TOWARDS CLOSE-TO-NATURE NEURAL NETWORKS

*R.Stoop** *and L.A.Bunimovich***

* Institut für Neuroinformatik, ETHZ/UNIZH, Winterthurerstr.190, CH-8057 Zürich-Irchel
** Southeast Applied Analysis Center, Georgia Institute of Technology, Atlanta GA 30332

ABSTRACT

When regularly spiking rat cortical cells are perturbed by periodic inhibition, for set of positive measure of specific ratios between stimulation and self-oscillation frequency, the resulting spiking pattern is chaotic. Contrary to earlier speculations, these connections do not desynchronize the network. The optimal network performance is characterized by the transition from local chaos to global chaos dominance. When a phase-coincidence detection algorithm is applied, quick convergence towards nontrivial phase patterns is observed. Distinct "sensory" inputs to the network are reflected in localized, input- specific differences of the observed attractors.

1 INTRODUCTION

Although considerable progress has been achieved in the past, the way the brain works is still far from being understood [1]. Understanding the brain is intrinsically connected with questions such as how information is stored and propagated. The connection of neurons to a network clearly exceeds the complexity of its elements. However, one may expect that the behavior of the whole brain can be related to the behavior of single functional elements.

Questions which recently obtained considerable interest are whether or not brain activity can be chaotic [2] and whether or not it may be useful to use a phase-coding strategy to process the information in the brain, instead of the frequency-coding which sets up the usual model for artificial neural networks. This issue was raised in a special news report in science [3], where ongoing experimental work of B.N.Farhat [4] with the aim of building near to biology neural networks was discussed.

In the present article, we report on the results we have achieved into a closely related direction. In our approach, as a starting point instead of artificial neurons we use *experimentally measured response of rat cortical neurons* in a slice preparation. Using a nonlinear dynamics approach, on the basis of this experimental data *it is possible to demonstrate that single cortical cells may respond with chaotic firing patterns to periodic inhibitory stimulation* [5]. In order to derive from the experimental facts the behavior of a network, we use a *coupled map lattice approach* [6-8]. We are able to demonstrate that in a network our *inhibitory connections and not the excitatory connections lead to a coherent pulsing of the phases.*

When a neuron gets a large enough number of temporally uncorrelated, small-size stimuli, it suddenly starts to spike in a periodic way. From the point of view of nonlinear dynamics, the neuron has undergone a Hopf, or, as in our case, a homoclinic saddle-node bifurcation [10] and is now on a limit cycle solution [9][11]. By means of a Poincaré section, which by now has become a widely applied procedure, the associated differential equation system can be converted into a discrete map. This leads to a considerable simplification of the problem. In the case of a regularly spiking neuron, the map displays a fixed- point behavior. Information arrives at the neuron in the form of substantial packages of stimuli; this amounts in the mathematical picture to a perturbation of the limit cycle. In a similar context (that of the embryonic chicken heart cell beating) this point of view has been adopted with considerable success some time ago by Glass and Mackey [11]. In our experiment described in [5], slices of rat brain are investigated in an *in vitro* preparation. The limit cycle behavior is triggered by the application of a constant DC current to the cell. The perturbation is achieved by means of stimulating exciting nerve fibers leading to the neuron (this produces a *synaptic input*). The synaptic input leads to an addition (excitatory stimulation) or a subtraction (inhibitory stimulation) of a short-time current pulse of the duration of about $5ms$ to the DC current. The response of the neuron upon an incoming perturbation results in a *modified phase at which the next spike appears.* In the experiment, this phase dependence can be determined by using the relation the equation [11] [5] $T + t_2 = t_1 + T_s$, where T_s is the time between successive perturbations, T is the perturbed cycle length, t_1 is the time

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after spiking at which the perturbation was applied, and t_2 is the time after the spike at which the next perturbation will appear (t_2 can be viewed as encoding the length of the perturbed cycle). Expressing this relation in terms of phases is achieved by dividing the equation by T_0, the cycle time of the unperturbed limit cycle. This immediately leads to the equation

$$P : \phi_2 = \phi_1 + \Omega - T/T_0 \pmod 1, \tag{1}$$

where $\Omega = T_s/T_0$ is the frequency ratio between the periodic perturbation and the periodic limit cycle. This equation has the form of a circle map [14] and should be interpreted as a *Poincaré return map* [11]. The reaction of the cell upon the stimulation is essentially contained in the last right-hand-side contribution in this equation, that can be called the *phase-response* function [11]

$$g : \phi = t_1/T_0 \to T/T_0. \tag{2}$$

Map g is typical for the considered cell type, the perturbation strength or the cell excitability and the stimulation type. In our work, it will emerge that the forms these phase return maps can assume are sufficient to determine the behavior of the network.

2 POINCARÉ MAPS

For the stimulated neuron, typically phase response functions as shown in Figs. 1 a), b), emerge, for the cases of inhibitory stimulation and for excitatory stimulation, respectively (we show only the interpolating functions of the experimental data points, for more details see Ref. [12]).

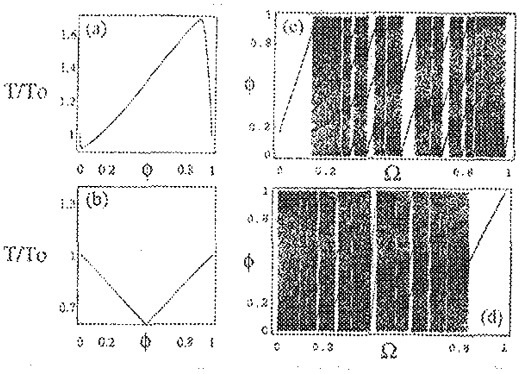

Figure 1: Phase response functions $g : \phi \to T$ for a) inhibitory and b) for excitatory stimulation. c), d): Corresponding bifurcation diagrams, stimulation strength: $k = 0.2, 0.4$, respectively.

In the experiment, the effects of isolated perturbations are measured in order to derive the phase-response function. By iteration of the associated Poincaré maps P, predictions of the phases can be made which should be observed upon periodic perturbation of the system. For the perturbed system, periodic behavior, for example, is identified by a set of observed phases of finite cardinality. It is worth emphasizing that the phases that are obtained from the application of the return map are not determined by the phase response map g alone, but also depend in an essential way on the value of the phase shift Ω. This additive constant of Eq. (1), which expresses the relation between self-oscillation frequency of the neuron and the frequency of the perturbation, has a strong influence on the grammatical structure of the system. An investigation of the generated phases in dependence of Ω results in a bifurcation diagram. The typical bifurcation diagrams for our experiment for both cases of stimulation are displayed in Figs. 1 c), d). Starting with periodic behavior at small phase shifts, soon bands of phases arise which indicate irregular response of the neuron upon the perturbation. Calculation of the Lyapunov exponents [15] corresponding to the bifurcation diagram shows that inhibition can lead to chaotic spiking behavior. Recently, first numerical evidence [5] has been corroborated by analytical investigations [13]. For excitation we found no experimental evidence of chaotic behavior, since under biological conditions the phase return map has always found to be always invertible (these statements are consistent with the phase response maps of Figs. 1 a), b)).

The bifurcation diagram also depends on the perturbation strength. Our experimental evidence indicates that within a broad range of biologically meaningful perturbation strengths k, this dependence can be modeled as

$$g(k, \phi) = (g_{ko}(\phi) - 1)k + 1, \tag{3}$$

where $g(k, \phi)$ is the phase response function at perturbation strength k, and g_{ko} denotes the phase response function obtained for a chosen model perturbation strength ko. It has emerged that for our purpose it is not useful to separate perturbation strength from the excitability of the targeted neuron. We therefore chose for k_o the perturbation strength which leads to a maximal lengthening of the inter-spike interval by a numerical factor of 1.8.

