

Complete Synchronization in Coupled Neuromodules of Different Types *

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Abstract

We discuss the parametrized dynamics of two coupled recurrent neural networks comprising either additive sigmoid neurons in discrete time or biologically more plausible time-continuous leaky-integrate-and-fire cells. General conditions for the existence of synchronized activity in such networks are given, which guarantee that corresponding neurons in both coupled sub-networks evolve synchronously. It is, in particular, demonstrated that even the coupling of totally different network structures can result in complex dynamics constrained to a synchronization manifold M . For additive sigmoid neurons the synchronized dynamics can be periodic, quasiperiodic as well as chaotic, and its stability can be determined by Lyapunov exponent techniques. For leaky-integrate-and-fire cells synchronized orbits are typically periodic, often with an extremely long period duration. In addition to synchronized attractors there often co-exist asynchronous periodic, quasiperiodic and even chaotic attractors.

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1 Introduction

There is experimental evidence that coherent firing of spatially separate neurons in biological brains appears as a response to specific external stimuli. This led to the famous “binding hypothesis” which states that selective synchronization of neural activity is a fundamental temporal mechanism for binding spatially distributed features into a coherent object representation (cf. e.g. [5, 6, 24]). In this context conceptual discussions and biologically motivated models were mainly based on the synchronization of oscillatory dynamics in large, e.g. high-dimensional systems (cf. [26, 27]). Dynamical modes more complex than oscillations have been rarely taken into consideration. But, since complex dynamics and chaos are known to exist already on the single neuron level in real brains, it seems, that brain theory is often unaware of the rich phenomenology of coupled nonlinear subsystems.

On the other hand, since 1990 the synchronization of chaotic physical systems has been extensively investigated experimentally as well as theoretically. Although a large part of the work has been motivated by its potential for technical applications there is still an ongoing discussion of the theoretical aspects of this phenomenon [8, 18, 21, 22, 23].

On this background we investigate the parametrized dynamics of two coupled neural networks with recurrent connectivity. The subsystems are called *neuromodules* because in the wider context of cognitive systems they can be considered as building blocks for larger functional neural networks. Basic concepts along this line of ideas are outlined in [14]. The neuromodules considered in the sequel belong to two different main classes: the first class describes modules as low-dimensional dynamical systems with nonlinearities introduced by the sigmoidal transfer (or rate) functions of standard additive neurons. The second class employs *spiking neurons* of the *leaky-integrate-and-fire* type, which are often envisaged as being biologically more plausible than additive sigmoid neurons. In both cases as parameters we will consider bias terms and/or stationary inputs, the synaptic weights between module neurons, and the mutual coupling strengths between neurons of different modules. Comparison of networks comprising graded respectively spiking neurons will show that the principal synchronization phenomena discussed in the following appear to be similar in both network variants.

We will use the term “synchronization” in the sense of *complete synchronization*; i.e. the states of the systems will coincide, while their dynamics in time remains periodic or chaotic. This requires, that the coupled networks under consideration have the same number of neurons. The term “state” here refers to the state of a whole module and not to that of a single cell; if two modules are completely synchronized, only the temporal activity of

corresponding cells in both modules will evolve identically. Cells inside a particular module, need not - and, in general, will not - be synchronized.

Often it is claimed that complete synchronization appears only if the interacting systems are identical. For instance, synchronous chaos has been discussed for two coupled intrinsically chaotic neurons in [15] as well as for coupled identical neuromodules in [16]. The synchronization conditions derived in section 2, however, show that synchronization of corresponding neurons can be achieved even if the systems are different; complete synchronization is possible in coupled networks that have different recurrent architectures. This will be demonstrated in section 3 for networks of additive sigmoid neurons and in section 6 for leaky-integrate-and-fire cells.

Outline of the paper is as follows: in the next section we introduce the terminology used throughout the paper for the special case of time-discrete additive sigmoid neurons. Furthermore, we present the main lemma guaranteeing complete synchronization of coupled modules. Section 3 gives an example for the synchronized dynamics in neuromodules of different architectures: a three neuron ring is coupled with a bi-directional chain of three neurons. The dynamical features of the isolated systems are quite different: besides fixed point attractors 3-rings can have period-2, -3 and period-6 attractors [13], whereas 3-chains can have p -periodic attractors for all p , and chaotic attractors as well [14]. Nonetheless, there are many different coupling schemes which ensure the existence of completely synchronized dynamics. Computer simulations demonstrate stable synchronous chaos for the case of a “minimal” coupling scheme in section 3. Sections 4 to 6 afterwards transfer the results to spiking neuron networks. The dynamical equations for leaky-integrate-and-fire neurons are stated and discussed in section 4; section 5 gives an example of a spiking neuron network comprising 3 neurons organized in a ring-architecture. An example for complete synchronization in a coupled network consisting of a 3-ring and a 3-chain are shown in section 6. General aspects of synchronizing neuromodules are finally discussed in section 7.

