

# Coexistence of synchronized "oscillatory" and desynchronized "rate" activity in cortical networks

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## **Abstract**

The basis of MRI and PET experiments is the finding that neuronal cell firing levels are modulated in a task dependent manner. Results from EEG and MEG experiments on the other hand point to the importance of synchrony, *e.g.* the peak frequency may depend on the difficulty of the task. In most models only one of these activity modes of firing is desirable or possible to produce. In this work we show how a cortical microcircuit can produce either synchronized or desynchronized firing, and how this solves problems of present day rate and synchronization models.

# 1 Introduction

The basis of MRI and PET experiments is the finding that neuronal cell firing levels are modulated in a task dependent manner. Results from EEG and MEG experiments on the other hand point to the importance of synchrony, e.g. the peak frequency may depend on the difficulty of the task. A coexistence of synchronized and desynchronized activity in the same region is also consistent with the observation in local field potentials, that the synchronization is limited in time and is preceded and succeeded by epochs of desynchronized activity.

Seen on a cellular scale, pyramidal cells in a local region of neocortex may thus fire more or less synchronized. In most models only one of these activity modes of firing, synchronized or desynchronized, is generated. In some cases only one mode can be generated, in other cases only one mode is desirable, the other is viewed as destructive or at least non-productive. In this work we describe a model that can produce either of the two modes depending on the drive to different local interneurons. We also show advantages from having the two modes coexist in a network.

## 2 Features and problems of present day models

**Synchronization models** (Studied by Abeles, Bienenstock, Hertz, Singer *etc.* ) An advantage of synchronized (e.g. synfire chain) activity is its larger impact on a target cell, a desynchronized set of EPSPs may fail to elicit an action potential. Modulating the degree of synchrony may thus change the impact at the postsynaptic target without a need for change in rate. In synchronization models, one of the problems is how to keep a self-sustained activity for extended times (more than one or a few spikes). The proposed model offers the possibility to drive the synchronized population by desynchronized portions that have a stable activity.

**Rate models** (Studied by Amit, Brunel, Fransén, Fuster, Lansner *etc.* ) An advantage of a rate (e.g. attractor) model is that the persistent firing may provide a basis for recurrent feed-back to settle the activity according to synaptic efficacies tuned by learning. In rate models, one of the problems is how to end the activity, and for example to go to a new stable state. The proposed model offers the solution of termination by synchronization.

**Bump models** Bump models are used to model prefrontal cortex working memory (studied by Abbott,

Chow, Compte, Brunel, Tegnér, Wang *etc.* ), as well as M1 population vector activity [4], V1 orientation selectivity [5] and head direction cells [13]. One of the main problems in bump models is that a perturbation in the rate on one side of the bump, or including neuronal spike frequency adaptation or synaptic short term plasticity, will send the bump traveling (Fransén, and Lansner unpublished observations) and [6, 13]. In the proposed model, the bump may be stabilized by synchronized regions on the sides of the bump.

### 3 Cell and network model

Biophysical compartmental models of pyramidal cells and interneurons in cortex layer II/III were constructed. The cell models use Hodgkin-Huxley representations of intrinsic currents and 1-D diffusion models of the intracellular calcium. The cell morphology is reduced to 6 compartments. Simulations were done using the simulation package GENESIS.

The basic network is a set of pyramidal cells contacted by two different types of interneurons. It has 24 pyramidal cells and 4 interneurons of two types. Pyramidal cells are connected to the nearest 2 neighbors as well as to interneurons. The two types of interneurons connect to two different pools of 12 pyramidal cells. In the figures, the 3 upper interneurons connect to the upper pyramidal pool, the lower interneuron to the lower pool. The interneurons differ in their synchronizing effect on the pyramidal cells as described in the next section. A pyramidal cell contacts the two types of interneurons as well as other pyramidal cells. Anatomically, this is consistent with the synaptic triade as described in White [11]. Depending on the individual balance of inputs to the interneurons, a group of pyramidal cells may either synchronize or desynchronize when activated by afferent excitatory input or local recurrent activity.