3 UNIVERSAL RESPONSE

For the dependence of the bifurcation diagram on the perturbation strength k we stress the following facts (c.f. [13]): Within a broad parameter range of the stimulation strength, the qualitative features of the bifurcation diagram (i.e., its topology) remains unchanged. This is a *consequence of universality properties of the circle map class* [9]. As a general tendency, valid for both types of stimulation, we observe that with increasing perturbation strength the bands observed in Fig. 1 get narrower. Moreover, as a further consequence of circle map universality, the exact interpolation function is irrelevant for topological properties of the bifurcation diagrams. Seventh-order polynomials and linearized versions of the inhibitory phase response map shown in Fig. 1 a) yield qualitatively identical results. It is this universality principle which makes indicates that our results can be of a far-reaching significance. This interpretation is corroborated by the observation that at those thresholds above which our biological experiments cannot be continued (because the cells would be destroyed), also in our mathematical description abrupt changes set in: inhibitory stimulation ceases to be able to generate chaos. At the same time, excitatory stimulation acquires this ability.

It is furthermore of importance to compare the predictions made by the bifurcation diagram with the results obtained from experiments of continued perturbations, to prove that under the given conditions the assumption of a stable enough limit cycle still is valid. To this end, we stimulated the neuron periodically with inhibition at fixed values of Ω, classified the obtained set of phases as periodic or as chaotic and then compared these findings with the predictions made by the bifurcation diagram. The agreement between prediction and experiment was good; it even improved when we included into our iterative approach additive Gaussian distributed white noise of the size observed in our experiment.

4 NEURON CONTROL

For phase-coded information, the question arises whether the computational unit has the ability to adjust the firing behavior to a given required periodicity. On first sight, the usual controlling chaos techniques which start off from a chaotic "ground" state and then apply control to obtain the desired periodicity [17], look very attractive, because, in this way the phase return map could essentially be preserved. Biologically, such a fact implies that the biophysical processes remain unchanged, with possible exception of the localized part where the control is applied. However, we found no evidence for the occurrence of this mechanism. Instead, the adjustment is established in the following way. It is possible to show that all periods exist if the value of the phase-shift Ω is appropriately chosen. This is a consequence of the fact that both phase return functions are of circle map type (to our surprise, this universality class is sufficiently large to include both types of stimulation [13]). The required periodicity then can be selected by switching to the appropriate Ω. In practice, this is done via *a change of the frequency of the perturbing neuron.*

5 NETWORK PROPERTIES

In order to investigate possible effects arising from local chaos generated by inhibitory connections, we investigated *networks built up from our experimentally measured Poincaré return maps.* In 'purely' biological networks of neocortical neurons, large-scale ordering and coherence in firing over large distances are observed abundantly. So far, this effect has not been explained microscopically in a satisfactory manner, when starting from site maps. For some time it was widely believed that excitatory stimulation is responsible for the observed synchronization effects [18]. However, evidence originating from purely inhibitorically connected, but strongly coherently periodically spiking cells in the thalamus, later questioned this point of view [19]. In the light of the former belief, chaotically spiking neurons could be speculated to be needed to break global synchronization obtained in this way.

We focused on small-scale networks with our experimental Poincaré return maps as site maps (network size varying between 150-700 sites on a rectangular $M_1 \times M_2$-grid) on which we put diffusive next-neighboring coupling. In simple words, this model describes a situation where (not necessarily spatially localized) pair-stimulations dominate the network activity and can be separated from the higher-order background activity. From a mathematical point of view, due to the fact that generally circle-type maps lack the property of absolutely continuous invariant measure, very few analytical statements can be expected. This is in contrast to networks of, e.g., fully chaotic tent maps [8], or identically distributed ensembles of sigmoid neurons [16]. We therefore resorted to performing numerical simulations. Our networks were of; fully excitatory, fully inhibitory, and mixed type. In the last case, we chose 0.8 excitatory and 0.2 inhibitory connections. The coupling was characterized by an over-all coupling strength k_2, and random coupling strengths $\tilde{k}_{i,j}$ between site maps and next neighbors, taken from a uniform distribution over $[0.5, 1.5]$. For the site maps, we similarly chose $\Omega \in [0, 1]$. The corresponding excitabilities k (c.f. Eq. 3) were taken from the interval $[0.4, 0.8]$, monitoring in this way rather strong synaptic connections. As a consequence, for the phases the update-rule

$$N_{i,j} = (1 - k_2 \tilde{k}_{i,j}) P_{i,j} + \frac{k_2}{|\, nn \,|} \tilde{k}_{i,j} \sum_{m,l}^{nn} P_{m,l} \qquad (4)$$

emerges, where $N_{i,j}$ denotes the phase at site $\{i, j\}$, P is the phase return map at the indexed site and