2 Coupled neuromodules

In this section we consider a neuromodule with n units as a time-discrete parametrized dynamical system on an n -dimensional activity phase space \mathbf{R}^n . With respect to a set ρ of parameters it is given by the map $f_\rho : \mathbf{R}^n \rightarrow \mathbf{R}^n$ defined by

$$a_i(t+1) = \theta_i + \sum_{j=1}^n w_{ij} \sigma(a_j(t)) , \quad i = 1, \dots, n , \quad (1)$$

where $a_i \in \mathbf{R}^n$ denotes the activity of the i -th neuron, and $\theta_i = \bar{\theta}_i + I_i$ denotes the sum of its fixed bias term $\bar{\theta}_i$ and its stationary external input I_i . The output $o_i = \sigma(a_i)$ of a unit is given by the standard sigmoidal transfer function $\sigma(x) := (1 + e^{-x})^{-1}$, $x \in \mathbf{R}$, and w_{ij} denotes the synaptic weight from unit j to unit i . If there exists a parameter set $\rho = (\theta, w)$ for which the dynamics (1) has at least one chaotic attractor, the module will be called a *chaotic neuromodule*.

Now, let A and B denote two neuromodules (1) with parameter sets $\rho^A = (\theta^A, w^A)$ and $\rho^B = (\theta^B, w^B)$, respectively. Connections going from module B to module A are given by an $(n \times n)$ -coupling matrix w^{AB} . Correspondingly, connections from module A to module B are given as a matrix w^{BA} . Thus, the architecture of the $2n$ -dimensional coupled system is given by a matrix w of the form

$$w = \begin{pmatrix} w^A & w^{AB} \\ w^{BA} & w^B \end{pmatrix}. \quad (2)$$

The neural activities of module A and B will be denoted a_i, b_i , $i = 1, \dots, n$, respectively; and $F_\rho : \mathbf{R}^{2n} \rightarrow \mathbf{R}^{2n}$ denotes the parametrized dynamics of the coupled systems with respect to $\rho := (\rho^A, \rho^B, w^{AB}, w^{BA})$.

In the following we will consider the process of *complete synchronization*, which means that there exists a subset $D \subset \mathbf{R}^{2n}$ such that $(a_0, b_0) \in D$ implies

$$\lim_{t \rightarrow \infty} |a(t; a_0) - b(t; b_0)| = 0,$$

where $(a(t; a_0), b(t; b_0))$ denotes the orbit under F_ρ through the initial condition $(a_0, b_0) \in \mathbf{R}^{2n}$. We are interested in the case where corresponding neurons of the modules have identical activities during a process. A *synchronized state* S of the coupled system is defined by $S := (a, b) \in \mathbf{R}^{2n}$ with $a = b$, and the *synchronization manifold* $M := \{(s, s) \in \mathbf{R}^{2n}\}$ of synchronized states corresponds to an n -dimensional hyperspace $M \cong \mathbf{R}^n \subset \mathbf{R}^{2n}$. Note, that in a synchronized state defined this way individual neurons inside a single module need not have identical activities. A straightforward calculation then proves the following general synchronization condition:

Lemma 1 *Let the parameter sets ρ^A, ρ^B of the modules A and B satisfy*

$$\theta^A = \theta^B, \quad (w^A - w^{BA}) = (w^B - w^{AB}). \quad (3)$$

Then every orbit of F_ρ through a synchronized state $(s, s) \in M$ is constrained to M for all times; i.e. M is an F_ρ -invariant manifold.

The prove of lemma 1 as well as some generalizations can be found in [17]. Condition (3) shows that synchronization can be achieved for modules

with different weight matrices w^A and w^B , as well as with different coupling matrices w^{AB} and w^{BA} , as long as (3) is satisfied. Using the definitions $\theta := \theta^A = \theta^B$ and

$$w_{ij}^+ := (w_{ij}^A + w_{ij}^{AB}) = (w_{ij}^B + w_{ij}^{BA}), \quad (4)$$

the corresponding synchronized dynamics $F_\rho^s : M \rightarrow M$ is given by the n equations

$$s_i(t+1) = \theta_i + \sum_{j=1}^n w_{ij}^+ \cdot \sigma(s_j(t)), \quad i = 1, \dots, n. \quad (5)$$

Thus, the synchronized dynamics corresponds to that of an n -module with weight matrix w^+ . It depends on the intrinsic dynamics of the two coupled modules as well as on the choice for the coupling matrices w^{AB} and w^{BA} .

Although the persistence of the synchronized dynamics is guaranteed by condition (3), it is not at all clear that the dynamics constrained to the manifold M is asymptotically stable with respect to the dynamics F_ρ ; i.e. whether a small perturbation of the system in a synchronous mode will desynchronize the system or not. A periodic or chaotic orbit in M may be an attractor for the synchronized dynamics F_ρ^s but not for the dynamics F_ρ of the coupled system [3]. We therefore have to discuss stability aspects of the synchronized dynamics with the help of Lyapunov exponents, and will discern between *synchronization exponents* λ_i^s and *transversal exponents* λ_i^\perp , $i = 1, \dots, n$ (compare e.g. [16]). They are derived from the linearizations $L^+(s(t))$ and $L^-(s(t))$, respectively, of the systems dynamics F_ρ along synchronized orbits $s(t)$ constrained to M . For $i, j = 1, \dots, n$ we have

