

SYNCHRONIZATION OF SPIKES IN POPULATIONS OF LATERALLY COUPLED MODEL NEURONS

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The synchronization of impulse generation in non-oscillating networks of laterally coupled model neurons is investigated. The influence of network parameters and of the external stimulation on the quality of synchronization is quantified. It turns out that synchronization accuracy in the order of few tenths of the impulse duration can be achieved and that it is barely influenced by moderate deviations from optimum parameter values.

1. INTRODUCTION

There is general agreement about the fundamental rôles 'feature linking' and 'perceptual grouping' play in the biological evaluation of sensory signals (for a review see [1]). The perceived velocity of an object which must be derived from independent measurements of local changes in the retinal intensity distribution, is one example for such mechanisms. Perceptual integration of elementary data according to common properties or features (here: sufficiently similar and spatially coherent, local velocities within an appropriate flow-field paradigm) is called linking, binding, or grouping.

In the following we present results from simulations concerning a possible neural basis of a prerequisite operation for *feature linking*, namely stimulus-dependent *feature labelling*. Our approach, which is related to that of Hartmann and Drüe [2], essentially differs from those [3,4,5,6] that aim to describe the experimentally observed phenomenon of so-called stimulus-dependent phase-locking of oscillatory spiking activity in some areas of cat visual cortex [7,8]. However, we want to know some of the principal conditions under which stimulated, i.e., sufficiently depolarized model neurons (units) synchronize their generation of action potentials. With regard to feature labelling we presuppose that the units of a network stand for properties of the stimuli and that units within subsets, each representing for instance a specific property, are locally coupled. Thus, the labelling condition for units in a subset is the spatially coherent presence of the same feature, and a 'label' is represented by the synchronism and rate of action potentials of such units.

2. THE MODEL NEURON

For the digital simulations with the temporal resolution Δt , we describe the somatic potential $D_i(t)$ of a model neuron "i" by the non-linear first order difference equation

$$D_i(t+\Delta t) = \begin{cases} D_i(t) + \frac{-D_i(t) + I_i(t) + N_i(t)}{\tau_{so}/\Delta t} & \text{for } \{D_i(t) < \theta\} \vee \{D_i(t-T_{re}) = D_{re}\} \\ D_i(t) & \text{for } \{D_i(t) \geq \theta\} \wedge \{D_i(t-T_{sp}) < \theta\} \\ D_{re} & \text{else} \end{cases}$$

and the generation of the output signal $A_i(t)$, i.e., of action potentials (axonal spikes or impulses) at the axon hillock, with two optional impulse shapes (cf. Fig. 1), by the threshold condition:

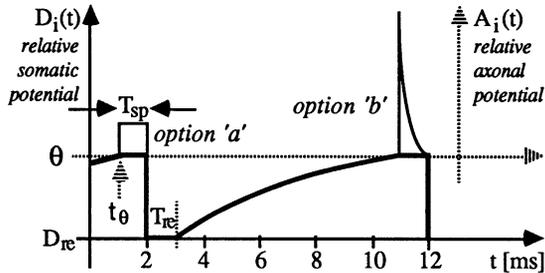
$$A_i(t) = \begin{cases} 0 & \text{for } \{D_i(t) < \theta\} \\ \text{option 'a': } P & \text{for } \{D_i(t) \geq \theta\} \\ \text{option 'b': } 5P \cdot \exp[-(t-t_0)/\tau_{sp}] & \text{for } \{D_i(t) \geq \theta\} \end{cases}$$

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$I_i(t)$ integral signal-input at time t ;	t_θ initiation of the past action potential
$N_i(t)$ noise voltage at time t ;	T_{sp} duration of a single action potential (1ms)
D_{re} potential during refractory period;	T_{re} refractory period (1ms)
P peak potential of an impulse;	τ_{so} somatic integration time constant (10ms)
θ threshold voltage;	τ_{sp} spike decay time constant (144 μ s)

FIGURE 1

Typical time-courses of the somatic potential and of the axonal impulses



3. SYNCHRONIZATION OF AXONAL IMPULSE GENERATION

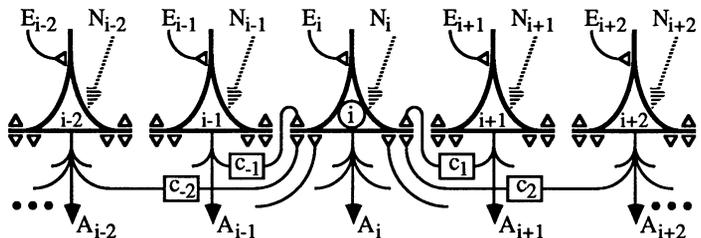
We consider one-dimensional "subset-networks", i.e., cyclic chains consisting of n units that are laterally coupled according to Fig. 2. All interconnections are excitatory. We distinguish two types of input signals to each unit: An external input $E_i(t)$, reflecting the equivalent mean impulse rate R_{E_i} of, e.g. the integral sensory stimulation, as well as lateral inputs, i.e., $2k$ symmetrically weighted (synaptic coefficients c_v) and delayed (time delay τ) signals $A_{i+v}(t)$ from neighbouring units.

