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Synchronization of Spikes in Populations of Laterally Coupled Model Neurons

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The synchronization of impulse generation in non-oscillating networks of excitatorily coupled formal neurons is investigated. The influence of network parameters and of the external stimulation on the attainable level of synchrony is quantified. It turns out that synchrony accurate to a of few tenths of the impulse duration can be achieved and that it is barely influenced by moderate deviations from the 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 that must be derived from independent measurements of local changes in the retinal intensity distribution, is one example for such mechanisms. Such integration of elementary data, according to common properties or features (e.g. within an appropriate flow-field paradigm: local velocities that are sufficiently similar and spatially coherent), 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 labeling*. Our approach, which is related to that proposed by 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]. In contrast, we are interested in some of the principal conditions for which stimulated, i.e., sufficiently depolarized formal neurons or units synchronize their generation of action potentials. With regard to feature labeling we presuppose that the units of a network stand for properties of the stimuli and that units in subsets – each representing for instance a specific property – are locally coupled. Thus, the labeling condition for units in a subset is the spatially coherent presence of the same feature, and a 'label' is represented by the synchrony (and rate) of the emitted action potentials.

2. THE FORMAL NEURON

For the digital simulations with the temporal resolution δt, we describe the somatic potential $\varphi_i(t)$ of a formal neuron 'i' by the non-linear first order difference equation

$$\varphi_i(t+\delta t) = \begin{cases} \varphi_i(t) + \dfrac{-\varphi_i(t) + \psi_i(t) + n_i(t)}{\tau_{so}/\delta t} & \text{for } \{\varphi_i(t) < \theta\} \vee \{\varphi_i(t - T_{re}) = \varphi_{re}\} \\ \varphi_i(t) & \text{for } \{\varphi_i(t) \geq \theta\} \wedge \{\varphi_i(t - T_{sp}) < \theta\} \\ \varphi_{re} & \text{else} \end{cases}$$

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

$$p_i(t) = \begin{cases} 0 & \text{for } \{\varphi_i(t) < \theta\} \\ \left.\begin{array}{ll} \text{option 'a':} & P \\ \text{option 'b':} & 5P \cdot e^{-(t-t_\theta)/\tau_{sp}} \end{array}\right\} & \text{for } \{\varphi_i(t) \geq \theta\} \end{cases}$$

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$\psi_i(t)$	integral signal voltage 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	(1 ms)
φ_{re}	voltage during refractory period;	T_{re}	refractory period	(1 ms)
P	peak voltage of an impulse;	τ_{so}	somatic integration time constant	(10 ms)
θ	threshold voltage;	τ_{sp}	spike decay time constant	(144 µs)

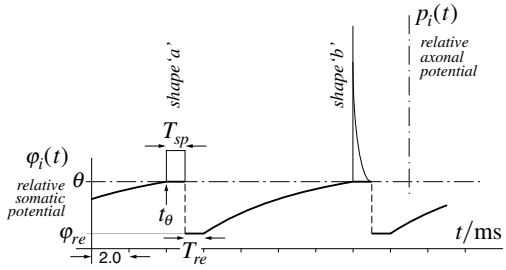

FIGURE 1

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

3. SYNCHRONIZATION OF AXONAL IMPULSE GENERATION

We consider one-dimensional "networks", i.e., cyclic chains of n units that are laterally coupled according to Figure 2. All interconnections are excitatory. We distinguish two kinds of input signals to each unit: An external input $e_i(t)$ – that stands for the equivalent mean impulse rate of, for example the integral sensory stimulation – and lateral input, i.e., $2k$ symmetrically weighted (synaptic coefficients or weights w_ν) and delayed (delay time ϑ) signals $p_{i+\nu}(t)$ from neighboring units.

$$\psi_i(t) = e_i(t) + \sum_{\substack{\nu=-k \\ \nu\neq 0}}^{k} w_\nu \cdot p_{i+\nu}(t-\vartheta) \quad \text{with } k = 1,2\ldots; \quad \text{and} \quad \vartheta = \lambda\cdot\delta t \quad \text{with } \lambda = 0,1,2\ldots;$$

We assume the coefficients w_ν to linearly decrease with $|\nu|$ and their sum $W = \sum w_\nu$ to be the same for every unit. Furthermore, all units receive the same constant external input $e_i(t>0) = E$ and individual random numbers $n_i(t)$, from the interval $\pm E/2$, are added to the somatic potentials.