$$L_{ij}^+(s) := w_{ij}^+ \cdot \sigma'(s_j), \quad L_{ij}^-(s) := w_{ij}^- \cdot \sigma'(s_j), \quad (6)$$

with σ' denoting the derivative of the sigmoid σ , w^+ as in equation (4), and w^- given by

$$w_{ij}^- := (w_{ij}^A - w_{ij}^{BA}) = (w_{ij}^B - w_{ij}^{AB}). \quad (7)$$

Synchronized chaotic dynamics will be characterized by the largest synchronization exponent satisfying $\lambda_1^s > 0$. On the other hand, a positive transversal exponent λ_1^\perp indicates unstable synchronized dynamics. Thus, if an unstable synchronous chaotic orbit exists in M then the system naturally must have entered a *hyperchaotic* regime [20]; i.e. at least two Lyapunov exponents of the system F_ρ are positive.

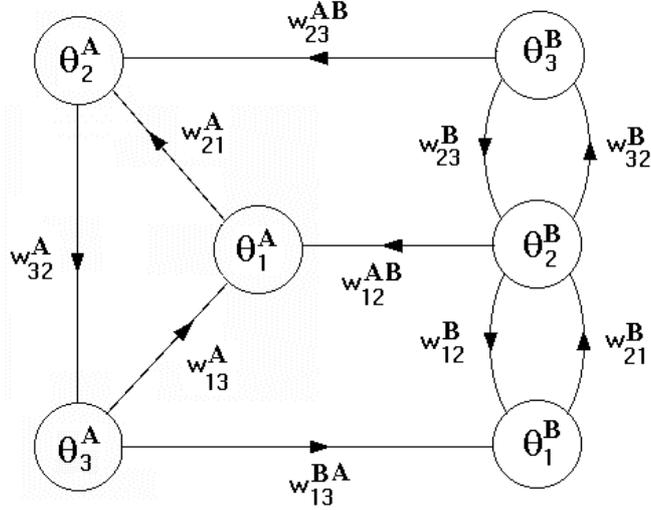


Figure 1: A minimal coupling configuration for complete synchronization of a 3-ring (module A) with a bidirectional 3-chain (Module B).

3 Example: Coupled 3-neuron modules

To demonstrate the complete synchronization of two different types of networks, we will study the following setup where an (oscillatory) 3-ring is coupled to a (chaotic) bi-directional 3-chain. The modules and their couplings are shown in figure 1, and the dynamics of the coupled system is given by

$$\begin{aligned}
a_1(t+1) &:= \theta_1^A + w_{13}^A \sigma(a_3(t)) + w_{12}^{AB} \sigma(b_2(t)) , \\
a_2(t+1) &:= \theta_2^A + w_{21}^A \sigma(a_1(t)) + w_{23}^{AB} \sigma(b_3(t)) , \\
a_3(t+1) &:= \theta_3^A + w_{32}^A \sigma(a_2(t)) , \\
b_1(t+1) &:= \theta_1^B + w_{12}^B \sigma(b_2(t)) + w_{13}^{BA} \sigma(a_3(t)) , \\
b_2(t+1) &:= \theta_2^B + w_{21}^B \sigma(b_1(t)) + w_{23}^B \sigma(b_3(t)) , \\
b_3(t+1) &:= \theta_3^B + w_{32}^B \sigma(b_2(t)) .
\end{aligned}$$

A possible realization of the synchronization condition (3) for this special case is given by the parameter values

$$\begin{aligned}
w_{12}^B = w_{12}^{AB} = w_{21}^A = w_{21}^B = w_{32}^A = w_{32}^B = 8 , \\
w_{13}^A = w_{13}^{BA} = w_{23}^B = w_{23}^{AB} = -8 , \\
\theta_1 = -1 , \quad \theta_2 = -3.6 , \quad \theta_3 = -4 .
\end{aligned}$$

For these parameter values the coupled system has a stable synchronized 2-cyclic chaotic attractor, which is depicted in figure 2. Recall [1], that a chaotic

attractor is called *p-cyclic* if it has p connected components which are permuted cyclically by the map F_ρ ; i.e. every component of a p -cyclic attractor is an attractor of F_ρ^p . Figure 2 shows the projections of the chaotic attractor onto the (o_1^A, o_2^A) -subspace and onto the subspaces (o_1^A, o_1^B) , (o_2^A, o_2^B) , and (o_3^A, o_3^B) . The (o_1^A, o_2^A) -projection clearly shows the chaotic nature of the dynamics inside module A and the two components of the 2-cyclic attractor. On the other hand, the remaining 3 projections demonstrate that the chaotic orbit is in fact constrained to a three-dimensional manifold M ; i.e. to the main diagonal in the last three subspaces. This implies, that corresponding neurons in both modules are perfectly synchronized.

