



# Nonlocal synchronization mechanism in firing dynamics of neural networks

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**Abstract**—Simulations of Hodgkin Huxley population dynamic networks with unidirectional connectivity and synaptic noise indicate a new nonlocal mechanism governing the periodic activity mode: the greatest common divisor (GCD) of network loops. For a stimulus to one node, the network splits into GCD-clusters in which cluster neurons are in zero-lag synchronization. For complex external stimuli, the number of clusters can be any common divisor of loops. The synchronized mode and the transients to synchronization pinpoint the type of external stimuli. The findings supported by an information mixing mechanism, call for reexamining sources of correlated activity in cortex and shorter information processing time scales.

## 1. Introduction

The spiking activity of neurons within a local cortical population is typically correlated [1, 2]. As a result, local cortical signals are robust to noise, which is a prerequisite for reliable signal processing in cortex. Under special conditions, coherent activity in a local cortical population is an inevitable consequence of shared presynaptic input [3, 4, 5]. Nevertheless, the mechanism for the emergence of correlation, synchronization or even nearly zero-lag synchronization (ZLS) among two or more cortical areas which do not share the same input is one of the main enigmas in neuroscience [4, 5]. It has been argued that nonlocal synchronization is a marker of binding activities in different cortical areas into one perceptual entity [5, 6, 7]. This prompted the hypothesis that synchronization may hold key information about higher and complex functionalities of the network. To investigate the synchronization of complex neural circuits we studied the activity modes of networks in which the properties of solitary neurons, population dynamics, delays, connectivity and background noise mimic the inter-columnar connectivity of the neocortex.

## 2. Neuronal circuit

We start with a description of the neuronal circuits and define the properties of a neuronal cell, the structure of a node in a network representing one cortical patch, and the connection between nodes. Each neural cell was simulated using the well known Hodgkin Huxley model [8, 9]. Each

node in the network was comprised of a balanced population of 30 neurons, 80/20 percent of which were excitatory/inhibitory (Fig. 1a). The lawful reciprocal connections within each node were only between pairs of excitatory and inhibitory neurons and were selected at random with probability  $p_{in}$ . In terms of biological properties it was assumed that distant cortico-cortical connections are (almost) exclusively excitatory whereas local connections are both excitatory and inhibitory [10]. In this framework, cortical areas are connected reciprocally across the two hemispheres and within a single hemisphere, where small functional cortical units (patches) connect to other cortical patches in a pseudo random manner. The number of patches to which a single patch connects varies considerably, where typically, it grows like the square root of the number of cortical neurons [11] resulting for a mouse in 3 to 6, and most likely for humans roughly 150. Hence, we investigated excitatory strongly connected oriented graphs; i.e., if neurons belonging to node A project to neurons belonging to node B, then connections from node B to node A are forbidden; however there is a legal path between any pair of nodes. The connection between neurons belonging to different nodes was excitatory and was selected with probability  $p_{out}$ . In terms of biological properties, distant cortico-cortical unidirectional connections were exclusively excitatory whereas local connections within one node of the network were both excitatory and inhibitory [10].

The delay between a pair of neurons belonging to the same node was taken from a uniform distribution in the range [1.5, 2.5] ms, whereas neurons belonging to different nodes came from a uniform distribution in the range  $[\tau - 0.5, \tau + 0.5]$  ms where  $\tau$  was the average time delay including the internal dynamics of a neuron. Results are exemplified below in simulations with  $p_{in}=0.2$ ,  $p_{out}=0.8$  and  $\tau = 20$  ms, unless otherwise indicated. The robustness of the results was tested under the influence of background synaptic noise generated from the synaptic input of a balanced random population of 1000 neurons. In the absence of a stimulus, an isolated node as well as the entire network has no consistent or periodic firing activity or chaotic activity [9].

Figure 1a depicts a neuronal circuit consisting of four nodes and two loops having total delays of  $3\tau$  and  $4\tau$  with  $GCD(3,4)=1$ , where at time  $t=0$  node A is stimulated for

