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SYNCHRONIZATION, CHAOS AND SPIKE PATTERNS IN NEOCORTICAL COMPUTATION

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ABSTRACT

From simulations relying on detailed physiological data, cortical layer IV recurrent network topology and small thalamic input currents, a novel synchronization paradigm emerges. Coarse synchronization, where small temporal variations due to individual characteristics of neurons are still allowed, is mediated by the bursting of intrinsically non-bursting spiny stellate and basket neurons. Using advanced methods of noise removal, we concluded that the collective behavior is of low-dimensional chaotic nature. The model observations are compared with data from anesthetized cats, where three fundamental groups of neuronal firing are distinguished. Using variable thalamic input currents, the characteristic in vivo behaviors and statistical properties are reproduced. Model and experimental data lead us to the conclusion that a large group of neurons fire in terms of patterns which may have a significance in information transfer in the brain.

Keywords: *Chaotic biological neural networks, synchronization and control, patterns.*

I. INTRODUCTION

One question in mankind's struggle to understand its own intellectual capacity has attracted particular attention. It is the puzzle of how the human cortex can be so variable and efficient, in cognitive tasks and in storage, although the cycle time of cortical computation - if a typical interspike interval is taken as the basic unit of the clock time - is of the order of milliseconds, a time that is far slower than what is currently (easily) achieved by computers. This observation leads to the expectation that there may be hidden, still undiscovered, computational principles within the cortex that, if combined with the speed of modern computers, could lead to a jump in the computational power of artificial systems, from both the hard- and software points of view. In the explanation of the computational properties of the human brain, an important issue of current interest is the feature-binding problem, which relates to the cortical task of associating one single object with its different features [1]. As a solution to this problem, synchronization among neurons firing has been proposed.

2. NEURON GROUND-STATE AND BEYOND

We consider the case where a silent neuron obtains a number of excitatory, and inhibitory, inputs with small temporal variation. Increasing

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the excitatory input, the neuron undergoes a Hopf bifurcation and starts to fire in a regular fashion. When two or more neurons are strongly connected, their firing locks in an universal manner [2]. Experimental observations of this locking can therefore be taken as the proof that neurons are on limit-cycle solutions in their ground state. Beyond this bi- or n-ary strong interaction, a weaker exchange of activity can be modeled as diffusive coupling-mediated interaction among the more strongly coupled centers. In this way, we arrive at a next-neighbor coupled map lattice model, which is based on measured binary interaction profiles at physiological conditions (including all kinds of variability, e.g., interaction, coupling strengths).

Within this paradigm, generalized synchronization would lead from initially independent to coherent macroscopic behavior, which then could be taken as the expression of a corresponding perceptional state. However, extended simulations show that, for biologically reasonable parameters, the generic response of the network is unsynchronized, despite the coupling. Extrapolations from simpler models, for which exact results are available [2], provide us with the explanation why: They show that it is extremely difficult to obtain synchronization from network architectures involving only pyramidal neurons (typically residing in cortical layers II-III and V-VI).

3. SYNCHRONİZATİON VİA THALAMİC İNPUT

Maintaining the assumption that synchronization is needed for computational and cognitive tasks, the question remains where such behavior might be generated. In simulations of biophysically detailed models of layer IV cortical architecture, (see Fig.1 and [3]), we discovered a strong tendency to produce coarse-grained synchronization.

This synchronization is based on intrinsically non-bursting (non-pyramidal) neurons that develop the bursting property as a consequence of the recurrent network architecture and the feed-forward thalamic input in the major part of the accessible parameter space. In spite of their individual characteristics, all individual neurons are collectivized, and give rise to, on a coarse grained scale, synchronized dynamics (see Fig.2).

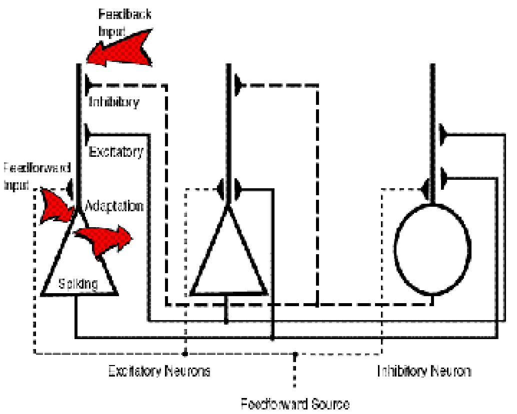

Figure 1. Layer IV architecture used for the simulation, involving (excitatory) spiny stellate and (inhibitory) basket cells. Note the recurrent connectivity.

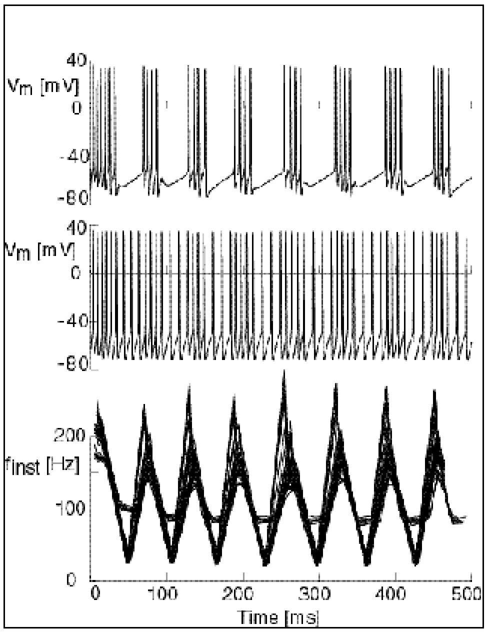

Figure 2. Coarse-grained synchronized activity of layer IV dynamics. Excitatory (upper trace), inhibitory (middle trace) and from several neurons superimposed (bottom, containing excitatory as well as inhibitory neurons).

4. CHAOS AND CONTROL

In fact, using methods of noise cleaning, we find that the collective behavior can be represented in a four-dimensional model, having a strong positive, a small positive, a zero and a very strong negative Lyapunov exponent, with identical values for all involved neuron types [3]. The latter characterization has been checked by comparing the Lyapunov dimension ($d_{KY} \sim 3.5$) with the correlation dimension ($d \sim 3.5$). Moreover, different statistical tests have been performed to confirm that the noise-cleaning did not bias the statistical behavior of the system.

The question then arises of what functional, possibly computational, relevance chaos could be associated with? When we allowed in our layer IV-model the (thalamic) feed-forward input to vary, we observed an astonishing ability to generate well-separated characteristic interspike interval lengths. This supports the view that cortical chaos may reflect the ability of the system to express its internal states (e.g., a result of a computation) by choosing among different interspike intervals or, more generally, among distinct spiking patterns, analogously to the chaos control paradigm. In the case of artificial systems or technical applications, strategies on how to use chaos to transmit information, are well developed. One basic principle used is that small perturbations applied to a chaotic trajectory are sufficient to make the system follow a desired symbol sequence, containing the transmitted message [4]. This control strategy is based upon the property of chaotic systems known as "sensitive dependence on initial conditions". Another approach, which is currently the focus of applications in areas of telecommunication, is the addition of hard limiters to the system's evolution [5]. This very simple and robust control mechanism can, due to its simplicity, even be applied to systems running at Giga-Hertz frequencies, and it leads to convergence onto periodic orbits in less than exponential time [6].In spite of these insights into the nature of chaos control, it is still unclear which kind of control governs cortical chaos. In layer IV chaos, one possible biophysical mechanism would be a small excitatory / inhibitory post-synaptic perturbation at the end of a collective burst, which enables / disables firing of additional spikes. Another possibility, is the use of local recurrent loops to establish delay-feedback control [7]. In fact, such control loops could be established via the abundantly occurring recurrent neuron connections. The relevant parameters in this approach are the time delay of the re-fed signal, and the synaptic efficacy, where especially the latter seems biologically well accessible.