### 4 Mechanisms of synchronization and desynchronization

Interneuron types show specificity in their localization on target pyramidal cells. Further, there are interneurons with only a  $GABA_A$  component [7]. If dendritic localization, IPSP decay time constant ( $GABA_A$  or  $GABA_B$ ), synaptic efficacy or release probability varies among the contacts on pyramidal cells, the IPSP of the interneuron may be able to delay the upcoming spike of the pyramidal cell to a variable extent, and thereby desynchronize or synchronize the pyramidal cells to variable extents.

Based on this type of data, a number of mechanisms for synchronization have been proposed, including fast  $GABA_A$  synapses [9], IPSP doublets [12] and short-term synaptic plasticity [8]. Likewise, a number of

mechanisms for desynchronization have been proposed, including distal synaptic placement [3], modulator reduced spike frequency adaptation [2], and slow NMDA-like EPSPs [2, 10].

We will here show that a local circuit of pyramidal cells, which are contacted by different types of interneurons, may either synchronize or desynchronize. Which activity mode that dominates is controlled by differences in drive onto the interneuron types. This drive may be external afferent input or local activity in the network. Thus, the same circuit can produce either type of activity, and different groups of pyramidal cells will subsequently interact on the basis of their firing mode.

In the present model, using moderate sized IPSPs, the interneuron giving somatically located  $GABA_A$ -type synapses produces a desynchronized pyramidal cell population, and the interneuron with dendritically located mixed  $GABA_{A/B}$  synapses produces a synchronized population. We suggest that a slow time constant, here decay of  $GABA_B$ , produces a slow repolarization upon which fast depolarizations, here recurrent pyramidal inputs, produce a synchronizing effect of the type described by Ekeberg [1].

Using these mechanisms for synchronization and desynchronization, we have studied if synchronized and desynchronized activity can coexist but stay separated. In Fig. 1, we show an example of how synchronized and desynchronized populations can coexist in the same network without interfering or enforcing its own activity pattern on the other population. Different types of inhibitory input produces synchronization and desynchronization respectively.

**(figure 1 somewhere here)**

We have also studied how a population of desynchronized cells can drive activity in a synchronized population, as well as how synchronizing a desynchronized population can end the activity. In Fig. 2, we show an example of how persistent rate activity is ended by synchronized activity. At time 1.4 sec the inhibitory input is changed to the synchronizing type. We also demonstrate that persistent rate activity can drive the neighboring synchronized cells to spiking, but that the synchronizing cells themselves can not sustain any activity. Thus, a synchronized population can prevent rate activity to spread, and could therefore stabilize the position of a bump.

**(figure 2 somewhere here)**

## 5 Discussion

We have shown how a cortical microcircuit can generate both synchronized and desynchronized activity depending on the excitability or synaptic drive onto the interneurons. In this model, fast IPSPs produce

desynchronized and slow IPSPs produce synchronized activity. The model displays the following features:

- 1) Coexistence: One and the same network can generate synchronized as well as desynchronized activity.
- 2) Stabilization of bump: Synchronizing regions surrounding a rate “bump” may prevent the bump to drift.
- 3) Input drive: Desynchronized regions may provide the continuous input to maintain synchronized activity.
- 4) End of rate activity: A shift toward synchronization can end the persistent activity in a rate model.
- 5) Stop of propagation: A shift toward desynchronized activity can prevent cells (in a synfire chain) from producing spiking at their target cells.

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Fig. 1

(top)

Bands of desynchronized activity do not invade the synchronized population. The synchronized activity does not lead to synchronicity in the desynchronized population. Note that there is no apparent difference in average frequency between the synchronized and the desynchronized population. Activity starts desynchronized by differential timing of onset of the external input. Top 4 cells are interneurons. Soma membrane potential v.s. time (sec).

(middle)

Spike histogram of upper 12 pyramidal cells. These cells receive input from the top 3 interneurons. The input is medially at the dendrite and is of a mixed  $GABA_A$  and  $GABA_B$  type. Using 3 interneurons could have enabled a larger variation in spike timing, but synchronization dominates. Spikes per bin v.s. time (sec). Bin width is 15 ms.

(bottom)

Spike histogram of bottom 12 pyramidal cells. These cells receive input from the lowest interneuron. The input is at the soma and is of the  $GABA_A$  type. Using only 1 interneuron could have enabled synchronization, but desynchronization dominates. Spikes per bin v.s. time (sec). Bin width is 15 ms.