$$I_i(t) = E_i(t) + \sum_{\substack{v=k \\ v \neq 0}}^k c_v \cdot A_{i+v}(t-\tau) \quad \text{with } k=1,2,\dots; \quad \text{and } \tau=\lambda\Delta t \text{ with } \lambda=0,1,2,\dots;$$

We assume the coefficients c_v to linearly decrease with $|v|$ and their sum $C=\sum c_v$ to be the same for every unit. Furthermore, all units receive the same constant external input $E_i(t>0)=E_0$ and individual random numbers $N_i(t)$, taken from the interval $\pm E_0/2$, are added to the somatic potentials.

FIGURE 2

Interconnection scheme of the one-dimensional network

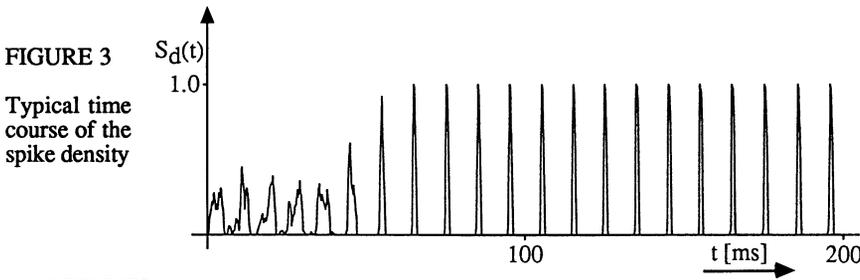


According to the above given definitions, we characterize a network by the following set of parameters: impulse shape, Δt , τ , k , C , n , and E_0 . In order to quantify the influence of these parameters on the degree of synchronization we introduce a quality factor η . It uses the spatio-temporal spike density $S_d(t)$ which refers to the spiking activity (option 'a') of all n units during the time interval T_{sp} .

$$S_d(t) = 1/(nm) \sum_{\mu=1}^{m-1} \sum_{i=1}^n A_i(t-\mu\Delta t)/P \quad \text{with } m=T_{sp}/\Delta t$$

Consequently, $S_d(t)=1$ holds, iff all n units start firing at the same time. Owing to the lower bound $R_A=20s^{-1}$ of the units' impulse rates in our simulations, we determine the quality factor η as the maximum of the spike density $S_d(t)$ taken from intervals of 50ms. In order to give an impression of the temporal evolution (cf. Fig. 3) of the quality of the synchronization we show our results for four successive intervals, ending 50ms, 100ms, 150ms and 200ms after $t=0$.

Because the starting potential is randomly chosen from the interval $D_{re} \leq D_i(t=0) < \theta$ – individually for every unit and run –, we display results representing averages over 50 runs.



4. RESULTS

We observe good synchronization for the standard parameter values: impulse shape option 'b', $\Delta t_s=100\mu s$, $\tau_s=0\mu s$, $k_s=8$, $C_s=0.2$, $n_s=64$, and an excitation E_{0s} that causes a unit to fire at the rate $R_{As}=100s^{-1}$. Now, we report the effects of deviations from these values on the synchronization.

- i) For variations of the external input E_0 that cause output rates in the range $40s^{-1} \leq R_A \leq 200s^{-1}$, we observed changes in the quality of synchronization ($\eta_{>50}$) of only $\pm 7\%$.
- ii) Above $n=32$, synchronization linearly decreases with $\ln(n)$ and levels out at $\eta_{200}(512) \approx 0.30$.

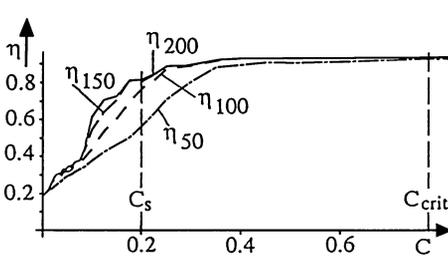


FIGURE 4

Synchronization and lateral coupling

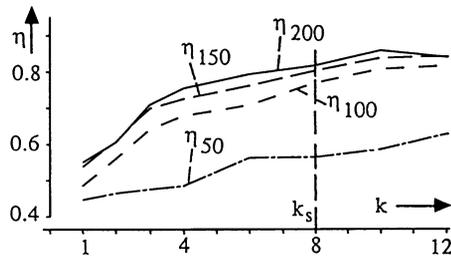


FIGURE 5

Sync. and number of bilateral interconnections

iii) The synchronization rapidly improves with increasing strength of the integral lateral coupling. According to Fig. 4, the synchronization quality starts saturating around the value $C_{sat} \approx 0.3$. Up to a critical value $C_{crit} = 0.78$ lateral triggering of an externally unstimulated unit is prevented. In other words, for $C \geq C_{crit}$ the labelling condition is violated (cf. the introduction).