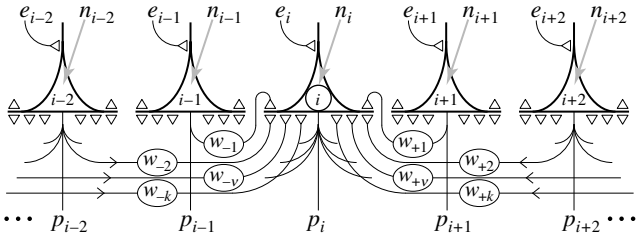

FIGURE 2

Interconnection scheme of the one-dimensional network

According to the above definitions, we characterize a network by the parameters: n, impulse shape, ϑ, k, W, E, and its simulation by δt. To quantify the influence of these parameters on the resulting level of synchrony, we introduce a quality factor η. It is based on the spatio-temporal spike density $S(t)$ that refers to the spike activity (option 'a') of all n units during the temporal interval T_{sp}.

$$S(t) = \frac{1}{n\cdot m}\sum_{j=1}^{m-1}\sum_{i=1}^{n} p_i(t-j\cdot\delta t)/P \quad \text{with } m = \frac{T_{sp}}{\delta t};$$

Consequently, $S(t) = 1$ holds, iff all n units fire at the same time. Owing to the lower bound of the impulse rates in our simulations of 20/s, we determine the quality factor η as the maximum of the spike density $S(t)$ taken from intervals of 50 ms. To give an impression of the temporal evolution of the quality of synchronization (cf. Fig. 3), we show results for four successive intervals, ending at times x of 50 ms, 100 ms, 150 ms and 200 ms.

Because the initial depolarization is randomly chosen from the interval $\varphi_{re} \le \varphi_i(t=0) < \theta$ (individually for every unit and run), the displayed quality factors η_x are averages taken from 50 runs.

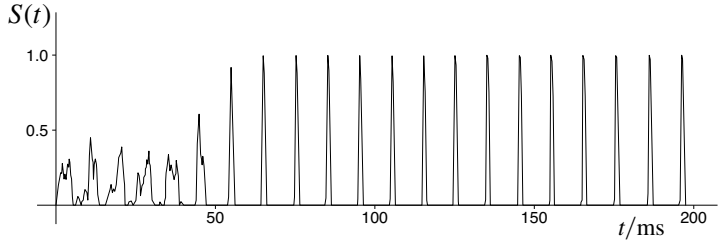

FIGURE 3

Typical time-course of the spike density

4. RESULTS

In nets of $n_S = 64$ units, simulated with $\delta t_S = 100\,\mu\text{s}$, we observe good synchrony for the parameter values: impulse shape 'b', $\vartheta_S \approx 0\text{ms}$, $k_S = 8$, $W_S = 0.2$, and an input E_S that causes a unit to fire at a rate of $R_S = 100/\text{s}$. We now report on how synchrony is affected by deviations from these values.

i) The measures of synchrony $\eta_{>50}$ change only ±7% for variations of the external input E that cause impulse rates in the range of $40/\text{s} \le R \le 200/\text{s}$.

ii) For $n > 32$, synchrony linearly decreases according to $\text{ld}(n)$ and levels off at $\eta_{200}(n{=}512) \approx 0.3$.

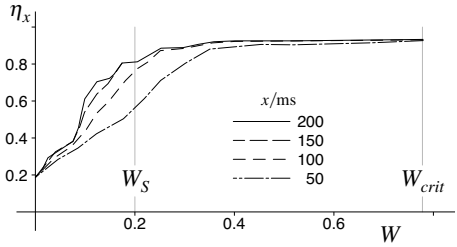

FIGURE 4
Synchrony as function of coupling strength

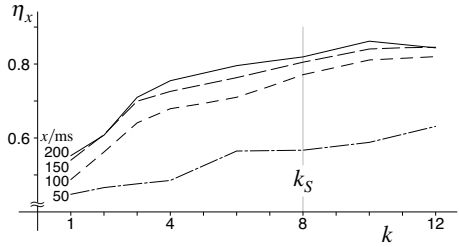

FIGURE 5
Synchrony as function of bilateral coupling width

iii) The synchrony rapidly improves with increasing strength of the lateral coupling and typically saturates at $W_{\text{sat}} \approx 0.3$ (Fig. 4). Up to the critical value $W_{\text{crit}} = 0.78$, lateral triggering of a unit that is not externally stimulated is prevented or, in other words, the labeling condition – mentioned in the introduction – is violated for $W \ge W_{\text{crit}}$.

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

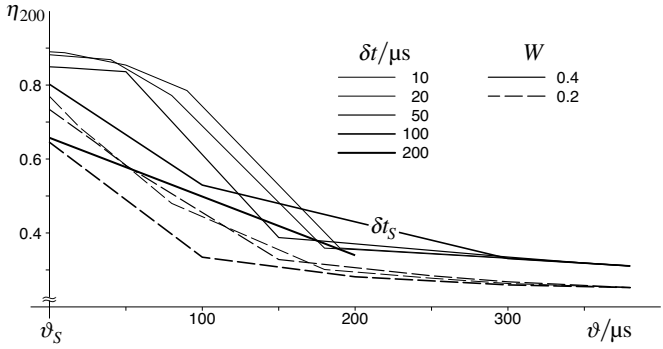

FIGURE 6
Synchrony as function of delay ϑ and temporal resolution δt of the simulation

