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networks of spiking neurons**

by

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# Generalized Types of Synchronization in Networks of Spiking Neurons\*

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## Abstract

The synchronization of neural signals has been proposed as a temporal coding scheme in distributed cortical networks. Theoretical studies in that direction mainly focused on the synchronization of coupled oscillatory subsystems. In the present work we show that several complex types of synchronization previously described for graded response neurons appear similarly also in biologically realistic networks of spiking and compartmental neurons. This includes synchronized complex spatio-temporal behavior, partial and generalized synchronization. The results suggest a similarly rich spatio-temporal behavior in real neural systems and may guide experimental research towards the study of complex modes of synchronization and their neuromodulation.

## 1 Introduction

The synchronization of neural signals has been proposed as a temporal coding scheme expressing the cooperated computation in distributed cortical networks [1, 8]. Theoretical studies in that direction mainly focused on the

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synchronization of coupled oscillatory subsystems [1, 3, 4, 7]; they usually neglected more complex dynamical modes, that are known to exist already on the single-unit level [2, 7]. Recently we described synchronization phenomena - considerably more complex than synchronized oscillations - in two small mutually coupled recurrent networks comprising graded response neurons [5, 6]. For instance, we observed that (1) attractors of the coupled system can contain *completely synchronized* periodic, quasiperiodic or even chaotic orbits; (2) the synchronization can also be only *partial*, referring to a situation where subsets and not all of the neurons in each subnetwork synchronize; (3) or it can be *generalized*, meaning that a non-trivial function maps the state of one subsystem onto that of the other (a special case of this situation is p:q-locking). Moreover, (4) attractors of different types, dynamic complexity and degree of (partial) synchronization can coexist for the same set of parameters, and (5) any single attractor can comprise cells that are asynchronous, partially synchronized, or synchronized in the generalized sense. Finally, (6) all this is possible even if the coupled networks have different architectures or a different number of neurons; especially, even non-identical systems can often synchronize perfectly. The type of synchronization depends in an intricate way on external stimuli, modulatory signals, the history and connectivity of the network as well as other parameters.

These results were obtained in [5] for networks comprising artificial time-discrete graded response neurons. The present work now aims to demonstrate that phenomena very similar to those in [5] appear also in biologically more plausible spiking neuron networks. This suggests a similarly rich spatio-temporal behavior in real neural systems and may guide experimental research towards the study of complex modes of synchronization and their neuromodulation.

## 2 Example with integrate-and-fire neurons

We first demonstrate different types of synchronization in a network of integrate-and-fire neurons. This should also make our conceptual approach clear. The dynamics of an integrate-and-fire neuron reads (cf. e.g. [3, 4])

$$\tau_i \frac{dx_i}{dt}(t) = -x_i(t) + I_i(t) + \sum_{j=1}^N w_{ij} z_j(t) . \quad (1)$$

Here,  $x_i(t)$  is the membrane potential of neuron  $i$  and  $\tau_i$  is its membrane time constant.  $I_i(t)$  is some external input and the sum represents input from other cells. The  $w_{ij}$  are synaptic weights and  $z_j(t)$  is the output of cell  $j$ . 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  $\vartheta_i = 1$  at that time. In addition, right after firing the potential is reset to zero, i.e.  $x_i(t_f+) = 0$ .

Using these standard equations, spikes arriving at a target cell, say neuron  $i$ , evoke a discontinuous jump in the potential  $x_i$ . This discontinuity is an artefact of the simple model, but it has intricate implications on the time-order of spikes in the network. In especially, it destroys the possibility for stable synchrony in networks of excitatorily connected identical integrate-and-fire cells (cf. [3]). Arguments for this conjecture are given in [5] and are not repeated here. To resolve this problem, we proceed as in [3, 4, 5] and 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 implements some kind of refractoriness [5].