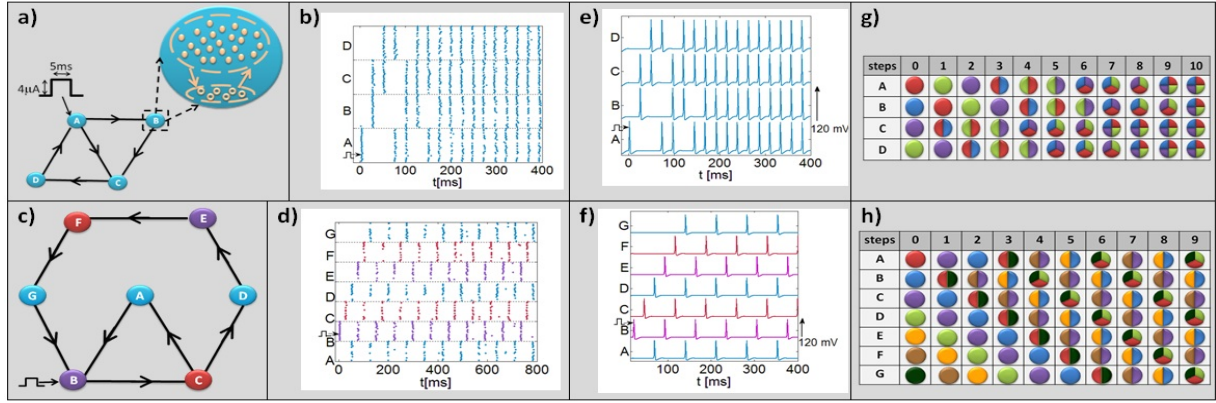


Figure 1: ZLS and clusters in small neural circuits. (a) Schematic of ZLS of an oriented circuit consisting of four nodes, where node A is stimulated for 5 ms by an external current  $I_{ext} = 4\mu A/cm^2$ . Detailed structure of each node is depicted for node B where filled-circles/empty-circles stand for excitatory/inhibitory neurons and arrows represent reciprocal connections between excitatory and inhibitory neurons. (b) Raster diagram of the firing activity of neurons in (a). (c) Schematic of an oriented circuit consisting of seven nodes which splits into 3-clusters represented by 3 colors. (d) Raster diagram of the firing activity of neurons in (c). (e) Spike train for (a) with simplified node consisting of only one neuron. (f) Spike train for (c) as for (e). (g) Mixing mechanism (see text) for (a) where steps are measured in units of  $\tau$  and synchronized nodes are composed of an identical set of colors. (h) Mixing mechanism for (c).

5 ms by an external current  $I_{ext} = 4\mu A/cm^2$ . The raster diagram of the firing activity of the neurons in each node is presented in Fig. 1b. Although the graph does not contain reciprocal connections after a short transient,  $\sim 200$  ms, the neuronal circuits reach ZLS among all nodes. Figure 1c depicts a neuronal circuit consisting of seven nodes and two loops with total delays of  $6\tau$  and  $3\tau$  with  $GCD(6,3)=3$ , where at time  $t=0$ , node B for instance is stimulated for 5 ms by an external current  $I_{ext} = 4\mu A/cm^2$ . The raster diagram of the diluted firing activity of the neurons in each one of the seven nodes is presented in Fig. 1d. Results indicate that after a short transient of less than 200 ms, the neuronal circuit splits into 3-clusters as labeled by three different colors in Figs. 1c and 1d.

There are two sources for the low firing rate in the neuronal circuits [13, 14]. The first source is the local inhibitory connections that hyperpolarized the membrane potential resulting in a relatively diluted firing pattern in each node. The second source is the emergence of m-clusters leading to the periodic activity with a period of  $m\tau$  of each node rather than  $\tau$  as in the case of ZLS. However, the model described here is but a toy model compared to the full biological reality [13, 14].

### 3. GCD-clusters and mixing mechanism

In the absence of inhibition and background noise, the firing pattern of each neuron becomes regular and all neurons in a node are synchronized; however, the phase among nodes is unaltered. For the sake of clarity, below we present results for neural circuits where each node was reduced to one excitatory neuron with no background noise, although

similar results were obtained in simulations for structured nodes and background noise. The results of this simplified node characterized by a single neuron for the neural circuits in Figs. 1a and 1c are presented in Figs. 1e (ZLS) and 1f (3-clusters), respectively. The interplay between the number of clusters and the GCD of the loops that compose a neuronal circuit can best be understood by the self-consistent argument, *mixing mechanism*, that nodes with identical color are in ZLS and must be driven by the same set of "colors". The trivial solution is always one "color", ZLS; however, the alternative solution consists of exactly GCD "colors", GCD-clusters. An attempt to consistently color nodes serially with a greater number of colors fails, because nodes of the same color have different drives. In the case of  $GCD > 1$ , GCD-clusters take over the ZLS solution following the mixing mechanism [15]; the initial condition is a distinct color for each node, time steps are rescaled with  $\tau$  and at each time step a node is colored by the union of colors of its driven nodes. The colors of a node at step  $t$  indicate the set of nodes/colors at  $t=0$  which are now mixed (integrated) by the node. The mixing mechanism for the circuit in Fig. 1a is shown in Fig. 1g where after 10 steps all nodes are identical, and colored by 4 colors, indicating a ZLS solution. Similarly the mixing mechanism for the circuit in Fig. 1c indicates 3-clusters ((A,D,G), (B,E), (C,F)) as depicted in Fig. 1h.