Different read-out mechanisms able to decode the signal at the receiver's side can be imagined, starting from simple threshold units up to spike-pattern detection mechanisms. For the latter, besides simple straightforward implementations that lead to supra-threshold summation only for some patterns, more sophisticated approaches, such as the recently discovered general activity-dependent synapses (e.g., [8]) seem natural candidates for this task.

5. COMPARISON WITH IN VIVO DATA

For particular in vivo-measurements, the emergence of firing in patterns is obvious. When sharply separated interspike interval lengths emerge, they can directly be mapped onto symbols (of the same number as there are classes of distinguishable interspike interval lengths). A suitable transition matrix then specifies the allowed, and forbidden, succession of interspike intervals. I.e., this transition matrix provides an approximation to the grammar of the natural system (see Fig. 3). The majority of in-vivo neuron data, however, behaves more similarly to our layer IV-simulations, where firing patterns distinguish more clearly than single length scales. Instead of using a transition matrix method, this case should be analyzed using methods developed for intermittent systems (corresponding to the grand-canonical approach in statistical mechanics).

When we compared the model data with in vivo anesthetized cat measurements (17 time series from 4 unspecified neurons from unspecified layers), we found agreement that, to this extent, would not be expected. Not only were the measured in vivo dimensions in the range predicted by the model; specific characteristic patterns found in vivo could also be reproduced by our simulation model. Of particular interest are step-wise structures found in the log-log-plots used for the evaluation of the dimensions. These steps have previously been associated with low dimensions [9], but can be proven to be indicative for firing in terms of patterns. The coincidence of modeling and experimental aspects of visual cortex firing leads us to believe that the observed ability of the network to fire in well-separated characteristic time scales, or in terms of whole patterns, is not accidental. Rather, it seems to be generated in layer IV, serving to evoke corresponding responses within other layers by means of resonant cortical circuits. The deeper interpretation, of course, would be that its final task is to efficiently transmit information.

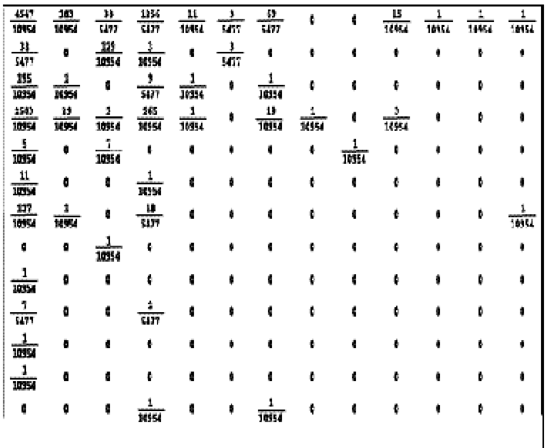

Figure 3. Matrix representation for one particular neuron when stimulated by a square-wave grating, for which the neuron responds optimally. The case corresponds to group III neuronal firing in Fig. 4.