v) To facilitate the simulations that resulted in the graphs of Figure 6, we applied impulse shape 'a' and $n_i(t) = 0$. The two sets of graphs show that, for good synchrony, the tolerable delay ϑ_{lmt} depends on the coupling strength W, a finding that conforms well with the pronounced saturation in Figure 4. Delays $\vartheta > \vartheta_{\mathrm{lmt}}(W = 0.4) \approx 100\mu\mathrm{s}$ cause the synchrony measure η_{200} to rapidly decrease from the saturation level. This decline is virtually independent of the temporal resolution of the simulation but, for obvious reasons, it is best observed for $\delta t \leq 50\mu\mathrm{s}$.

vi) Except for those described above, we performed all simulations with either impulse shape. In general, shape 'b' results in better synchrony, with η_{200}('b') = 0.82 when compared to η_{200}('a') = 0.51. For equal impulse integrals, the time-course of the synchronization does not differ significantly.

5. DISCUSSION

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

- The number of bilateral interconnections must exceed $k = 4$.
- A unit's integral coupling strength must be restricted to $W_{\mathrm{sat}} < W < W_{\mathrm{crit}}$.
- The delay in the lateral interconnections must be limited to $\vartheta_{\mathrm{lmt}}(W < W_{\mathrm{crit}})$.
- Simulations must be performed with a temporal increment $\delta t < \vartheta_{\mathrm{lmt}}$.

In addition, impulse shapes of high initial energy concentration are of advantage. Over a wide range, the external stimulation E only slightly affects the attainable synchrony.

For the purpose of feature labeling, one must know about the number of labels that can reliably be distinguished (cf. [3]). Obviously, this number depends on the impulse rate and on the temporal resolution of the simulation. With $R \leq 100/\mathrm{s}$ we achieve up to hundred labels, while other groups report only up to ten [2]. As can be seen from Figure 3, such labeling is possible after a synchronization process that takes typically 50 ms, which, physiologically regarded, is too long. Hence, further investigations must reveal whether and how this restriction can be overcome. We conjecture that two-dimensional networks may result in some improvement.

The limitation of the delays to values in the order of the estimated synaptic transmission time means that additional delays, for example in dendrites, can hardly be tolerated. In two-dimensional networks W_{crit} will even be much smaller which aggravates the situation. Whether it can be relaxed by refinements of the approach, or solely by forward coupling [9], is to be clarified by future investigations.

The absence of any oscillating circuitry or direct feedback onto the same unit makes the crucially difference to most of the presently discussed labeling approaches [3, 4, 5, 6]. With the approach reported in [2] as well as with the here described, single spikes – not bursts – are synchronized.

We showed that spike synchrony, accurate to a few tenths of the impulse duration, can be achieved by excitatory lateral coupling of sufficiently stimulated formal neurons. Despite certain neurobiological deficiencies, we think that the presented principle can serve as a basis for neural labeling which opens attractive perspectives for neural processing as they are discussed for synfire chains in [9].

REFERENCES

[1] Rock I. and Palmer S., The legacy of Gestalt psychology, *Sci. Am.* **263** (1990) 48.

[2] Hartmann G. and Drüe S., Self organization of a network linking features by synchronization, in: Eckmiller R., Hartmann G. and Hauske G. (eds.) *Parallel Processing in Neural Systems and Computers* (North-Holland, Amsterdam, 1990) pp. 361-364.

[3] Atiya A. and Baldi P., Oscillations and synchronizations in neural networks: an exploration of the labeling hypothesis, *Int. J. Neural Syst.* **1** (1989) 103.

[4] Eckhorn R., Reitboeck H.J., Arndt M. and Dicke P., Feature linking via synchronization among distributed assemblies: simulations of results from cat visual cortex, *Neural Comput.* **2** (1990) 293.

[5] Schillen T.B., Simulation of delayed oscillators with the *MENS* general purpose modelling environment for network systems, in: Eckmiller R., Hartmann G. and Hauske G. (eds.) *Parallel Processing in Neural Systems and Computers* (North-Holland, Amsterdam, 1990) pp. 135-138.

[6] Epstein I.R. and Marder E., Multiple modes of a conditional neural oscillator, *Biol. Cybern.* **63** (1990) 25.

[7] Eckhorn R., Bauer R., Jordan W., Brosch M., Kruse W., Munk M. and Reitboeck H.J., Coherent oscillations: a mechanism of feature linking in the visual cortex? *Biol. Cybern.* **60** (1988) 121.

[8] Gray C.M., König P., Engel A.K. and Singer W., Oscillatory responses in cat visual cortex exhibit intercolumnar synchronization which reflects global stimulus properties, *Nature* **338** (1989) 334.

[9] Abeles M., *Local Cortical Circuits. An Electrophysiological Study* (Springer, Berlin, 1982).