Artificial Neural Networks
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Dynamics of Synchronous Neural Activity in the Visual Cortex

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Abstract:

Recent experiments by Singer et al. have shown synchronous firing activity in the visual cortex of cat among neurons coding similar features. The observations suggest that synchronization may be an important coding principle for information processing in the brain. We have earlier proposed a mechanism for the synchronous neural activity based on a dynamical description of single neurons as excitable elements with stochastic activity. Such weakly coupled neurons can readily develop synchronous firing when subject to coherent excitation, and, thereby, can segment images (figure-ground). In this contribution, we provide further simulations and an analysis of the model and discuss processing capabilities made possible through synchronous neural activity.

1. Introduction

Many neural network models assume that the state of a network is fully described by the firing frequency or activity of its neurons. Recent experiments by Gray and Singer [1, 2] and Eckhorn et al. [3], performed on area 17 of the visual cortex of cat, have focussed interest on details of the firing pattern of neurons. In particular, the observation that the firing of neurons of distant parts of area 17 is synchronous if these parts are excited by the same object, e.g. a continuous light bar presented to the retina, while the firing is asynchronous, if the neurons are excited by disjunct objects, has renewed interest in the hypothesis [4] that synchronicity of firing is a mechanism for feature linking in neural networks.

We have earlier proposed [5] that synchronous firing in networks can develop through neurons which are *stochastic excitable elements (SEE)* as described by the Bonhoeffer–van-der-Pol (BVP) or Fitzhugh–Nagumo (FN) equations [6, 7, 8, 9]. The behaviour of a network of coupled SEE's was shown to undergo a transition to synchronous and periodic firing for proper parameters of the SEE's. Furthermore a neural network of BVP/FN neurons connected in a way to simulate the visuo-cortical lateral connectivity develops firing patterns in good agreement with experimental findings. In this paper, we want to discuss in more detail the parameters that control synchronization, and discuss the possible significance of such firing pattern.

In chapter 2 we introduce the BVP/FN equations. In chapter 3 we discuss the advantages of SEE networks over networks of nonlinear oscillators. In chapter 4 we investigate in detail which parameters control the transition from asynchronous to synchronous activity. In chapter 5 finally, we discuss the information processing capacity of SEE networks.

2. Dynamics of the Bonhoeffer–van-der-Pol/Fitzhugh–Nagumo Equations

To describe the dynamics of N coupled neurons we extended the BVP/FN equations by including a coupling to Gaussian noise $\eta_1(t)$ and $\eta_2(t)$ [10] and an interaction term $\sum_j W_{j\to i}(t)$, which couples the voltage of neuron i to the voltages of all other neurons in a network [5].

$$\begin{aligned} \dot{x}_{1,i} &= c(x_{1,i} - x_{1,i}^3/3 + x_{2,i} + z) + \eta_1(t) + \textstyle\sum_j W_{j\to i}(t) \\ \dot{x}_{2,i} &= (a - x_{1,i} - b x_{2,i})/c \quad + \eta_2(t) \end{aligned} \tag{1}$$

with

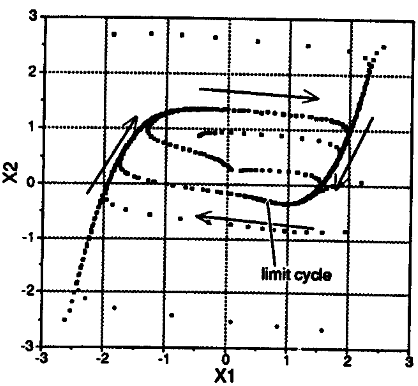
$$\begin{aligned} <\eta_j(t_1)\eta_k(t_2)> &= \sigma^2 \cdot \delta_{j,k} \cdot \delta(t_1 - t_2) \\ W_{j\to i}(t) &= \theta(-x_{1,j}(t)) \cdot (x_{1,j}(t) - x_{1,i}(t)) \cdot w_{ji}, \quad i,j \in \{1,2,\ldots N\}, \end{aligned} \tag{2}$$

$a = 0.7$, $b = 0.8$, and $c = 3.0$. The interaction $W_{j\to i}(t)$ is switched on only when neuron j is firing, i.e. for $x_{1,j}<0$. The $w_{i,j}$ can be chosen such as to represent the lateral cortical connectivity (see [5]). In the present investigations, they will all be set to a uniform value w.

