].

2 Synfire Chains

Synfire chains consist of diverging/converging links connecting a number of groups of neurons. A diverging/converging link can be described by two structural parameters, the width $w$ and the multiplicity $m$, defining the number of neurons in a group and the minimum number of connections from a member neuron to the next group.

In simulation studies we found, that successful transmission from one group to the next requires two conditions to be fulfilled. First, the number of firing neurons within the sending group has to be larger than some minimum number $a_0$. Second, their spike time distribution must be narrower than some critical width $\sigma_0$. These critical values $a_0$ and $\sigma_0$ depend both on the structural parameters $w$ and $m$, as well as on the details of the single neuron dynamics [7]. In order to characterize the dynamics, we need to assess the influence of the degree of synchrony in the spike arrival time distribution. Unfortunately, existing measures of neural transmission focus on two limiting cases, full synchrony and random arrival [2, 3]. Intermediate cases with a finite degree of temporal dispersion are not addressed.
3 Pulse-Packets

We introduce here the concept of pulse packets [7, 8], in order to overcome these restrictions and to quantify the degree of temporal synchrony in propagating volleys of neural activity. A pulse packet is a probabilistic description of the activity of a group of neurons, represented by a pulse density function $\rho(t)$. This pulse density function is determined by two parameters: the activity $a$, defining the number of active neurons in a group and the width $\sigma$, defining the temporal dispersion of the group activity (Fig. 1). This parametric description of synfire activity provides a conceptual framework that allows us to derive an appropriate neural transmission function and, thereby, to enhance our analytical insight into the role of the single neuron dynamics.

Using this approach, we investigated the response of a model neuron [9] to input activity with varying degrees of synchrony. From the model neuron we recorded the response (time of first spike), collected in a PST-histogram over many trials. After normalization for the number of trials, the resulting output distribution was similarly described as a pulse packet, and the associated pulse density $\rho(t)$ along with the values of $a$ and $\sigma$ were determined. Thus, we could investigate how the output distribution changed, depending on the input distribution. To this end, the input was varied systematically from a sharp synchronous volley of spikes (small $\sigma$, large $a$) to an asynchronous rate variation (large $\sigma$, small $a$). For each pair of input parameters $(a_{\text{in}}, \sigma_{\text{in}})$, we measured the corresponding output pair $(a_{\text{out}}, \sigma_{\text{out}})$. As an alternative approach, we simplified the model neuron such that an analytical treatment was possible. This yielded a relationship for the input-output relation of pulse packets that could be solved numerically. Again, for each pair of input parameters $(a_{\text{in}}, \sigma_{\text{in}})$, we measured the corresponding output pair $(a_{\text{out}}, \sigma_{\text{out}})$.

4 Results

The resulting input-output relation between incoming and outgoing pulse packets can be visualized in so-called iterative maps. These yield a compact characterization of the neuron’s firing dynamics. In contrast to earlier approaches where the neuron’s firing probability is measured quasi-statically as a function of DC-current, this new transmission function takes full account of the dynamic properties of the input distribution $\rho(t)$. One appropriate way to look at it is to plot $\sigma_{\text{out}}$ versus $\sigma_{\text{in}}$ for constant $a_{\text{in}}$. The result from the numerical study is shown in Fig. 1; observe that for small values of $\sigma_{\text{in}}$, the outgoing pulse packet is wider than the incoming one. Synchronous input is thereby dispersed in time. With increasing $\sigma_{\text{in}}$, however, the curve crosses the diagonal

and runs below it. Thus, testing whether the neuron exhibits chaotic behavior, the intersection is an unstable attractor of an invariant set. These features of the single neuron can be carried over to description of groups of neurons. In the completely connected group, appropriately scaled number of neurons in a group, or the group’s temporal response, can be extended to completely connected groups, where ‘sees’ only a fraction of the chain. Hence, we can determine the chain of such groups, and in and those of the chain.

5 Conclusions

The formalism of pulse packets and the notion of coincident firings whether the cortical neuron is a question which was raised. The notion of pulse packets provides one unified concept. Our model either of the two, depending on the situation. The temporal structure of events is emphasized.