### 4. Nonlocal mechanism

A more complex circuit is presented in Fig. 2a consisting of three directed loops with total delays of  $6\tau$ ,  $12\tau$  and  $18\tau$  and 25 nodes. The  $GCD(6,12,18)=6$  and 6-clusters

(6-colors) were identified in simulations. Small changes in topology can dramatically alter the number of clusters, such that the addition/deletion of one connection can serve as a remote switching mechanism in the circuit [17, 18]. Figures 2b, 2c and 2d show that an additional unidirectional connection between two nodes induces a loop with a total delay of  $5\tau$ ,  $4\tau$  and  $3\tau$ , respectively. Hence the GCD modifies and switches the 6-cluster solutions to ZLS, 2-clusters and 3-clusters, respectively. One might conclude that in order to generate large loops the number of cortical patches, nodes, needs to increase accordingly, nevertheless Figure 2e indicates that an oriented graph consisting of 6 nodes with diluted connectivity generates loops of sizes  $6n\tau$  where  $n$  is an integer. Furthermore a shortcut in this condensed representation, as shown by the dashed arrow in Fig. 2e, changes the GCD in a way similar to the expanded representation, Figs 2a-d.

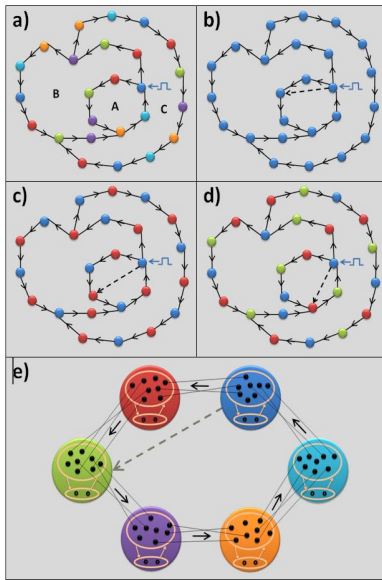


Figure 2: Non-local mechanism for clustering of complex and condensed circuits. (a) A circuit consisting of 25 simplified nodes, loops with total delays of  $6\tau$ ,  $12\tau$  and  $18\tau$  (boundaries of areas A, A+B and C, respectively where  $\tau$  is a unit delay between two connected nodes), and a stimulus to one node as in Fig. 1. Nodes split into 6-clusters following the  $\text{GCD}(6,12,18)=6$ . (b) With an additional unidirectional connection (dashed arrow) and a loop of  $5\tau$ , the  $\text{GCD}(5,6,12,18)=1$  and the circuit is in ZLS. (c) An additional loop of  $4\tau$  as in (b), where  $\text{GCD}(4,6,12,18)=2$  and the circuit is in 2 clusters. (d) An additional loop of  $3\tau$  as in (b), where  $\text{GCD}(3,6,12,18)=3$  and the circuit is in 3 clusters. (e) Schematic condensed representation of  $6n$  loops where  $n$  is an integer, emerging in a ring of 6 nodes, each one representing one cortical patch, and with diluted connectivity where the in/out connectivity of each neuron is at least 1. The gray dashed arrow depicts a similar effect as in 2b.

## 5. Complex external stimuli

A temporal stimulus to one node of the neural circuit splits the firing pattern of nodes into GCD-clusters and in addition the firing pattern cycle of a node is also equal to the GCD. For a neural circuit with  $\text{GCD}=6$  (Figs. 2a and 2e), the firing pattern cycle of a node is exemplified in the first row of Fig. 3a together with its binary representation and the degeneracy of this class of stimuli. Under cyclic permutation symmetry in the 6-clusters arrangement, there are 13 classes of simultaneous stimuli for nodes belonging to one or more clusters as summarized by the first column of Fig. 3a, and as expected, the sum of their degeneracy is  $2^6 - 1 = 63$ . The firing pattern cycle and its binary representation are given by the second and third columns of Fig. 3a.