$| nn |$ denotes the cardinality of the set of all next-neighbors of the site $\{i, j\}$. The coherence of the overall network performance was measured by calculation of the metric

$$\delta(t) = (M_1 M_2)^{(-1)} \sum_{i,j} | (N_{i,j}(t) - N_{i,j}(t_0)) | . \quad (5)$$

This coherency measure was usually applied after $t_0 = 5500$ discarded initial iterations for $t = 100$ consecutive time steps. $\delta(t) = 0$ indicates a returning pattern; periodic structures in $\delta(t)$ are indicators of periodicity on a larger time scale (possibly connected with a small stochastic or chaotic component, if zero is not reached). A comparison of the results obtained for the three types of networks (see Figs. 2) shows clearly that the *coherent pulsing of the network is due to the influence of inhibitory and not of excitatory connections.*

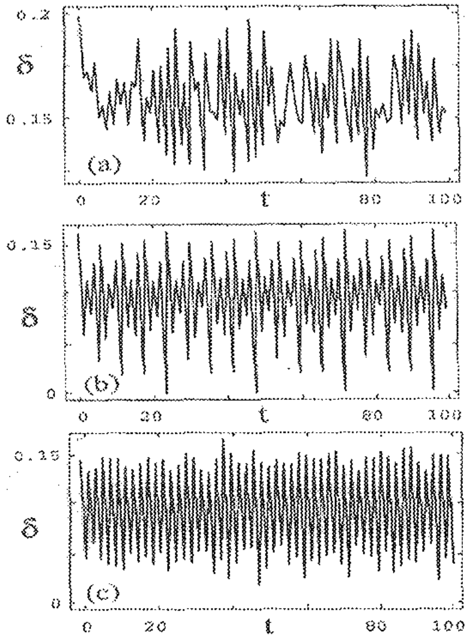

Figure 2: Network coherency measured in terms of $\delta(t)$ for 100 time steps, for networks of a) full excitatory, b) full inhibitory and c) mixed excitatory-inhibitory type (see text). Coupling strength $k_2 = 0.8$. Identical initial conditions.

6 CODING SITES

At this point, only the properties of self-organization of the network have been active (no information arriving from outside of the network, no learning rules has been considered). According to our findings

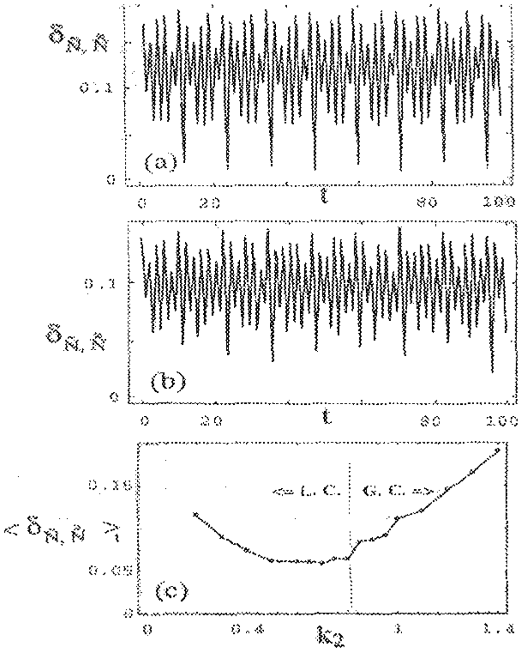

Figure 3: Network coherency $\delta(t)$ for input patterns consisting a) of a fixed phase, b) of random phases, for 100 time steps. Nearly periodic behavior emerges in b) on much longer time scales. Coupling constant $k_2 = 0.8$. c) The time-averaged difference between the coherency measures generated by different patterns $\delta_{\tilde{N}\tilde{\tilde{N}}}$ shows a clear minimum as a function of the coupling strength k_2. Identical initial conditions for all measurements.