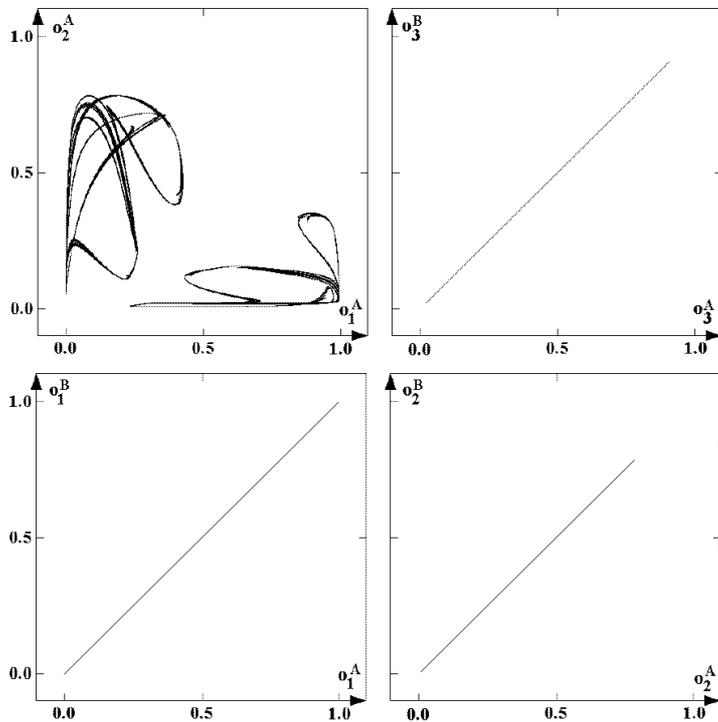


Figure 2: Completely synchronized chaos for two coupled 3-modules having different architectures. Parameters: see text.

Furthermore, we simulated the system with parameters from a neighborhood of the values given above. The completely synchronized 3-dimensional dynamics of this coupled system is given by equation (5). That it has interesting dynamical features can be read from the bifurcation sequence with respect to the variation of $\theta_2 := \theta_2^A = \theta_2^B$ shown in figure 3. The parameters are here given by $w_{12}^+ = w_{21}^+ = w_{32}^+ = -w_{23}^+ = -w_{13}^+ = 8$, $\theta_1 = -1$, $\theta_3 = -4$. Starting from a fixed point attractor for $\theta_2 = -8$, the system jumps into a period doubling route to chaos followed by windows of periodic, quasi-periodic

and chaotic dynamics. There are also θ_2 -intervals where we observe coexisting synchronous periodic and chaotic attractors. In fact, for this special coupled system the synchronized dynamics will always be stable. This can be easily seen by the fact that the only nonzero elements of w^- in (7) are w_{21}^- and w_{32}^- , and thus the matrices $L^-(s)$ in (6) have zero eigenvalues for all synchronous states s . Therefore the largest transversal Lyapunov exponent λ_1^\perp will be negative for all orbits constrained to M .

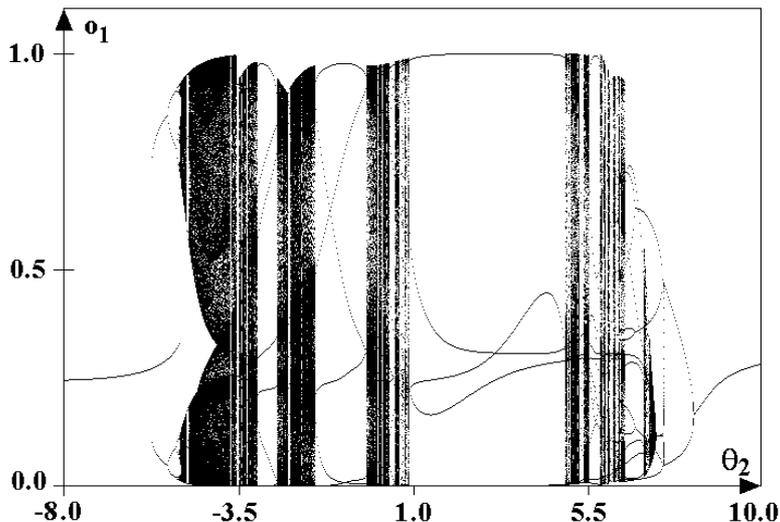


Figure 3: Bifurcation sequence for the completely synchronized dynamics of coupled 3-modules. Parameters: see text.

4 Spiking neurons

Sofar we considered standard additive neurons with sigmoid output functions. Although widely used in neuroinformatics and technical applications this neuron model only crudely approximates the behavior of real biological cells; whereas the graded output signal may be suitably envisaged as a firing probability or short-time average of a neuron's actual firing frequency, the time-discreteness of the model is not so easily interpreted. In addition, in the context of synchronized oscillations in cortex the precise timing of action potentials seems to be important. Obviously, such timing effects can only be studied, when time and spikes are modelled in an appropriate way.

Therefore, in the following we employ a simple spiking neuron model and extend the previous work to networks of coupled modules consisting of such

neurons. The main purpose is to show that the previously described synchronization effects appear very similarly also in those networks. In particular, it will be shown, that synchronization can be reached even if the network dynamics is complex (i.e. more complex than just oscillatory), and that even neuromodules of different architectures can be synchronized.

Many different spiking neuron models exist, ranging from biologically very detailed conductance based multi-compartment neurons to extremely simplified models that reduce biological complexity to just a few essential features covering current integration on cell membranes and the spike generation mechanism. One such simplistic spiking neuron model is the *leaky-integrate-and-fire cell* (see e.g. [25]). Since the present paper adopts an abstract viewpoint motivated by the theory of nonlinear dynamical systems we will also choose the leaky-integrate-and-fire cell as the basic neuron model in the following. However, we expect that the principal phenomena described below are generic and appear also in more complex spiking neuron models.

The leaky-integrate-and-fire neuron model can be derived from conductance based models, as for example described by the Hodgkin-Huxley equations [25, 11]. To this end, it is basically assumed, that the time-scale of the fast variables for sodium spiking (mainly mediated by fast Na^+ and delayed rectifier K^+ currents) separate from the slower time-scale for sub-threshold membrane properties (leakage currents at first approximation). The fast time-scale variables are then skipped in the model, and sodium spikes are approximated by Dirac-spikes that are elicited when the membrane potential reaches a certain firing threshold. The slow time-scale is kept in form of a linear (sub-threshold) membrane low-pass. In addition after-hyperpolarization present in many real neurons is incorporated in form of a reset of the membrane potential from firing threshold to some hyper-polarization level just after firing. This reset prevents the cell from immediately firing again, but it also makes the membrane behave discontinuously in time, an issue further discussed below.

Formally the membrane dynamics of a single cell is described as follows

$$\tau_i \dot{x}_i(t) = -x_i(t) + I_i(t) + \sum_{j=1}^N w_{ij} z_j(t) . \quad (8)$$

Here, $x_i(t)$ is the membrane potential of neuron i , τ_i is its membrane time constant, $I_i(t)$ is some external input, and the sum represents recurrent input from other cells in a network. The w_{ij} are synaptic weights as before, and the $z_j(t)$ are the outputs of the connected cells, i.e. sequences of Dirac-pulses.

Neuron i emits a Dirac-spike, $z_i(t) = \delta(t-t_f)$, at time t_f when its potential reaches a fixed firing threshold ϑ_i at that time. In addition, right after firing

the potential is reset to a fixed value r_i , i.e. $x_i(t_f+) = r_i$. In the sequel we will choose $\vartheta_i = 1$ and $r_i = 0$ for all model neurons.

When a spike from neuron j reaches neuron i it leads to a discontinuous jump in the potential $x_i(t)$ of size w_{ij}/τ_i due to the first order low-pass integration of the Dirac-spikes in (8). These discontinuities together with the discontinuous reset after firing have intricate implications for the precise dynamics of coupled leaky-integrate-and-fire cells. Consider, for example, two identical cells mutually excitatorily connected with weight w (and no selfconnections, for simplicity). If at some time the potentials of both cells are the same and their input I is above firing threshold they will both reach the threshold at the same time, exchange spikes, and afterwards will again have identical potentials. So they will evolve in perfect synchrony. On the other hand, if their potentials differ by an arbitrary small amount, one of the neurons will reach threshold earlier, send a spike to the second neuron, which will also fire - formally at the same time - driven by the incoming spike. But, now consider the potentials just after firing: The first neuron resets and then receives the spike of the second one; so its potential will be w/τ . The second neuron, however, receives the spike of the first one before it fires, it is reset and this way the influence of the incoming spike is perfectly canceled, its potential after firing is zero. This means, although both neurons fire virtually at the same time, their potentials afterwards are different. Accordingly, an arbitrarily small perturbation immediately destroys the synchrony that appears for initially identical potentials.

These difficulties are of course an artefact of the very simple nature of the model, and in particular of its discontinuities. In the present context, however, they suggest that synchronous states in coupled networks of leaky-integrate-and-fire cells as described above are generically unstable. Interestingly, Mirollo and Strogatz mathematically proved quite the opposite, i.e. that excitatorily connected networks of an arbitrary number of identical leaky-integrate-and-fire neurons under certain mild conditions always synchronize in finite time for almost all initial conditions [12]. The reason for this apparent contradiction is, that the synaptic interactions in [12] are different from the standard model described above. The keypoint is that (identical) neurons that virtually fire at the same time should have identical potentials just after firing. Otherwise synchronization can never be reached from non-synchronized states as explained for the two-neuron example above.

For that reason, we extend the standard update scheme by the following rule: if a neuron has fired at time t , then spikes that appear immediately afterwards but virtually at the same time $t+$ have no impact on the membrane potential. Such spikes, for instance, may stem from neurons that are raised above threshold by the firing of the cell itself. This rule is not perfectly

the same than that used in [12], but the effect is the same: synchronization becomes non-singular, i.e. basins of attraction become finite.

We should mention that the rule to some extent can be justified biologically. In principle it represents some kind of *absolute refractoriness* restricted to the time during and just after firing. Spikes impinging on a target cell during firing of a real neuron also have a neglectable effect on that cell, mainly because the evoked postsynaptic currents are orders of magnitude smaller in comparison with the spike-mediating Na^+ and K^+ currents which dominate the dynamics during firing. Since the leaky-integrate-and-fire model condenses the finite spike-time of real neurons into a Dirac-pulse of duration zero, refractoriness in our model is also restricted to the time of firing only. More elaborate refractory mechanisms are certainly possible, but are not considered here.

