Synchronization in Complex Dynamical Networks

Karsten Kube, Andreas Herzog, Bernd Michaelis, *Member, IEEE*, Ana D. de Lima, and Thomas Voigt

Abstract— Excitatory recurrent networks, while confirmed in theory, have not been intensely studied by simulation focused on synchronization properties. In our research, we validate on the basis of complex network models, the refinement of degree and link-level deepness, which embodies principles of topological structural nature with emphasis on the relationship between the topology and the dynamics of such complex networks. Biologically plausible excitatory networks that are maintaining this structure, develop a stable synchronized pattern of activity depending on spontaneous activity and synaptic refractoriness. We show that by fixed synaptic weights the synchronous bursts of oscillatory activity are stable and involve the whole network. As a result, by investigating conditions for synchronized oscillatory activity in several types of networks, we found that 'small world' networks with a higher proportion of long connections can sustain a higher degree of synchronization.

I. INTRODUCTION

Cultured networks of the neocortex show a similar development as in the brain, whereas spontaneous large-scale wave-like activity during early development can be observed, using imaging techniques and electrophysiological patch-clamp-measurements [1]. The synchronous activity appear in culture at the beginning of the second week and eventually includes the entire neuronal population about 1 week later [2]. In standard culture conditions neurons become electrically active spontaneous and independently. Next neurons connect to each other, form synapses, and begin to burst simultaneously, discharging collectively about once per minute. Time histograms show that the portion of synchronously firing neurons increases with time. Because non-active neurons die before the end of the second week in vitro [3], the participation in synchronous oscillatory activity seems to play an important role in the early development of the mammalian cortex. In [4] we have investigated conditions and parameters for the emergence of oscillatory network activity by accumulated activity of distinct single cells in intrinsic driven networks. Tabak et al. [5] described a global model to transform spontaneous activity in random connected networks in episodic events of synchronized activity. This behaviour is coherent with a locally connected network. On the other hand, 'small world' networks [6] contain a majority of local connections between cells, but a few of the connections are long distance connections.

Karsten Kube, Andreas Herzog, and Bernd Michaelis are with the Institute of Electronics, Signal Processing and Communications, Otto-von-Guericke University Magdeburg, P.O. Box 4120, 39114 Magdeburg, Germany (email: kkube@iesk.et.uni-magdeburg.de).

Ana D. de Lima and Thomas Voigt are with the Institute of Physiology, Otto-von-Guericke University Magdeburg, Department of Developmental Physiology, 39120 Magdeburg, Germany.

II. METHODS

Networks of neurons were modelled using the NEURON environment [8]. Single neurons were represented as electrical models with two compartments for the purpose of decoupling synaptic integration and impulse generation dynamics in different compartments [9] [10] [11]. The cell model reflects electrical effects caused by neuron dimensions. The dynamic of the membrane potentials V_m results from

$$C_m \frac{d}{dt} V_m = \frac{E_m - V_m}{R_m} + \sum_k I_{syn} + \frac{V_m - V_m(soma)}{R_a} \tag{1}$$

$$C_m \frac{d}{dt} V_m = \frac{E_m - V_m}{R_m} + \frac{V_m - V_m(dend)}{R_a} + I_{HH} + I_\zeta \tag{2}$$

for the dendric and somatic compartment. The equations describe the synaptic integration signal and action potential generation of the neuron model, respectively. $\frac{E_m - V_m}{R_m}$ is the leaky current, I_{HH} is a current resulting from active Hodgkin-Huxley conductions (approximated by standard HH equations [12] for squid axon) and $\sum_k I_{syn}$ is the sum of all k synaptic currents. I_ζ is a discrete stochastic component, which spontaneously elicits action potentials with highly variable intervals between spikes, erratically but Poisson-distributed [13]. I_ζ is implemented as a current pulse, activated at distinct time points driven by a Poisson-process. The time of an action potential is determined as the first point in the rising phase in the somatic compartment that exceeds 0 mV.

At the beginning of each simulation the neurons are initialized first to a resting membrane potential of -65 mV. In order to induce a spontaneous activity in the network, single, i.e. non-repetitive action potentials are triggered by pulsed driving currents, which are fed in the dendritic compartment (I_ζ, 0.1nA, lasting 10 ms). Triggering times were selected randomly after a poisson distribution with the average value λ, which describes the characteristic form of the distribution of firing during the spontaneous activity [13], and corresponds to the observed behavior of isolated neurons in cultures [1].