Figure 1 shows an example simulation. On the left side the network architecture is depicted showing a 3-ring coupled to a 3-chain (i.e. 2 subnetworks of *different architecture* are coupled). Complete synchronization of complex firing patterns in a ring-chain architecture has been demonstrated in [5]. The four frames on the right hand side of figure 1 show a more complicated mode of synchronization. Displayed in each frame are the potential values of two neurons sampled whenever anyone of the 6 neurons in the network fires. The upper left frame displays potentials of cells 1 and 2 inside the ring-subnetwork (denoted by an A). Apparently, there is no obvious functional relationship between both neurons, which indicates that the firing pattern inside the ring is complex (perhaps chaotic, but we cannot rule out the possibility that it is cyclic with an extremely long period). The lower left plot shows potentials for neurons 1 in module A and B respectively. Because the plot is confined to the main diagonal these two neurons are perfectly synchronous. In contrast, neurons 3 in module A and B are essentially asynchronous, although the respective plot (upper right) shows some structure. Accordingly, the synchronization of the whole system is only partial. Furthermore, neurons 2 in A and B give an example for generalized synchronization. They are not perfectly synchronous (i.e. confined to the diagonal), but the potential value

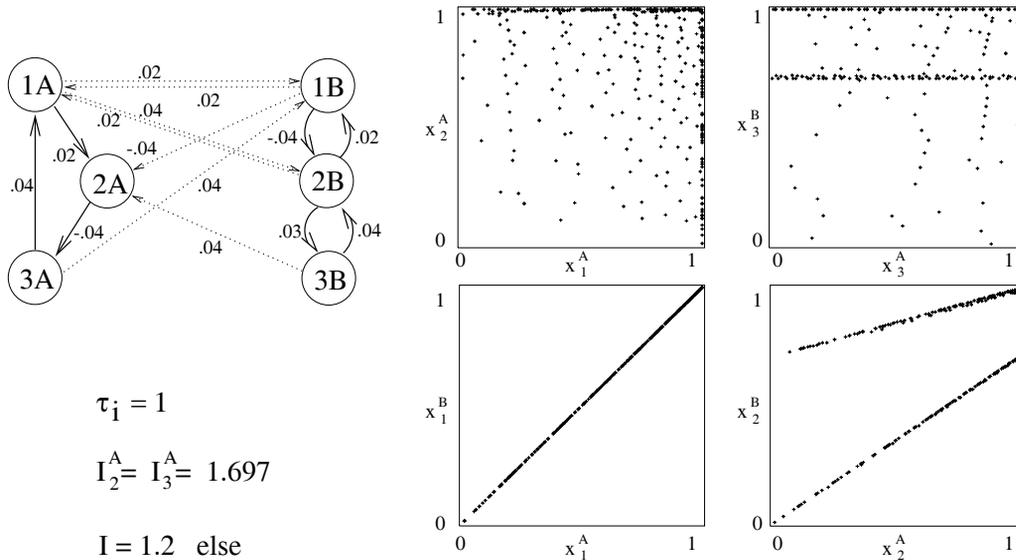


Figure 1: Differently synchronized neurons in a network of integrate-and-fire cells. Left: Network architecture. Right: Example simulation.

$x_2^B$  can be predicted with high accuracy from  $x_2^A$ . Neuron 2 in A fires two spikes, when the corresponding neuron in B fires only a single spike.

### 3 Biological examples

For demonstration purposes the previous section gave a still somewhat technical example of complex synchronization. We now briefly discuss some examples, where comparable phenomena may appear in real neural systems.

*Complete synchronization* has, of course, often been demonstrated in the context of binding by synchronization using networks of oscillatory subunits (e.g. [1, 3, 4] and many more).