With these preliminaries we can proceed as before and define neuromodules, complete synchronization, synchronization manifolds, etc. just as for the case of additive sigmoid neurons. The definitions are straightforward and not repeated here. In addition, it is quite simple to show, that the synchronization Lemma 1 exactly keeps its form also for coupled neuromodules comprising leaky-integrate-and-fire cells (plus the refractory mechanism described above). It is not clear to date whether also the synchronized dynamics can be given by just specifying the reduced $n \times n$ matrix w_{ij}^+ . Similarly, the conditions for stability are currently under investigation and may turn out to be more complicated than for additive sigmoid neurons in discrete time.

5 Example: 3-ring of spiking neurons

In this section we briefly investigate the dynamics of a single 3-module organized in a ring-architecture and discuss some of its main properties, which appear similarly also in modules of different type or containing a different number of neurons. The 3-ring will also appear as a sub-module connected to a 3-chain in the next section.

Dynamic equations of the module are given by (8) and the spike mechanisms described earlier. As parameters we (somewhat arbitrarily) choose $\tau_i = 1$ and $I_i = 1.29$ for $i = 1, 2, 3$, and the connectivities $w_{13} = .12$, $w_{21} = .06$, $w_{32} = -.12$; other connections are zero.

For these parameters and initial conditions $(.17, 0, 0)$ the network settles into a cyclic firing state, displayed in figure 4. The left plot shows the mapping between consecutive interspike intervals of neuron one, $T_{1,n} \rightarrow T_{1,n+1}$. A fractal nature of this map would indicate chaotic dynamics and a finite set of m points a limit cycle; for $m = 1$ the cell would fire oscillatory in

regular intervals. Observe, that the range of the plot extends from 1.1 to 1.55. Accordingly, the neuron fires more or less regularly every 1.3 units of time. The exact times, however, scatter around that value. Furthermore, we should mention that the map in figure 4A is cyclic, although a complete cycle comprises 33 spike-events of neuron one and lasts for roughly 42 units of time (to be compared with the membrane time constant of 1).

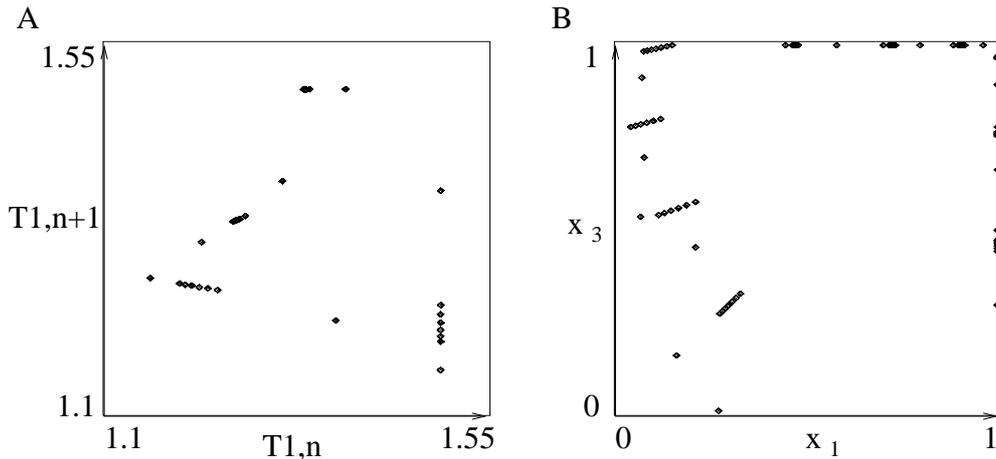


Figure 4: Dynamics of a ring network containing three spiking neurons. The left plot displays the mapping between consecutive interspike intervals of neuron one, $T_{1,n} \rightarrow T_{1,n+1}$. The right plot shows instantaneous potential values of neurons 1 and 3 sampled whenever a cell in the network fires. The network dynamics is periodic, although the period duration is very long.

Figure 4B plots potential values of neurons 1 and 3 whenever any of the three neurons fires. If for some of the displayed points $x_1 = 1$ then neuron 1 fired; if $x_3 = 1$ then neuron 3 fired; if both potentials are different from one then neuron 2 fired. The figure again reveals the complex firing pattern reached asymptotically by the network.

Complex firing patterns are a quite general feature observed in simulations at least for small or moderate coupling strengths. After initial transients have died out, typically firing patterns are periodic and relatively long compared with the intrinsic membrane time-constant. In addition, these patterns are rather sensitive against parameter changes. Moreover, in many cases extremely long transients can occur before an attractor is reached, somewhat in contrast to the fast relaxation times found by Hopfield and Herz in topologically organized networks of leaky-integrate-and-fire cells [10]. This difference may in part be due to different coupling strengths. As a trend, for stronger couplings firing patterns become shorter and less sensitive to pa-

parameter changes. Because firing patterns are often cyclic with long periods we are not certain whether chaos exists in the network; this is likely (cf. [4]), but it may be virtually undistinguishable from very long cycles or transients.