Fig. 2

(top)

To facilitate persistent rate activity, the network has, relative to Fig. 1, stronger intrinsic connections between pyramidal cells. Input is weaker relative Fig. 1, and is subthreshold to the synchronizing cells to show how these cells can be driven by the desynchronized cells. Soma membrane potential v.s. time (sec).

(bottom)

Spike histogram of pyramidal cells. Note that input onset is simultaneous to all cells, this does however not lead to synchronized activity in the desynchronized population (lower 12 cells). The rate varies from 5 to 40 Hz depending on the location, cells near the borders (top and bottom) have fewer inputs from neighbors. Spikes per bin v.s. time (sec). Bin width 15 ms.

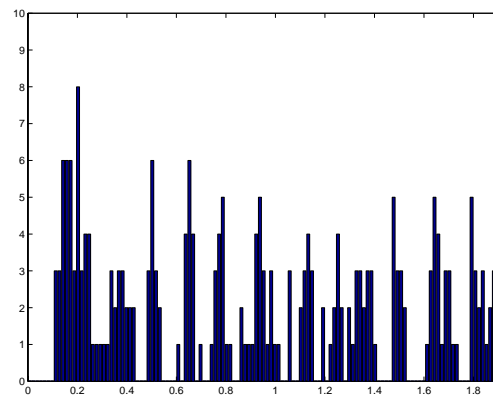
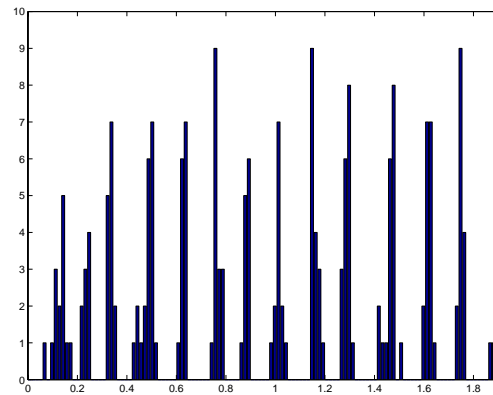
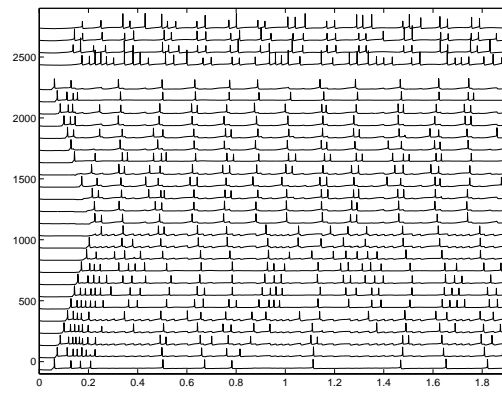


Figure 1:



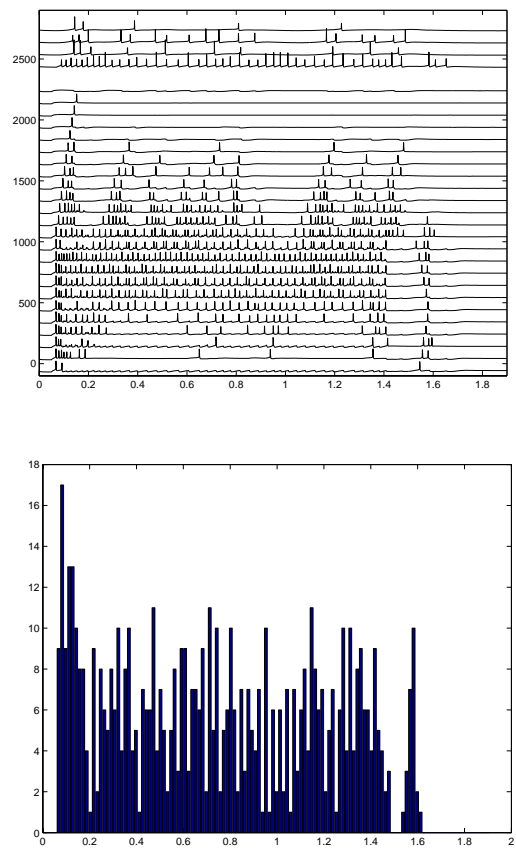


Figure 2: