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Synchronization and label-switching in networks of laterally coupled model neurons

A. Nischwitz, H. Glünder[*‡], A. von Oertzen and P. Klausner

Lehrstuhl für Nachrichtentechnik, Technische Universität München, Arcisstraße 21
D-8000 München 2, F.R. Germany, Email: alfred@lnt.e-technik.tu-muenchen.de

[*] Institut für Medizinische Psychologie, Ludwig-Maximilians-Universität, Gœthestraße 31
D-8000 München 2, F.R. Germany

Abstract

Necessary conditions for the impulse synchronization in non-oscillating networks of laterally coupled 'integrate-and-fire' model neurons are investigated. The behavior of such networks for homogeneous stimulations as well as for differently stimulated subpopulations is studied. In the first case, synchronization accurate to fractions of the impulse duration can be achieved by either lateral *inhibition* or lateral *excitation* and in the second case, good and independent synchronization is obtained within subpopulations, if they are separated by units without stimulation.

1. INTRODUCTION

Recent electro-physiological investigations of the visual cortex, mainly in the cat, revealed stimulus-dependent temporal correlations between spatially separate neural activity [1, 2]. It is currently conjectured that the (spatial) coherence of visual data, such as direction and speed of motion, contrast, texture or color, is expressed (labeled) by synchronized neural activity. In this sense, neurons that fire asynchronously but perhaps at the same rate, indicate non-coherent features, for example those belonging to different objects. Obviously, a thorough judgement of this hypothesis must be based on some knowledge about necessary conditions for the synchronized spike generation in networks of 'integrate-and-fire' model neurons. Consequently, we resume and extend last year's report on this issue [3], before we deal with responses of such networks to spatio-temporal stimuli.

2. NETWORK MODEL AND MEASURE OF SYNCHRONY

The formal neuron (unit) considered here behaves like a leaky integrator with a time constant of 10 ms. Hence, a unit's constant excitatory input increases its somatic potential $\varphi_i(t)$ according to the step response of a first order low-pass. When this potential surpasses the threshold θ, an exponentially declining impulse $p_i(t)$ of duration $T_{sp} = 1$ms is triggered and the somatic potential is reset to the resting potential φ_{re}. Following a refractory period of $T_{re} = 0.5$ms, the integration starts again (Figure 1). Investigated are single stage networks that are cyclically closed chains consisting of n laterally coupled units (Figure 2). All interconnections are either *inhibitory* or *excitatory* with coupling coefficients w_ν that linearly decrease with the distance. To quantify the level of synchrony, a quality factor η is defined as the maximum value of the spike density $S(t)$ taken from intervals of 50 ms. The instantaneous spike density in turn is the ratio of the binarized impulse activity in a spatio-temporal window (n units long and an impulse duration wide) and the window area (see Figure 5 for examples of $S(t)$). The spike density $S(t) = 1$ and therefore

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$\eta = 1$, is reached iff all n units start firing simultaneously. Two quality factors η_{50} and η_{200} are considered, that are the maxima of the spike densities $S(0\ldots50\text{ms})$ and $S(150\ldots200\text{ms})$ respectively. The synchrony η_{ref} refers to the uncoupled network and – due to the individually randomized starting potentials $\varphi_i(t=0)$ and to the noisy thresholds $\theta + n_i(t)$ – implies asynchronous impulse generation. Evidently, the reference quality increases with the firing rate $R(e, W, \vartheta)$ that depends on the stimulation e, the integral coupling strength W and the delay ϑ in the lateral interconnections (Figure 2). A more detailed description of the network is given in [3].

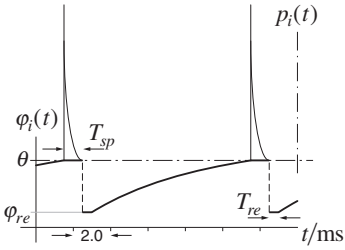

Figure 1. Typical time-courses of the somatic potential and of the axonal impulses of an isolated unit

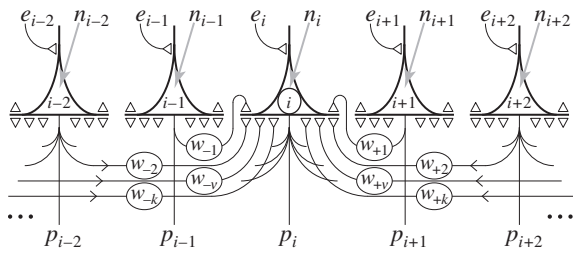

Figure 2. Interconnection scheme of the one-dimensional network composed of recurrently coupled units