According to Fitzhugh's derivation [8] of the BvP equations, x_1 represents the negative transmembrane voltage and x_2 is closely related to the potassium conductivity. The dynamical character of the solutions of this system of equations is determined by the parameter z, which represents the excitation of a neuron. In the absence of noise, z determines whether the system is an oscillator periodically changing its voltage, or an excitable element which rests at a fixed voltage. The phase portrait for these two dynamical modes is shown in Figs. 1 and 2.

In the presence of noise, the firing in the oscillator mode becomes less regular. In the excitable element mode, however, a neuron fires ramdomly whenever the noise drives the system far enough away from the stationary point. The correlation $C(t)$ of the firing activity can then be measured using the times $t_i(t)$ at which the last firing of neuron i has been initiated [5]:

$$C(t) = \frac{1}{N(N-1)} \sum_{i\neq j}^{N} cos(2\pi \frac{(t_j(t) - t_i(t))}{T}). \tag{3}$$



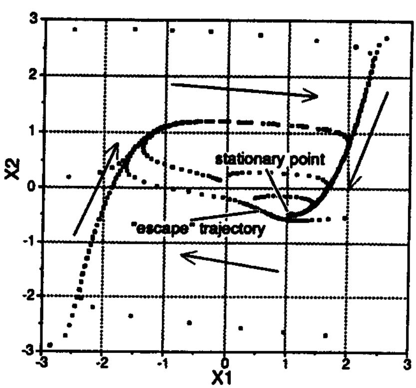


Figure 1: (left side) Some typical phase space trajectories for $z = -0.4$: All trajectories eventually lead into a stable limit cycle. Represented is a stroboscopic view of trajectories for 9 different initial states.

Figure 2: (right side) Some typical phase space trajectories for $z = 0$: All trajectories lead to the stable stationary point at about (1.1,-0.5). Note that a trajectory which passes very near by the stationary point may lead the phase point back to its stationary state only after a long path through phase space.

Here T is the average firing frequency of the population of SEEs. (T is of the order of typical interspike times and chosen such as to maximize C). In the following the term synchronicity refers to the time average of $C(t)$, averaged over a time span larger than the duration of typical fluctuations.

3. Comparision of SEE and Non-Linear Oscillator Networks

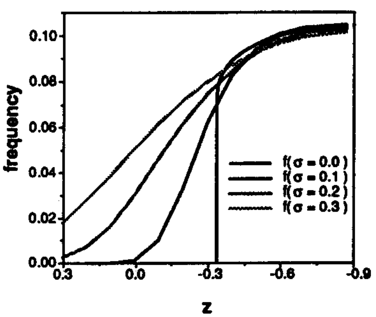
In order to understand the synchronous cortical oscillations, we avoided to investigate neuronal oscillator models and instead looked at the much richer dynamics of stochastic excitable elements. The parameter z in Eq. 1, which physiologically represents the external excitation of the neuron, turns out to be a crucial control parameter determining the dynamical properties of a single SEE: increasing the excitability of the neuron by decreasing the value of z increases the firing probability of a neuron. Therefore, variation of z in the presence of noise smoothly changes the average firing frequency of a neuron from zero to its maximal value (see Fig. 3) .

For coupled SEE's, variation of z additionally mediates a transition from synchronous to asynchronous firing (see Fig. 4). At the same time as the firing becomes synchronous, the averaged firing frequency of the synchronously firing neurons increases markedly. Synchronicity and high firing frequency thus appear to be intrinsically interdependent, which agrees with experimental observations by Gross and Kowalski [11].