*Generalized synchronization* most easily appears, when the cells in the network are not identical. For instance, Traub et al. [9] considered a network of excitatory and inhibitory compartmental neurons where the excitatory cells received differently strong input currents. The network revealed collective oscillations in the gamma-range, but less input current delayed firing of the excitatory cells relative to the collective oscillation. Accordingly, their

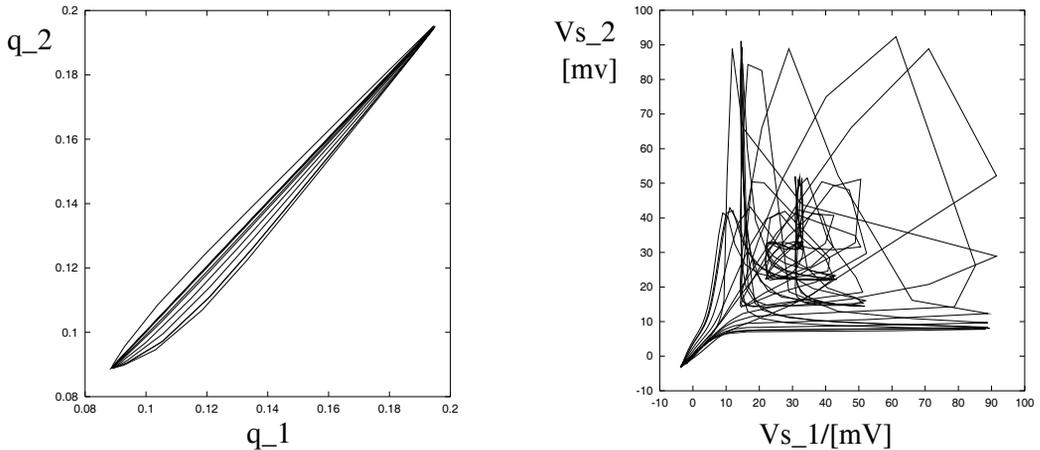


Figure 2: Example for partial synchronization in a network of 100 Pinsky-Rinzel neurons [7]. The slow variables  $q$  of two (arbitrary) neurons are almost synchronous (left side) but the fast sodium spikes are not (right side).

firing times were related by some static functional relationship (up to noise), and thus, the cells were synchronized in the generalized sense.

An example for (approximate) *partial synchronization* is shown in figure 2, where we simulated a network of 100 excitatorily connected two-compartment Pinsky-Rinzel-neurons. The network was virtually identical to that described in [7]. Each cell had 8 independent intrinsic variables including fast currents responsible for sodium spiking on a soma-like compartment and slower calcium and calcium-mediated currents on a dendrite-like compartment. Isolated neurons revealed several firing modes in response to input currents: regular spiking at moderate and high currents, different kinds of bursting at low inputs, and apparently chaotic dynamics in between (cf. [7]). When the cells were synaptically coupled, Pinsky and Rinzel observed a collective dynamical mode of burst-synchronization, where all cells fired brief, regular and roughly synchronized high-frequency bursts of spikes. This dynamical state is analyzed more closely in figure 2, where the (fast) soma-potentials,  $V_s$ , of two neurons are plotted against each other on the right hand side and the slow intrinsic variables  $q$  of these neurons on the left hand side. Apparently, the slow burst-mediating variables are almost confined to the main diagonal, indicating near synchrony, but the fast variables responsible for sodium

spiking remain asynchronous (presumably chaotic). This can be viewed as partial synchronization of the slow, but not the fast variables.

## 4 Discussion

In summary we have shown that several generalized types of synchronization previously described for networks of artificial time-discrete graded response neurons [5, 6] appear similarly also in biologically realistic networks of spiking neurons. Beyond the often considered synchronization of identical oscillators, *complete synchronization* can also be reached in complex spatio-temporal states of non-identical subsystems. Furthermore, the synchronization can be confined to only subsets of the dynamical variables of the coupled systems (*partial synchronization*), and it can be *generalized*, i.e. the relation between synchronized variables must not be the identity.

As in [6] we expect that external signals can easily switch the network behavior between different types of stable or unstable synchronization, or different degrees of synchrony. Neuromodulation should have similar effects by either influencing the intrinsic complexity of the single-cell dynamics or the effective connectivity structure of whole networks (cf. e.g. [2]). This way, the synchronization behavior of distributed networks may be changed dynamically also in real neural systems.

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