Symbols and default parameter values used in simulation. Number of neurons (n): 400; Current, duration (I_ζ): 0.1 nA,10ms; Mean of poisson distribution (λ): 0.001dt-1ms-1; Somatic diameter ($diam_{soma}$):10μm; Somatic length (L_{soma}): 10μm; Dendritic diameter ($diam_{dend}$): 5μm; Dendritic length (L_{dend}): 50μm; Connection length (l): 0.1 μm; Number of postsynaptic cells (k): 4; Conductance velocity: 0.5mm/ms; Monoexponential rise/decay parameter (τ_g):

3.0ms; Decay parameter for refractoriness (τ_m): 50.0ms; Synaptic resource threshold (m_{thr}): 0.8; Comsumption per spike (m_{spk}): 0.75; Reversal potential (E): 50.0mV; Initial synaptic strengths (w_{init}): 0.00165; Integration width (dt): 0.05ms.

Synapses: Synapses were simulated as an alpha-shaped postsynaptic conductance with refractoriness (differential short term depression effects): To implement refractoriness, the postsynaptic membrane conductances are determined by the amount of available transmitter and the synaptic currents are defined by a system

$$\tau_g \frac{d}{dt}a = -a \tag{3}$$

$$\tau_g \frac{d}{dt}g = -g + a \tag{4}$$

$$\tau_m \frac{d}{dt}m = 1 - m \tag{5}$$

If an isolated presynaptic event arrives, a peak conductance of magnitude strengths occurs at time τ_g after the event, $m \Leftarrow m - m_{spk}$ and $a \Leftarrow a + e^w$ with synaptic strength w, provided that $m \geq m_{thr}$, see Fig. 1a. The synaptic current then amounts to $I_{syn} = g(V_m - E)$. Synaptic latency was adjusted via parameter τ_m to endure about 85ms. In simulation, synaptic currents are calculated with initial values $a(0) = g(0) = 0$, $m(0) = 1$. An example with a test spiketrain is depicted in Fig. 1a. If m is below a critical threshold m_{thr} spikes are not transmitted.

Synchronisation analysis: Only perfect or nearly perfect synchronization, when all neurons fire synchronously (e.g. within a few milliseconds), can be easily detected visually by a raster plot of neuron activity. A modified version of the phase-locking-index by Davison et al. [14] is a mathematical tool for the detection and quantification of network synchrony. For each neuron $k = (1, .., n)$ in the network, for each spike i at time t_i^k of this cell, we find the closest spike j with the time t_j^l of cell l. The time lag for spike t_i^k in relation to spike t_j^l is defined as: $l_i^{kl} = t_j^l - t_i^k$ The mean distance for spikes from cell k to cell l is:

$$\phi^{kl} = \sqrt{\frac{1}{s_k}\sum_{i=1}^{n_k}(l_i^{kl})^2} \tag{6}$$

with s_k as number of spikes of cell k. The synchronisation index is now defined as:

$$\sigma = \frac{1}{n(n-1)}\sum_{k=1}^{n}\sum_{l=1|l\neq k}\phi^{kl} \tag{7}$$

The effect of the synchronization index is illustrated in Fig. 1c-d, by the example of an artificial spiketrain with perfectly synchronous spikes. The synchrony was decreased gradually by shifting the spikes from the ideal position. The shifts were selected in such a way that a normal distribution with the standard deviation results σ the spikes around the ideal position. Figure 1d shows the synchronization index for a test series with different standard deviations. It can be recognized that the synchronization index is zero at a perfect synchronization. The mean activity is calculated by a convolution with a Gaussian ($\gamma = 15ms$).

$$a(t) = \frac{1}{s(t)}\sum_{i=1}^{n_s}exp(\frac{(t - t(i))^2}{\sigma^2}) \tag{8}$$

with n_s as number of spikes per neuron and $t(i)$ as spike time i. $s(t)$ results from equivalent convolution of same number of regular spikes:

$$s(t) = \sum_{i=1}^{n_s}exp(\frac{(t - t_g(i))^2}{\sigma^2})t_s(i) = t_{min} + i\frac{t_{max} - t_{min}}{n_s - 1} \tag{9}$$

III. HIERARCHICAL NETWORKS

At the opposite of completely regular networks, networks with a completely random graph were studied first by Erdos et. al [15]. The main results of the random graph theory is to determine at what connection probability a particular property of a graph will most likely arise. A remarkable discovery of this type was that important properties of random graphs can appear quite suddenly. It was shown that, if the probability p is greater than a certain threshold , then almost every random graph is connected. The logarithmic increase in average path length with the size of the network is a typical smallworld effect. Because it increases slowly with the number of nodes, it allows the average path length to be quite small even in a fairly large network. On the other hand, in a completely random network, the probability that two of the nodes are connected is no greater than the probability that those of two randomly chosen nodes from the network. This means that a large-scale random network does not show clustering in general. For a large number of nodes, the algorithm generates a homogeneous network, where the connectivity approximately follows a Poisson distribution.

Watts and Strogatz examined structurally simple, circular networks, in a sliding transition of regular, locally coupled networks too purely randomly coupled networks adjusting only one free parameter ρ. In Fig. 2 we reproduced their experiments to show that even a very small portion of long distance connections ($\rho = 0.1$) is sufficient to decrease the path length (the average number of monosynaptic connections in the shortest way between two neurons) and consequently drastically improves the signal propagation. While path length grows linearly with increasing network size in locally coupled networks, it grows only logarithmically as a function of size in a network with 'small world' topology [16]. The effect of adding long distance connections was also demonstrated by Netoff et. al [7] in 'small world' networks using different neuron models, to explain different behaviours in the epileptical network synchronisation of CA1 and CA3-regions in the hippocampus.

When using the Watts-Strogatz model [6], the probability for rewiring a connection is assumed to be constant all over the network. In other models with similar characteristics (e.g. Barabasis 'scale free'-networks) [19] wiring probability is reduced with increasing distance between the
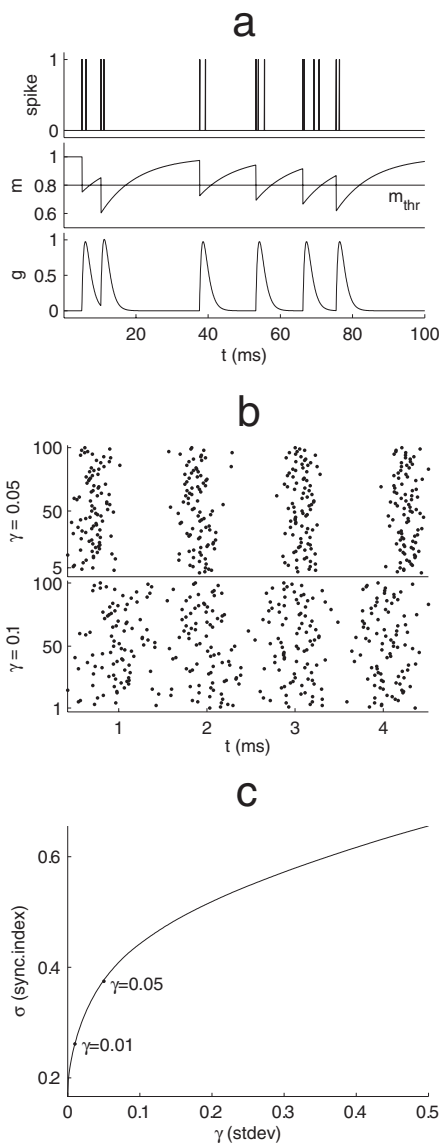
Fig. 1. Simplified alpha-model of synapse with refractoriness. (a) Conductance of synapse g, transmitter m, transmitter threshold m_{thr} and transmitter consumption m_{spk} per spike. Top panel: incoming spike train, middle panel: transmitter m and threshold mthr. Bottom panel: resulting synaptic conductance. (b) Raster plot for 100 neurons, each neuron showing 4 spikes. The spikes are normally distributed with respect to the time point of the ideal synchronization (here: t = 1, 2, 3, 4 ms) with standard deviation γ of 0.01 and 0.05. (c) Synchronization index for different standard deviations (from 0.0 to 0.050 in 50 steps). The points referring to (b) are marked. The synchronization index rises dependent on the standard deviation. When the spike train is perfectly synchronized, $\sigma = 0$.

Fig. 2. Parameter ρ of the "small world" networks. Left: Examples of networks with 25 neurons; top right: Distribution of neuronal degrees (Networks with 500 neurons); bottom right: Distribution of path length between two nodes. (a) $\rho = 0$, each node is connected with 4 neighbors. There are no long connections. The middle path length between two neurons is relatively long and directly dependent on network size. (b) $\rho = 0.1$, a small number of local connections is reconnected to other randomly chosen nodes, creating long distance connections and consequently a "small world" network. In this network each node have a mean of 4 neighbors. The long range connections create shortcuts, and the mean path length decreases significantly. (c) $\rho = 1$, In this completely randomly connected network each node has an average of 4 connections to other nodes, but the clusters are distributed: only few neurons have many common neighbors, and pairs of nodes are distant only a few grades from each other.

while the majority of nodes develops few connections. Although the structural concepts of 'small world' and 'scale free' networks probably may not completely correspond to the neural networks in the brain, the demonstration of the effectiveness of some few, but metabolic expensive long range connections in growing networks may contribute to the comprehension of the organization principles ruling CNS wiring in general [17].