One further important feature of this model which distinguishes it from oscillator networks is the fact that variation of z effects synchronization and desynchronization with a time lag of typically only one to two firing periods. This fast synchronization and desynchronization mechanism could be especially important in the visual cortex, in which moving images have to be processed by constantly changing neuronal populations.

4. Control of the Onset of Oscillations

We want to discuss in more detail, how the different parameters control the onset of oscillations in an SEE network. As shown in Figs. 5 and 6, increasing the interaction strength leads to a transition to synchronous firing at smaller excitation values and, furthermore, at higher excitation values, synchronicity is higher. Increasing the noise level leads also to a shift of the synchronous firing transition to smaller excitation values; at higher excitation values, however, the increased



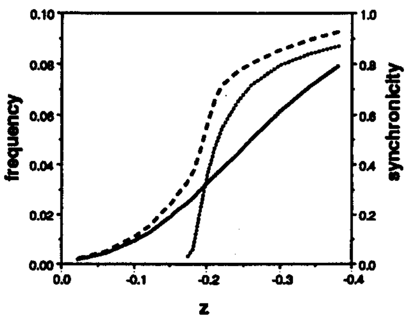
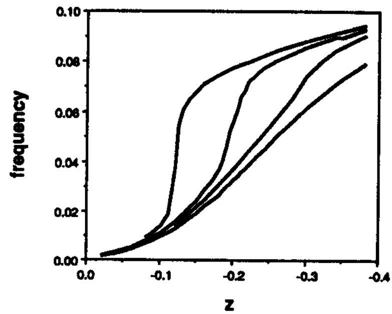


Figure 3: Firing frequency of a neuron as function of the excitation parameter z for different noise levels σ=0.0, σ=0.1, σ=0.2, and σ=0.3.

Figure 4: Firing frequency (dashed line) and synchronicity (dotted line) as function of the excitation parameter z for $\sigma = 0.1, N = 500$, and $w = 0.001$. For comparision, the solid line shows the firing frequency for noninteracting neurons ($w = 0$).



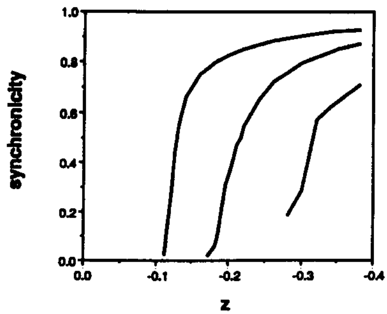
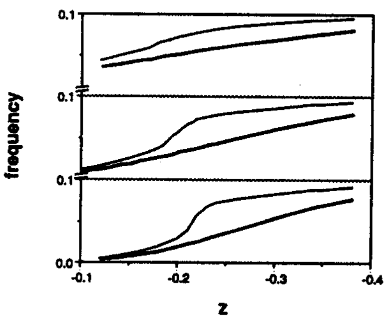


Figure 5: (left side) Dependence of the firing frequency on the excitation parameter z for different interactions strengths w=0 (lowest curve), w=0.0005, w=0.001, and w=0.002 (uppermost curve) and N=500, σ=0.1.

Figure 6: (right side) Synchronicity as function of excitation z for different interaction strengths w=0.05 (rightmost curve), w=0.1, and w=0.2 (uppermost curve). (N=500, σ=0.1)



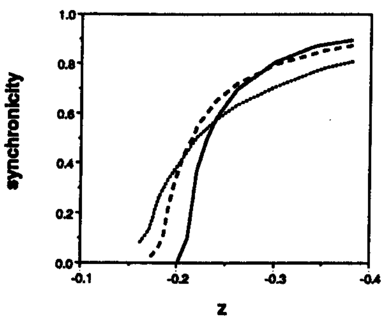


Figure 7: (left side) Comparision of firing frequencies of populations of coupled (w=0.001, N=500) vs. uncoupled (w=0) neurons for different noise amplitudes σ=0.08 (lowest curve), σ=0.10, and σ=0.15 (uppermost curve).