Finally, we should note, that besides the synchronized attractor displayed in figure 4 a second co-existing synchronized orbit exists, where the potentials and spikes of *all* cells are synchronized. This orbit can be traced with identical initial conditions for all cells. Although we have not particularly searched for multiple co-existing attractors, those are likely to exist at least in some parameter regimes.

6 Example: Coupled 3-ring and 3-chain

We now couple the ring network described in the previous section to a chain of three neurons. The architecture is essentially the same as the one used in section 3 and displayed in figure 1. The purpose of this example is to show that also for networks of leaky-integrate-and-fire cells, complete synchronization can be reached even when different network architectures are coupled.

Parameters ensuring synchronization can be easily found from Lemma 1. We choose $\tau_i = 1$ and $I_i = 1.25$ for $i = 1, 2, 3$. Nonzero weights inside the 3-ring (module A) are $w_{13}^A = .06$, $w_{21}^A = .03$, $w_{32}^A = -.06$ and inside the 3-chain $w_{12}^B = .03$, $w_{21}^B = -.06$, $w_{23}^B = .06$, $w_{32}^B = .045$. The mutual connections between modules A and B are $w_{21}^{AB} = -.06$, $w_{32}^{AB} = .045$, $w_{12}^{BA} = -.03$, $w_{13}^{BA} = .06$, $w_{21}^{BA} = .03$, and $w_{23}^{BA} = w_{32}^{BA} = -.06$.

For these choices and initial values $(.19, 0, 0)$ figure 5 exhibits the dynamics of the coupled network after transients have died out. The figure corresponds with figure 2 for the coupled ring-chain network containing sigmoid additive neurons. The upper left plot shows the instantaneous membrane potentials of neurons one and two in module A when anyone of the six neurons in the network fires (cf. figure 4B). Although it is again rather complex, the firing pattern inside module A is periodic - a complete cycle lasts for more than 120 units of time. In addition to the orbit shown in figure 5 a further synchronized orbit exists, for which all cells of both modules fire synchronously.

The other three plots in figure 5 show membrane potentials of corresponding neurons in both modules sampled whenever a cell fires. The restriction of the plots to the main diagonal implies that the coupled dynamics of the network is indeed constrained to a 3-dimensional completely synchronized manifold, i.e. that the spikes of the neurons in the chain - as well as their potentials - perfectly follow those of the neurons in the ring.

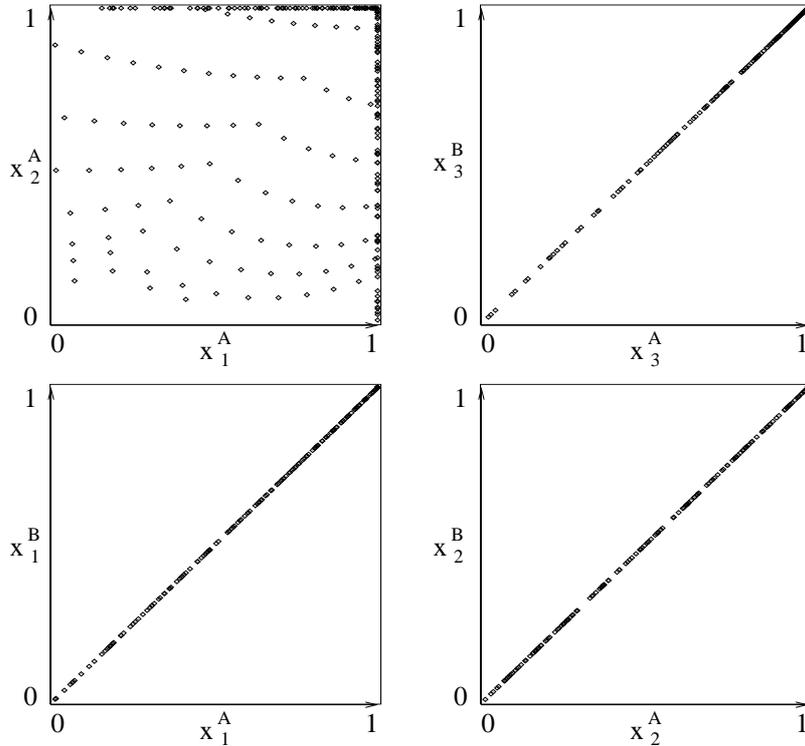


Figure 5: Complete synchronization in a spiking neuron network consisting of a 3-ring coupled to a 3-chain. Each of the four plots displays potential values of 2 cells sampled whenever any of the 6 neurons in the network fires. The upper left figure (x_1^A displayed against x_2^A) shows that the orbit inside the ring-module is rather complex (although periodic, see text); nonetheless, the restriction of the remaining 3 plots to the main diagonal proves that corresponding neurons in the ring and the chain are synchronized.