IV. NETWORK CONNECTIVITY:

For the network, we use the model of Watt and Strogatz [6] with neurons evenly located on a circular line. Here the

neurons according to a power-law distribution. The number of connections in such 'scale free' networks fits a negative exponential distribution. During the rewiring procedure, few nodes develop an exponentially large number of connections
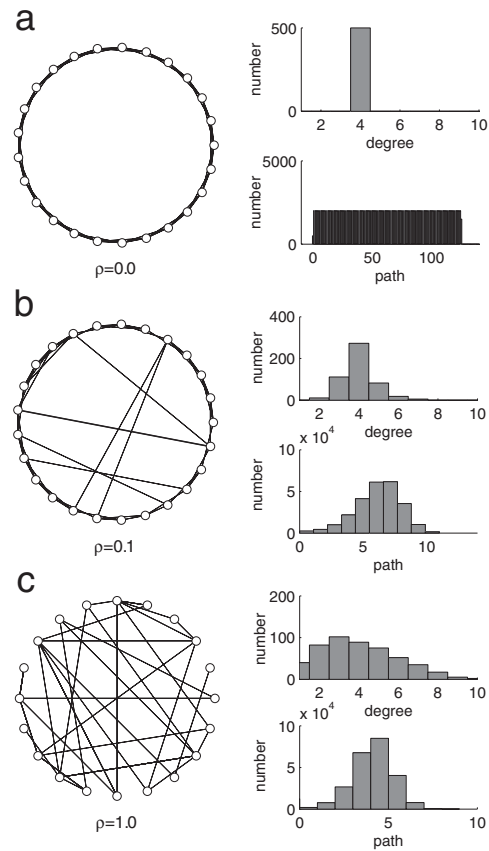
number of connections of a neuron, k, is called 'degree' [16]. As the connections are bi-directional rewired, the incoming degree (number of pre-synaptic neurons) equals the outgoing (number of postsynaptic) degree. At first, the neurons are only connected with the k neares neurons in the direct neighbourhood. A randomly selected part (parameters ρ) of these neurons that are involved in connections is then disconnected and other likewise randomly selected neurons is interconnected. By this 'rewiring' procedure the number of connections remains stable, independent of the selected ρ value. The connections described in the original model are non-weighted and non-directional. For simplicity reasons, we replaced the non-directional graph edges by bi-directional synaptic couplings with two separated synapses, thus mutually connecting pairs of neurons. The weighting of the connections corresponds to the synaptic strengths. The delay time of the connections results from their euclidean length. The used signal speed (conduction delay) was assumed to be $0.5 \frac{m}{s}$ [18], which leads to synaptic delays for each pre-post-pair. During the rewiring procedure, few nodes develop an exponentially large number of connections while the majority of nodes develops few connections.

V. RESULTS

First, we examined the effects of different parameters that can affect the synchronous activity. On the basis of empirically determined default values (selected operating point, see Methods), the weight of the synaptic conductivity w, synaptic refractory time τ_m and the proportion of long distance connections ρ were purposefully varied (see Fig. 3). A minimum synaptic weight, which represents a measure for the connectivity, is necessary to synchronize network activity (Fig. 3a). Under this value only isolated spontaneous activity of single neurons or coincidentally synchronous events occur. The synaptic refractory time parameter τ_m describes the duration of the synaptic depression by the exhaustion of the neurotransmitter. τ_m directly affects the time between the bursts and therefore the oscillation period. Fig. 3b (2nd row) shows that small, local excitation waves arise in the spike plot for $\tau_m = 20ms$. With a sufficiently large τ_m these excitation waves synchronize and produce a synchronous network activity. With further increasing of τ_m, the synchronization index rises further, indicating a decreased network synchrony, because with longer tm, more spontaneous spikes occur in the interburst interval. This behavior reflects a correlation between the length of the interburst intervals and the duration of the synaptic refractory phase also found in biological experiments [2].