Figure 8: (right side) Degree of synchronization as function of the excitation value z for different noise amplitudes $\sigma = 0.08$ (continous curve), $\sigma = 0.10$ (broken curve), and $\sigma = 0.15$ (dotted curve). (w=0.001, N=500).

noise level leads to a smaller degree of synchronicity. By adjusting both the average interaction strength and the noise level simultaneously, one can thus tune the z-value of the onset of oscillations and the maximally obtainable degree of synchronization independently.

The firing frequency and the synchronicity of SEE networks also depend on the number N of interacting neurons. As the N is increased, a smaller interaction strength w will suffice to obtain the same firing frequency and degree of synchronization. As suggested by Fig. 9, the value which determines the firing frequency is the product $(N \cdot w)$ which we will call the *total interaction strength*.

Another interesting aspect of the firing of SEE neurons is shown in Fig. 10. The continuous line shows the quotient of the firing frequencies of coupled SEE and uncoupled SEE for $\sigma = 0.1, w = 0.001$, and $N = 500$. The augmentation of the firing frequency of a neuron due to coupling with a

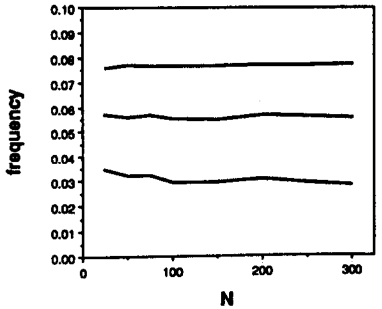


Figure 9: Firing frequency as a function of the number of coupled neurons with total interaction strength $N{*}w = 0.5$ held constant. Shown are the curves for $z = -0.24$ (upper curve), z=-0.20, and z=-0.16 (lower curve). (σ=0.1).

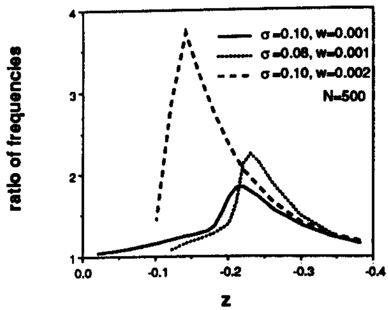


Figure 10: Ratio of firing frequencies of coupled vs. uncoupled neurons for different noise levels and interaction strengths.

large number of identical neurons is most pronounced in the vicinity of the z transition point between asynchronous and synchronous firing activity. The dotted and broken curves show how this augmentation peak changes with reduced noise level and increased interaction strength, respectively.

5. Information Processing Capacities of Synchronous Oscillations

Finally, we address the question of how a neural network could make optimal use of firing synchronicity for information processing. The noise in the suggested SEE network originates mainly from intrinsic sources such as fluctuating ion channels or quasi-random signals from adjacent networks. Therefore noise is probably a parameter which is independent of the state of a network. If the input to a neural network leads to z values of single neurons in some range $[z_1, z_2]$, the network may adapt the average interaction strength w such that firing activity will be asynchronous for excitation z_1 and synchronous for z_2.

The highly stochastic nature of neuron firing casts doubts on whether the phase of the synchronous oscillations is well enough defined as to allow it to carry information. However, such stochastic nature does not necessarily make oscillations insignificant for information processing. In fact, the mechanism providing synchronous oscillations in SEE networks also causes the firing frequency to increase. The emergence of synchronous activity does not only depend on the strength of excitation z but also on the number of neurons excited. Neurons coding different features of an object are more likely to engage in synchronous activity, if more of them are excited by the object. The synchronous oscillations might then act as a discriminating mechanism that selectively enhances the firing frequency of neurons if a significant part of the interacting neurons are excited by the object.

In this regard, synchronous activity would not be a feature which codes information through the phase of oscillations, but rather a mechanism which enhances the contrast of the signal coded in the firing frequencies of neurons.

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