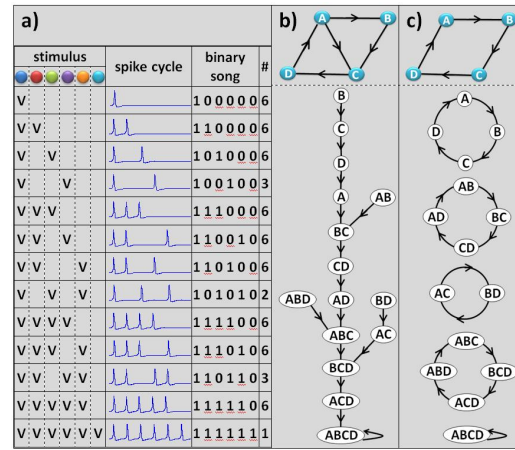


Figure 3: Complex external stimuli and transients. (a) Under permutation symmetry, the 63 different stimuli in the 6-cluster arrangement of the circuit in Fig. 2a are organized into 13 classes (first column), where the degeneracy of each class is given in the last column. The firing pattern cycle of a node together with its binary representation are presented in the second and the third columns, indicating that the number of clusters as well as the firing spike cycle of a node can be any common divisor of the loops. (b) Four node circuit which is in ZLS and the transients for the 15 different stimuli organized in a tree. (c) A square circuit and its 15 different stimuli organized in 5 distinct cyclic flows.

Results indicate that the period of the firing pattern can differ from the GCD, for instance the stimulus period in the 4<sup>th</sup> (8<sup>th</sup>) row of Fig. 3a is 3 (2) and in fact the number of clusters can be any common divisor of the loops composing the circuit as a result of stimuli inducing such periodicity, and an example is presented in Fig. 4.

The number of clusters as well as the spiking cycle of a given node can identify a class of possible stimuli applied to the circuits. Nevertheless, more detailed information about the stimuli can be deduced rapidly from the transients

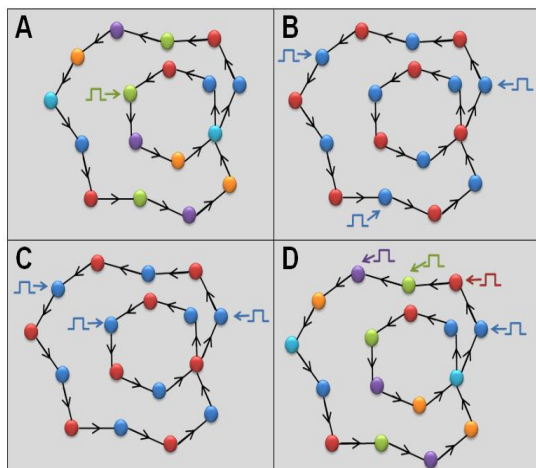


Figure 4: Simulation results of two connected loops with total delays of  $6\tau$  and  $12\tau$  consisting of 17 nodes. (a) A drive to one node resulting in  $\text{GCD}(6,12)=6$  clusters. (b) A drive to every fourth node in the loop of 12, represented by  $(1, 0, 0, 0, 1, 0, 0, 0, 1, 0, 0, 0)$ , results in  $\text{GCD}(4,6,12)=2$  clusters. (c) The drive can be given to any set of nodes with the same colors as in (b) and results in the same clusters. (d) A drive to four consecutive nodes in the loop of 12 represented by  $(1, 1, 1, 1, 0, 0, 0, 0, 0, 0, 0, 0)$ , which is characterized by a periodicity of 12. Hence, it results in  $\text{GCD}(6,12)=6$  clusters.

[19] to synchronization. Fig. 3b shows all the transients to ZLS from the 15 possible stimuli for the circuit in Fig. 1a, whereas Fig. 3c presents the 5 possible cyclic flows for a unidirectional square circuit. It is clear that the length and even knowledge of a partial time ordering of firing nodes in the transient quite clearly identify the stimulus, and the synchronized mode mainly serves as an indicator of the end of the transient.

Generalization of above homogeneous circuit results to *heterogeneous circuits* where the latency of neurons is taken into account is straightforward as discussed in [9].

## 6. Concluding remarks

The activity mode of the entire network cannot simply be described as a "Lego" of small connecting neural circuits with a given activity, since it is governed by a nonlocal quantity, the GCD. These findings challenge the emergence of significant topological motifs and the importance of their role in the functionality of the entire network [20] as well as the impact of statistical properties of complex neural circuits. Rather, they call for a reexamination of sources of correlated activity in cortex where addition/deletion of a connection or more realistically synaptic alternations that can induce transition between decaying and sustained activities can serve as a remote switching mechanism, and indicate that learning induced changes in some connections

affects the functionality of the networks more than others. The hypothesis that neural information processing might take place in the transient is suggestive of a much shorter time scale for the inference of a perceptual entity.

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