The approach outlined here can be characterized as ‘local dynamics beyond the language to describe the process of groups of neurons. At the level of single neurons, dynamics of information in such networks is the key analysis, using a dynamical systems approach. Finally, and most important, the spike time distributions and the spike time statistics in the system evolve separately and be used to test the synfire hypothesis.
ts [7, 8], in order to overcome temporal synchrony in propagating a probabilistic description of a pulse density function $\rho(t)$. The parameters: the activity $\sigma$, $\sigma_{out}$ and $\sigma_{in}$ of the neuron, the area under the curve represents the activity $\sigma$.

A pulse packet, the area under the curve, can have varying degrees of complexity and the response (time of first return) will be similarly described by $\rho(t)$ along with the values of $\sigma_{out}$, $\sigma_{in}$, and $\sigma_{out}$. For each pair of input and output pairs $(\sigma_{out}, \sigma_{in})$, the model neuron reaches an equilibrium, where the input-output relationship is established. Again, for each corresponding output pair $\sigma_{out}$, the curve crosses the diagonal and runs below it. Thus, beyond this intersection the neuron exhibits a synchronizing behavior, the intersection itself represents a stable attractor of an invariant pulse packet. These features of the single neuron dynamics can be carried over to describe the behavior of groups of neurons. In the simplest case of completely connected groups, the above distribution, appropriately scaled for the number of neurons in a group, directly describes the group's temporal response. This framework can be extended to the case of incompletely connected groups, where every neuron 'sees' only a fraction of the pulse packet. Hence, we can determine the stable point of synfire activity traveling along a chain of such groups, and investigate its dependence on the neuron parameters and those of the chain.

5 Conclusions

The formalism of pulse packets provides the appropriate framework to clarify the notion of coincident firing. This yields a natural solution to the question whether the cortical neuron acts as an 'integrator' or as a 'coincidence detector' - a question which was raised many years ago [3] and was revived recently [5, 11]. The notion of pulse packets conveniently embeds these two different modes into one unified concept. Our investigation shows that the neuron may behave as either of the two, depending on the degree of synchrony of the input activity. The temporal structure of the input determines which of the two aspects is emphasized.

The approach outlined here opens the way for a quantitative description of network dynamics beyond the single neuron level. It provides a parametric language to describe the propagation of synchronous activity in networks, that can be characterized as 'locally feed-forward', i.e. locally composed of chains of groups of neurons. At the same time, it provides a conceptual bridge to link the single neuron dynamics to the mechanisms involved in stable transmission of information in such networks. Both aspects accommodate an analytic treatment of the model. An example for such analytic treatment is the stability analysis, using a dynamical systems approach [4] (see also Arndt et al. in this Volume). Finally, and most interestingly from the experimental point of view, the spike time distributions obtained in our simulations can be compared with the spike time statistics in recurring patterns in physiological data, and thus be used to test the synfire hypothesis for activity in the working brain.
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References


1 Introduction

During the last years, several models and network approaches have been developed to address the problem of efficient and robust information processing in the brain (1-4). The focus of these models has been on the role of spatio-temporal spike patterns in the awake behaving monkey, and the role of synchronized activity in the cortex (1,2). These findings support the hypothesis that the stability of propagation of spike activity in the cortex is determined by the density of inter-node connections. In this work, we extend the results of Abeles et al. (1) on the stability properties of synfire propagation.

2 The ‘Synfire chain’

The theory we present here is based on the idea that information is processed in a simple feedforward network with a single layer. Each neuron in the layer receives input from a fully connected ('complete') chain of neurons. The number of neurons in each chain is determined by the number of input connections, and the multiplicity of the chain is determined by the number of neurons in each chain. The connectivity of the network is determined by the number of input connections, and the multiplicity of the chain is determined by the number of neurons in each chain. The connectivity of the network is determined by the number of input connections, and the multiplicity of the chain is determined by the number of neurons in each chain.