iv) Because wider interconnections permit the synchronization around single insufficiently depolarized units synchronization quality improves with the number k of bilateral interconnections (Fig. 5)

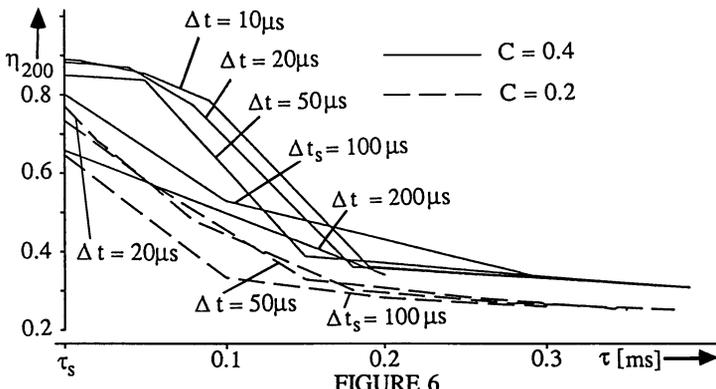


FIGURE 6

Synchronization as a function of the lateral time delay and temporal resolution

v) We applied impulse shape 'a' and $N_i(t)=0$ in order to speed up the investigations that led to the curves in Fig. 6. The two sets of graphs show that the tolerable time delay τ_{limt} crucially depends on the strength C of the lateral coupling, which conforms well with the pronounced saturation of the curves in Fig. 4. For $C=0.4 > C_{\text{sat}}$, time delays $\tau > \tau_{\text{limt}}(C=0.4) \approx 0.1 \text{ms}$ cause the quality of synchronization η_{200} to rapidly decline from the saturation level. This effect is essentially independent of the temporal resolution of the simulation but, for obvious reasons, it is best observed for $\Delta t \leq 50 \mu\text{s}$.

vi) Except for the previous, we performed all investigations with either impulse shape. Option 'b' generally leads to better synchronization, with $\eta_{200}('b')=0.82$ compared to $\eta_{200}('a')=0.51$. If the impulse integrals are the same, no essential difference in the time for synchronization is observed.

5. DISCUSSION

Our results reveal that the simulations of one-dimensional networks must meet basic conditions in order to produce satisfying impulse synchronization when judged according to our quality measure.

- The number of bilateral interconnections must exceed $k=4$.
- The integral coupling strength must be chosen from the interval $C_{\text{sat}} < C < C_{\text{crit}}$.
- The lateral time delay must be limited to $\tau_{\text{limt}}(C < C_{\text{crit}})$.
- The computations must be performed with a temporal increment $\Delta t \leq \tau_{\text{limt}}$.

Furthermore, it is advantageous to apply impulse shapes of high initial energy concentration.

- On the other hand, synchronization is only slightly affected by the external stimulation E_0 .

For the purpose of feature labelling one must know about the number of labels that reliably can be distinguished (cf.[3]). Obviously, this number depends on the impulse rate and on the temporal resolution of the system. While for $R_A \leq 100 \text{s}^{-1}$, we attain up to a hundred different labels other approaches, e.g. the one sketched in [2], reach only up to ten. Our data show (cf. Fig. 3) that this state is achieved after a synchronizing period of typically 50ms which, from a physiological point of view, is a bit long. Hence, further investigations must reveal whether and how this limitation can be overcome. We conjecture that two-dimensional networks may result in some improvement.

The limitation of the time delays to values in the order of the estimated synaptic transmission time means that additional delays, e.g. in dendrites, can hardly be tolerated. For two-dimensional networks C_{crit} will be much smaller which aggravates the situation. Whether it can be relaxed after refinements of the model, or solely by forward coupling [9], is to be clarified by future experiments.

A crucial difference between the labelling method reported in [2] as well as ours, and most of the presently discussed approaches [3,4,5,6], is the lack of any oscillating circuitry and direct feedback onto the same unit. Consequently, we deal with the synchronization of single impulses not bursts.

We showed for sufficiently stimulated model neurons that a synchronization accuracy of few tenths of the impulse duration can be achieved by excitatory lateral coupling. Despite some neurobiological deficiencies we think that the presented principle can serve as a basis for neural labelling which opens up attractive perspectives for neural processing as they are discussed for synfire chains in [9].

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