above, we expect that the inhibitory connections are needed for the emergence of a coherent reaction of the whole network onto arriving input. In order to investigate this aspect, we connected our network to different one-dimensional arrays of fixed phases, chosen either identically or uniformly distributed at random. As shown in Figs. 3 a), b), the input patterns generate additional fine-structures in the network output. In order to numerically compare different network outputs, the difference between two networks $\tilde{N}, \tilde{\tilde{N}}$ can be measured by using the metric

$$\delta_{\tilde{N}\tilde{\tilde{N}}}(t) = (M_1 M_2)^{(-1)} \sum_{i,j} | (\tilde{N}_{i,j}(t) - \tilde{\tilde{N}}_{i,j}(t)) | . \quad (6)$$

In our case, we use this quantity to calculate the deviations generated in a given network by different input patterns. A time average of this quantity can be used as an indicator of the ability of the network to *respond in a fine-tuned way to different input patterns.* It is natural to define the optimal performance working condition of the network at the nonzero minimum of $\delta(k_2)$, if it exists.

As is shown in Fig. 3 c), a clear minimum emerges just below a critical value $k_{2_c} \sim 0.83$. The latter value coincides with the value at which the networks make a transition from globally periodic behavior with dominating importance of local chaos (LC), to global chaos (GC).

If the phase is the important thing in the reaction of the neuron, how is information contained in the phase proceeded? The simplest way to think of this process consists in a learning algorithm designed for the detection of phase-coincidence emerged. That is, neighboring sites which fire in-phase enhance their connection strengths, among off-phase sites the connection strength is reduced. Under this phase-coincidence detection, formerly chaotic patterns converge, for all applied input patterns, to patterns whose highly nontrivial structures that are also time-dependent. By calculation of the local metric distance between the converged patterns, it emerges that the network changes are always confined to a small number of network sites. The location of these sites is *highly input specific* and robust in time.

7 CONCLUSIONS

We started our study by measuring the reaction of regularly spiking rat cortical neurons to periodic perturbations. For excitatory and for inhibitory stimulations, as a function of the parameter Ω expressing the relation between self-spiking and perturbation frequency, we found nontrivial bifurcation diagrams. For inhibitory stimulation, local chaos is possible at high excitabilities. As the next finding, using network simulations based on our experimentally measured phase response functions, we showed that it is the *inhibitory connections which make a coherent reaction of the considered network possible.* Possible chaotic behavior of these connections do not desynchronize, but rather help to synchronize the network. We then considered the ability of the network to store input patterns. Our findings are that different input patterns influence the over-all network behavior in a non-trivial way. At threshold k_{2c} the network makes a *transition from local chaos to global chaos dominance.* Just below this value, the network is able to respond in the most fine-tuned way to distinct input patterns. This specific behavior points out the importance of higher-order nonlinear effects for the explanation how the brain works. We then implemented a learning-like algorithm specified for the detection of phase-coincidence. As soon as this algorithm is applied, the neural network behavior converges to a stable, complex pattern development: We observed that when distinct input patterns are fed into the network at identical initial conditions, the induced phase changes are confined to a *sparse set of sites* in the network. This means that our network is able to react in very *input-sensitive way.*

Let us finally assume that connections exist which lead from the sites at which these phases changes occur, to other areas of the brain where results can be stored or used to trigger further actions. Let us further assume that a mechanism exists, by which the converged connection strengths are reset. We then have arrived at a theoretical picture of how the brain could work on the basis of phase properties. In our view, it will be a worthwhile challenge to investigate whether this point of view can be further substantiated in experiments on networks of natural neurons.

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