7 Discussion

In summary, we have shown that synchronized activity of groups of neurons in a system of coupled recurrent neural networks is always achievable, if the sum of bias terms and external inputs to corresponding module neurons are identical, and coupling weights are set appropriately. Then, even in systems of coupled neuromodules with the same number of neurons but *different* architectures completely synchronized complex activation patterns can exist. This holds for standard sigmoid neurons, and - as demonstrated - also for more realistical spiking neuron models. Accordingly, most results concerning the dynamics of coupled neuromodules presented earlier for the somewhat artificial time-discrete sigmoid neurons [16, 17] carry over to biologically more

plausible spiking neurons. Although the dynamical states that occur in both systems are different in detail, the fundamental synchronization phenomena are comparable from the abstract level adopted in the present work.

For additive sigmoid neurons the synchronized dynamics of the coupled system is describable as that of a reduced neuromodule with weight matrix given by the so-called synchronization matrix w^+ . The reduced system is typically - although not necessarily - different from each of the coupled subsystems. Depending on the module parameters (weights, bias terms, and inputs), synchronized orbits can be periodic, quasiperiodic or chaotic, and the synchronization will be stable, if these orbits, constrained to the manifold of synchronized states, are attractors for the dynamics of the coupled system. Stability of a synchronized orbit can be checked numerically by calculating the largest transversal Lyapunov exponent which is determined by the so-called obstruction matrix w^- .

In the present work, we did not find chaotic synchronized states in the example networks comprising leaky-integrate-and-fire neurons. This is probably the case because we did not yet search the parameter space exhaustively for these networks. Analytical results by Catsigeras and Budelli [4] suggest that chaotic orbits should exist if some inhibitory connections in the network are strong enough. Typically, in networks of leaky-integrate-and-fire cells, we found asymptotically periodic firing patterns, which often were very long compared with the membrane time constants when the coupling strengths were relatively weak. Stronger connections lead to less complex firing patterns. Moreover, starting from random initial conditions extremely long transients were observed in many simulations.

Module dynamics for both neuron types often show several co-existing synchronous attractors in large parameter domains. In addition to these synchronous attractors further asynchronous (periodic, quasiperiodic or chaotic) attractors can exist. This means, whether a system ends up asymptotically in a synchronous mode or not depends crucially on the initial conditions respectively on the internal state of the system. In this sense the reaction to external signals depends on the *history* of the system itself, whereby *memory effects* are introduced into the behavior of the networks.

Furthermore, a synchronized mode often persists even if external inputs are time dependent. Although the conditions for the existence of complete synchronization in Lemma 1 are formulated for constant inputs, it is straightforward to check, that the inputs may depend on time. Clearly, time-dependent inputs change the structure of the synchronous orbit, but they do not destroy synchrony as long as the conditions in Lemma 1 are satisfied in time. For example, if the input is only slowly varying, the synchronized dynamics may pass through a whole bifurcation sequence, or it may be driven

from stable synchronization conditions to unstable ones. Both effects modulate the sensitivity of the network against external input.

Desynchronization of module dynamics can be achieved in different ways. From the synchronization conditions it is clear that diverging external inputs or other inappropriate parameter settings will immediately desynchronize the modules. Depending on the coupling conditions a mode of lower degree of synchronization may be reached (cf. [17]) or the system may completely desynchronize.

Different from this standard situation, external signals may drive the composed system into domains where the - still existing - synchronized dynamics gets unstable. In such parameter domains, synchronization is particularly sensitive to perturbations orthogonal to the synchronization manifold. Accordingly, appropriate control signals may be used to transiently modulate the responsiveness of the coupled network in order to reach quick and active desynchronization of modules reacting to slightly different input signals.

In a similar way, parameters may also be used to decide, whether a system is responding to a given stimulus with a synchronous mode at all. Physiologically such parameters may be identified as subcortical input, which, for instance, is known to strongly modulate spatial ranges of synchronization of cortical oscillations in the alpha- and gamma-range (e.g. [19]). Alternatively, parameter changes may represent feedback from higher cortical areas either in the form of integrative input signals, that organize or “bind” otherwise isolated local submodules into larger functional networks [5, 6] or as part of some attentional mechanism.

One should note, that such feedback does not just provide electrical input into cortical cells. By varying excitability of cells, it is also capable to change the functional connectivity inside the network [2]. In this way different effective coupling schemes can be selected that support different kinds of collective dynamics. A very similar role may be played by neuromodulatory (e.g. the monoaminergic) transmitter systems in the brain. Their influence on functional connectivity as well as their capability to switch dynamical properties of complex collective modes of activation have repeatedly been demonstrated (e.g. [7, 9]).

We believe that the dynamical phenomenology of the presented results, although derived for small and simple neural networks, can stimulate the development of conceptually new dynamical models for cortical information processing or even cognitive capabilities [14]. As a direct application, the rather typical co-existence of synchronized modes with modes of asynchronous dynamics generalizes functional properties like “feature binding” often attributed to the synchronization of oscillations. At the same time it introduces memory aspects into these systems through generalized hys-

teresis effects. Furthermore, since synchronization and desynchronization of modules can be controlled by different parameters, attention-guided synchronization of subsystems is an additional interesting functional feature of coupled neuromodules.

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