3. GLOBAL HOMOGENEOUS STIMULATION

In networks consisting of $n_S = 64$ excitatorily coupled units that are simulated with a temporal increment $\delta t_S = 0.1\text{ms}$, good synchrony ($\eta > 0.7$) is observed for the standard parameter values: $k_s = 8$ bilateral connections per unit, integral lateral coupling strength per unit $W_S = \sum w_\nu = +0.2$, equal stimulation $e_i(t>0) = E_S$ of all units (that would cause an impulse rate of $R_S = 100/\text{s}$ in an uncoupled unit), and transmission delay $\vartheta_S \approx 0\text{ms}$. How deviations from these values affect the synchrony is described in [3]. Recent research reported below also deals with inhibitory lateral interconnections ($W < 0$) and more realistic delays $\vartheta > 0.5\text{ms}$. To avoid very low impulse rates in inhibitory networks (Section ii), stimulation is doubled ($2E_S$).

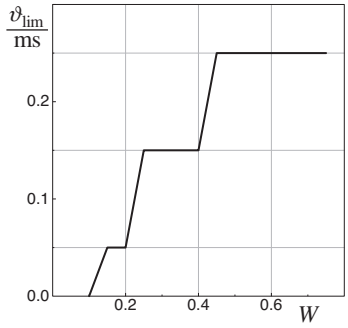

Figure 3. Tolerable delay ϑ_{lim} for $\eta_{200} > 0.7$ as a function of the coupling strength W

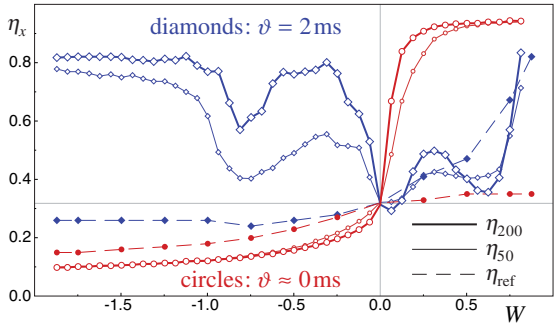

Figure 4. Synchrony as a function of the coupling strength W for transmission delays $\vartheta \approx 0\text{ms}$ and $\vartheta = 2\text{ms}$

i) In case of purely *excitatory* interconnections, the tolerable delay for $\eta_{200} > 0.7$ grows monotonously with the coupling strength W (Figure 3). It reaches $\vartheta_{\text{lim}} = 0.25\text{ms}$ for the critical

coupling strength $W_{\text{crit}} = +0.78$, at which a unit that is not externally stimulated starts being triggered by synchronous impulses from the k_S units of one side. As a consequence of the temporal sampling – which implies an average intrinsic delay of $\delta t/2$ (see e.g. [4]) – such simulations must be performed with temporal increments $\delta t \leq 0.5\text{ms}$.

ii) The data displayed in Figure 4 demonstrates that spike synchronization is feasible with either purely *inhibitory* or *excitatory* interconnections. The corresponding values for delay and coupling strength are complementary: Without delay, lateral excitation results in excellent synchrony ($\eta_{200} = 0.9$), whereas lateral inhibition de-synchronizes ($\eta_{200} \approx 0.1 < \eta_{\text{ref}} \approx 0.2$). For delayed ($\vartheta = 2\text{ms}$) excitation, synchrony stays in the range of the reference quality. (The increased synchrony and reference quality for $W > 0.7$ is caused by a steep increase of the impulse rate that reaches $R \approx 500/\text{s}$). In contrast however, delayed ($\vartheta = 2\text{ms}$) inhibition produces well synchronized activity ($\eta_{200} = 0.8$) that results from the temporally non-linear way in which inhibitory postsynaptic potentials (IPSPs) affect the generation of action potentials: The efficacy of an IPSP in delaying the triggering of a spike is higher for somatic potentials near the threshold than for those near the resting potential. Hence, advancing impulses are stronger retarded than late ones, a regime that results in synchrony.

4. SELECTIVE STIMULATION OF SUBPOPULATIONS

Following the brief outline of the network behavior for global and constant stimulation, first results from simulations with spatio-temporal stimuli are reported. For this purpose the randomized starting potentials are replaced by a deterministic pattern onto which a differently shaped stimulation pattern is superimposed for times $t > 0$. Effects of this so-called label-switching on the spatio-temporal synchronization process are studied. Except for initialization and stimulation, all network parameters conform to the values of the standard setting for excitatory coupling.