The parameter ρ mirrors the proportion of long distance connections in the Watt-Strogatz model (see methods), and its variation affects the connecting structure of the network. We could show that the proportion ρ of long distance connections increases first the synchrony (Fig. 3c), without a sufficient number of long distance connections no synchronous firing is possible. However, increasing the proportion of long distance connections present in the network, local

excitation waves does no longer occur, as the network synchrony decreases again. As a result, the synchrony is decreased again. The existence of an optimal relationship between short and long connections, with which the signals are best propagated, was already shown by Netoff et. al [7] and could be confirmed here. With the parameters selected here, the maximum synchrony occurs with $\rho = 0.3$ (example net with $\rho = 0.1$ in Fig. 2b).
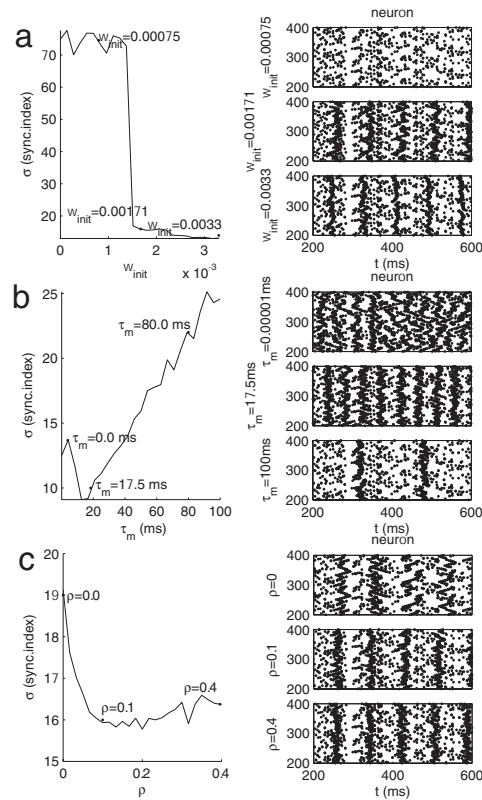

Fig. 3. Conditions and parameters for the generation of synchronous network activity. Each row represents a variation of one parameter close to the operation point; other parameters are fixed ($n = 500$ $\rho = 0.1$ $w_{init} = 0.00165$ $\tau_m = 50ms$). Left hand panels: Each of the graphs represents the progression of the synchronization index in function of a single parameter. Right panels show spike plots illustrating the synchronization of network activity in cross sections at the begin and end of the variation range. (a) w_{init}, initial synaptic weight for all connections; (b) τ_m, synaptic refractory time, and (c) ρ "small world" parameter = proportion of long-distance connections in the network.

VI. RELATED WORK

Networks of coupled dynamical systems have received a great deal of attention, mainly due to the fact that they can exhibit many complex and interesting dynamical phenomena, such as Turing patterns, auto- waves, spiral waves, and spatiotemporal chaos. Also, these networks are important in modeling many large-scale realworld systems. In the past decade, special attention has been focused on the synchronization of chaotic dynamical systems. These networks are

usually described by systems of coupled ordinary differential equations or maps, with completely regular topological structures such as chains, grids, lattices, and globally coupled graphs. Two typical settings are the discrete-time coupled map lattice [20] and the continuous-time cellular neural [21]. The main advantage of these simple architectures is that it allows one to focus on the complexity caused by the nonlinear dynamics of the nodes without worrying about additional complexity in the network structure, and another appealing feature is the ease of their implementation by integrated circuits. The topology of a network often plays a crucial role in determining its dynamical behaviors. For example, although a strong enough diffusive coupling will result in synchronization within an array of identical nodes [22], it cannot explain why many realworld complex networks exhibit a strong tendency toward synchronization even with a relatively weak coupling. As an instance, it was observed that the apparently independent routing messages from different routers in the Internet can easily become synchronized, while the tendency for routers towards synchronization may depend heavily on the topology of the Internet [23]. One way to break up the unwanted synchronization is for each router to add a sufficiently large component randomly to the period between two routing messages. However, the tendency to synchronization in the Internet is so strong that changing one deterministic protocol to correct the synchronization is likely to generate another synchrony elsewhere at the same time. This suggests that a more efficient solution requires a better understanding of the nature of the synchronization behavior in such complex networks as the Internet.

VII. Conclusion

We examined synchronization effects in probabilistic hierarchical network topologies, Watts-Strogatz-'small world' networks. Not only the 'small word' network topologies are considered biologically plausible, but they are also considered as fundamental structural principles in biological neural networks [16]. We showed that in such networks it comes to self-organizing processes in distinct parameter ranges: Initially the activity in the network synchronizes in dependence of the network architecture. This unique feature may cause an initialization of the synaptic strengths in the network and might prepare network properties for the later requirements of information processing.

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