

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

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Abstract

The basis for 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 points to the importance of synchrony. There may for instance be a shift in peak frequency depending on the difficulty of a cognitive task. In most models only one of these activity modes of firing is desirable, the other is viewed as destructive or at least non-productive. In this work we discuss the possibility to benefit from having the two modes coexist.

Introduction

The basis for 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 points to the importance of synchrony. There may for instance be a shift in peak frequency depending on the difficulty of a cognitive task.

Seen on a smaller 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 is desirable, the other is viewed as destructive or at least non-productive. In this work we discuss the possibility to benefit from having the two modes coexist.

A number of mechanisms to produce either synchronized or desynchronized activity have been proposed over the years. We will here build upon the assumption that a local circuit of pyramidal cells, which are contacted by two different types of interneurons, may either synchronize or desynchronize. Which activity mode that dominates is controlled by external afferent input and local activity in the network onto the interneurons. Thus, the same circuit can produce either type of activity, and different groups will interact on the basis of their firing mode.

Problems in single activity mode models

In synchronization models (Singer, Abeles, Hertz, Bienenstock etc), one of the problems is how to keep them going for extended times (more than one or a few spikes). In previous work sparse recurrency has been proposed as a solution. The proposed model offers the possibility to drive the synchronized population by desynchronized portions that have a stable activity.

In rate (attractor) models of cortical associative memory (Fransén and Lansner, Amit, Brunel, Fuster etc), one of the problems is how to end the activity, and for example to go to a new state. In previous work

inclusion of short term synaptic plasticity or cellular adaptation has been proposed. The proposed model offers the solution of termination by synchronization.

There is a popular special case of rate model, the bump model. Bump models are used to model prefrontal cortex working memory (Abbott, Wang, Tegnér, Compte, Brunel, Chow etc), M1 population vector direction (Lukashin and Georgopoulos 1993), V1 orientation selectivity (Sompolinsky 2001) and head direction cells (Zhang 2001). 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, Tegnér 2000, Zhang 2001). Previous work on bump stabilization includes using multiple types of interneurons (Tegnér and Wang 2000) or network asymmetry (Zhang 2001). In the proposed model, the bump may be stabilized by synchronized regions on the sides of the bump.

Mechanisms of synchronization and desynchronization

A number of mechanisms for synchronization have been proposed, including fast GABA_A synapses (van Vreeswijk, Abbott and Ermentrout 1994), IPSP doublets (Whittington, Traub, Kopell, Ermentrout and Buhl 2000) and short-term synaptic plasticity (Tsodyks, Uziel and Markram 2000).

Likewise, a number of mechanisms for desynchronization have been proposed, including distal synaptic placement (Lansner and Fransén 1992), modulator reduced spike frequency adaptation (Fransén and Lansner 1995), and slow NMDA-like EPSPs (Wang 1999).

More specifically, interneuron types show specificity in their localization on target pyramidal cells. Thus, interneurons with somatic (ie basket) or axon hillock (ie axo-axonic) localization may give a more pronounced synchronizing "reset" of the pyramidal cell. If dendritic localization (bitufted), synaptic efficacy and/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 the pyramidal cells.

Further, there are interneurons with only GABA_A or GABA_B components (Thomson and Destexhe 1999). Thus, cell types with only fast GABA_A inhibition may synchronize pyramidal cells and those with slow GABA_B may desynchronize.

The basic network is here a group of pyramidal cells contacted by two different types of interneurons. The interneurons differ in their synchronizing effect on the pyramidal cells as described above. The pyramidal cell contacts the two interneurons as well as other pyramidal cells. Anatomically, this is consistent with the synaptic triade as described in White (1989).

Additionally, there may also be a third type of interneuron (ie double bouquet) that contacts one or both of the other two types of interneurons (figure 1). This disinhibition may also shift the balance between the two interneurons.

Mechanisms for activity state modulation

Depending on the balance between the inputs from the two interneuron types on the pyramidal cells, the group of pyramidal cells either synchronize or desynchronize when activated by afferent excitatory input or local recurrent activity. With a changed afferent input to one or both of the interneuron types the balance can be changed. There may also be intrinsic connections between the pyramidal cells and the two (three) interneuron types that can shift the balance.

Also, differential effects of modulation on the different cell types may shift larger regions in favor of either state. A second role of modulators in synchronization could be to up- or down regulate a hyperpolarizing current, responsible for post hyperpolarization rebound spiking, in the pyramidal cell.

Discussion

A coexistence of bumps and fronts (waves of synchronized activity will here be termed fronts) is consistent with the observations in experiments focusing on synchronization, that the synchronization is limited in time and is preceded and succeeded by epochs of desynchronized activity. The fade in and out of synchronization may arise from fronts and bumps passing by the point of the recording electrode.

Finally, do we have to think simplistically in terms of a rate bump limited by synchronization boundaries, or synchronization fronts driven by desynchronized activity? Take a spatiotemporal pattern impinging on a collection of groups of pyramidal cells that can either synchronize or desynchronize. Present and recent input, diversified synaptic efficacies (memory) and modulatory drive decide what mode a group is in. Propagation of bumps and fronts in a "landscape" limited by the opponent mode. We thereby have a duality of computation by synchronization fronts and rate bumps. Fronts execute the position of bumps, or the transition between attractor states in a rate model. Desynchronized regions drive the trajectory of fronts.