Two independent, synchronous subpopulations at time $t = 0$ are simulated by an appropriately patterned initialization of the somatic potentials: Half of the units have their somatic potentials set to the threshold $\varphi_{16\ldots47}(t=0) = \theta$ (label 2) and those of the remaining units (closed chain) are set to the value $\varphi_{48\ldots15}(t=0) = (\theta + \varphi_{\text{re}})/2$ (label 1), which is the middle between threshold and resting potential. For times $t > 0$ the units 1...32 are stimulated by the sustained input E_S (label 1') and the units 33...64 by $0.7 \cdot E_S$ (label 2'), i.e., the stimulation pattern is shifted by 16 units with respect to the initialization pattern (see left part of Figure 5).

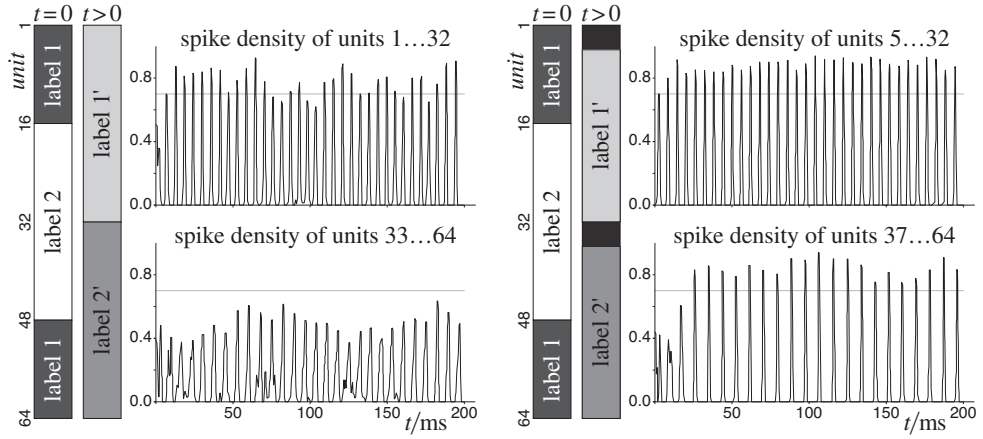

Figure 5. Patterns of initialization ($t = 0$) and stimulation ($t > 0$) of the excitatorily coupled network, and the resulting spike densities $S(t)$ for label-switching without (left) and with buffer units (right)

Under these circumstances, the stronger stimulated (E_S) subpopulation is moderately synchronized, whereas the less stimulated ($0.7 \cdot E_S$) subpopulation shows weak synchrony. Obviously, there is some destructive influence of label 1' on label 2'.

Good and undisturbed synchrony in differently stimulated subpopulations is observed if they are separated by units without external stimulation (right part of Figure 5: $i = 1 \ldots 4$, $i = 33 \ldots 36$). For this condition it is even possible to switch from 2 to 3 labels without loss of synchrony in the new subpopulations. If lateral transmission delays are introduced, more buffer units are required in order to maintain good and independent synchrony in subpopulations.

5. DISCUSSION

An essential difference between the presented approach and most of the presently discussed ones [5,6,7,8,9], is the lack of explicitly implemented oscillator *circuits*. Consequently, any spiking activity is due to sufficiently stimulated formal neurons that act as voltage-controlled and noisy impulse generators. Spatio-temporal activity patterns in the network output either result from the lateral coupling, or from the external stimulation, or they occur simply by chance. It is important to note that synchronization by lateral interconnections works over a large range (at least 1:10 for lateral excitation) of impulse rates (right part of Figure 5 and [3]) and only recently neurophysiological evidence of spatial correlations in aperiodic neural activity was reported [10].

The superiority of networks with inhibitory lateral interconnections – especially with respect to realistic delay times – is obvious: Delays $\vartheta > 0.25$ms permit only weak excitatory synchronization and neuroanatomically regarded, lateral inhibition is more likely as well [11].

The investigations demonstrate that synchrony accurate to fractions of the impulse duration and consequently, the encoding of up to 50 phase labels (at $R_S = 100/\text{s}$), is feasible by either inhibitory or excitatory lateral interconnections. And that there is no need for additional nonlinearities such as 'multiplying synapses' [6] – i.e., the threshold non-linearity is sufficient –, or different somatic time constants for external and lateral inputs [12].

According to Figure 5, the time needed for good synchronization after label-switching is quite short (less than 50 ms) which is well within a biologically relevant range. The interference between differently stimulated subpopulations demonstrates that there is only a minor spatial spread of synchronization and that synchronized activity in a coherently but weaker stimulated subpopulation in the immediate neighborhood can be destroyed. Whether lateral inhibition leads to a different behavior after label-switching is up to future experiments.

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