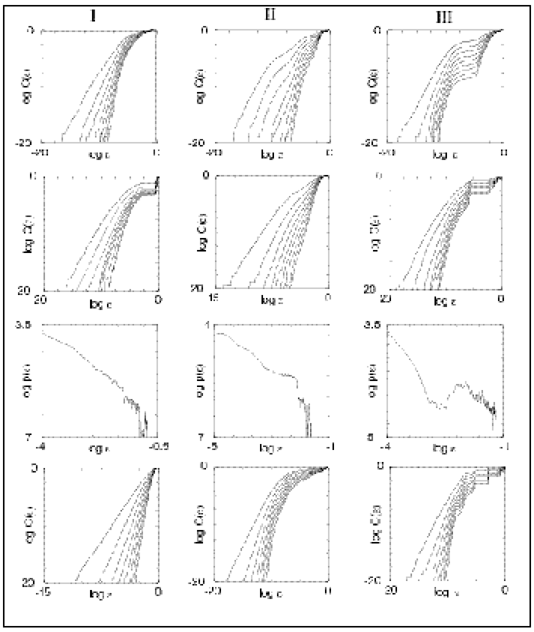

Figure 4. Fundamental neuronal firing classes. I) Firing in noise-dominated environment; II) intrinsic pattern firing that is incompatible with input patterns; III) firing in terms of well-resolved firing patterns. Dimensions: 3.5, 4.5-5.5, 2.5, resp. First row: experimental results; second row: layer IV simulation results (interactions of several layer IV feed-forward currents); third row: typical probability density distributions (experimental); fourth row: surrogate data (based on identical artificial spike interval distribution. I: Random selection of intervals, small noise, II: firing in patterns with small sinusoidal driving, small noise, III: pure firing in patterns, without noise, where interval patterns are chosen to reproduce the neuron of Fig. 3).

Obviously, not every neuron fires in terms of patterns. From our in vivo anesthetized cat data, we found three main groups of neuron firing, upon evoked or spontaneous neuron firing (where the distinction of the stimulation paradigms allowed for no further discrimination of the classes), see Fig. 4.

Based on the in simulations observed affinity of layer IV neurons to collectively generate firing patterns, we interpret these classes as follows. Class III corresponds to a situation, where the internal mode of operation of the neuron is compatible with the external stimulation. From step-like behavior that changes through the embedding dimensions, we associate class II with neurons that have incompatible stimulations/internal modes. Class I, finally, shows no patterns in the firing at all and may be driven solely by noise-like stimulation, possibly transmitted by decorrelated input over many neurons. Neurons of this class would primarily act as power engines for the transmission of information, but not transmit information in the first instance (see [2] for a deeper analysis). What support do we have for this interpretation ? The argument supporting the identification of step-wise behavior with firing in terms of patterns is our surrogate data analysis that yields compatible results (see Fig. 4). An argument supporting the characterization in terms of compatible stimulation modes is provided by the fractal dimensions and Lyapunov exponents which show that, when the firing is compatible, the dimensions decrease, whereas in the case of incompatible firing modes, additional degrees of freedom (corresponding to external stimulation) appear. Class I is between the two, but still seems to witness layer IV dynamics as the origin of the noisy stimulation. A last finding of interest is that in the absence of patterns, long-tail behavior of the interspike interval distribution is found. In the compatible case, a clean separation between patterns and individual firing is found, whereas the characteristics of the incompatible class are more typical of a mixture between the two length scales (see Fig. 4). In all cases, the firing seems hardly compatible with a Poissonian firing assumption, indicating that structures like patterns will play an important role in neuronal firing.

The methods by which patterns in neuronal firing should be detected, is presently highly disputed in the neuronscience community. Prevalently, the methods used in this field are based upon template matching. As a consequence, all of these approaches deal with the problem of predefined template structures and matching accurracies, which introduces a large bias. The method used in the present contribution, being a purely statistical one, is bias-free. Moreover, for the steps in the log-log plots indicating the patterns, a straightforward interpretation of macroscopic behavior can be given. They indicate states realized in the form of patterns, that during temporal evolution are lost, according to a power-law. More precisely, the slope of the steps indicates the stability of the patterns within the neuronal firing. In a forthcoming publication, the theoretical foundations of the used pattern recognition method are outlined in detail and the reliability of the method is demonstrated [10].

6. CONCLUSION

From our investigations we conclude that throughout the visual cortex, there is a characteristic, low-dimensional hyperchaotic neuron behavior (with a dimension of about 3.5) that can be reproduced by biophysically detailed models of neurons and architecture of layer IV. For a particular neuron, this behavior is modified according to its relationship with the stimulating environment, leading to the three firing classes worked out above. As a function of the particular experimental stimulation paradigm, the membership of a neuron to one of these classes remains relatively fixed; however, pattern sharpening stimulation paradigms have been observed. To understand the functional role of the occurrence / absence of patterns in the firing behavior still requires additional experimental and theoretical work.

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