

# CORTICAL DYNAMICS – EXPERIMENTS AND MODELS

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Electrophysiological studies of cortical function on the basis of multiple single-neuron recordings reveal neuronal interactions which depend on stimulus context and behavioral events. These interactions exhibit dynamics on different time scales, with time constants down to the millisecond range. Mechanisms underlying such dynamic organization of the cortical network were investigated by experimental and theoretical approaches. We review some recent results from these studies, concentrating on the occurrence of patterns of precisely timed spikes in cortical activity, both in physiology and in neural network models.

## 1 Introduction

Modern approaches to understand the mechanisms of higher brain function are increasingly concerned with neuronal dynamics. The task of organizing perception and behavior in a meaningful interaction with the external world prompts the brain to recruit its resources in a properly orchestrated manner. Contributions from many elements, ranging from individual nerve cells to entire brain areas, need to be coordinated in space and time. Our principal research goal is to understand how this organization is dynamically brought about, and how the brain uses such coordinated activity of neurons. To this end, we study the spatio-temporal organization of cortical activity recorded at many different sites at a time. The rules that govern this organization and the underlying mechanisms are brought to light by complementary approaches of neurobiological experimentation, advanced data analysis, and mathematical modeling.

According to the classical view, firing rates play a central role in neural coding [Barlow 1972, 1992]. The firing rate approach indeed led to fundamental insights into the neuronal mechanisms of higher brain function [Georgopoulos et al. 1993, Hubel and Wiesel 1977, Newsome et al. 1989]. In parallel, however, a different concept was developed, according to which the temporal organization of spike discharges within functional groups of neurons, so-called ‘cell assemblies’ [Hebb 1949], also contribute to neural coding [Von der Malsburg 1981, Abeles 1982a, 1991, Gerstein et al. 1989, Palm 1990, Singer 1993]. It was argued that the biophysics of synaptic integration favors coincident presynaptic events over asynchronous events [Abeles 1982b, Softky and Koch 1993]. Accordingly, synchronized spikes are considered as a property of neuronal signals which can be detected and propagated by other neurons. In addition, these spike correlations must be expected to be dynamic, reflecting varying affiliations of the neurons depending on the stimulus or behavioral context. Such dynamic modulations of spike correlation at different levels of precision have in fact been observed in a variety of cortical areas, amongst others visual [Eckhorn et al. 1988, Gray et al. 1989; for reviews see Engel et

al. 1992, Aertsen and Arndt 1993; Singer and Gray 1995, Roelfsema et al. 1996], auditory [Ahissar et al. 1992, Eggermont 1994, De Charms and Merzenich 1995, Sakurai 1996], somato-sensory [Nicoletis et al. 1995], motor [Murthy and Fetz 1992, Sanes and Donoghue 1993], and frontal [Aertsen et al. 1991, Abeles et al. 1993a,b, Vaadia et al. 1995, Prut et al. 1998]. Little is known, however, about the functional role of temporal organisation in such signals.

First important hints towards the importance of accurate spike patterns come from the work of Abeles and colleagues [Abeles et al. 1993a,b, Prut et al. 1998]. They observed that multiple single-neuron recordings from the frontal cortex of awake behaving monkeys contain an abundance of precisely timed spike patterns. These patterns had a total duration of up to several hundred milliseconds and repeated with an internal precision of  $\pm 1$  ms. Moreover, these patterns occurred in systematic relation to sensory stimuli and behavioral events. We investigated the mechanisms underlying such dynamic organization of the cortical network by experimental and theoretical approaches. Here, we present evidence—both from experimental data and from model studies—that volleys of precisely synchronized spikes can propagate through the cortical network in a stable fashion, thereby serving as building blocks for spatio-temporal patterns of precisely timed spikes. Taken together, these findings support the hypothesis that precise synchronization of individual action potentials among groups of neurons is an inherent mode of cortical network activity.

## 2 ‘Unitary Events’ in Cortical Multiple Single-Neuron Activity

It has been proposed that cortical neurons organize dynamically into functional groups, the so-called ‘cell assemblies’ [Hebb 1949, Gerstein et al. 1989]. It is widely assumed that this functional organization is reflected by the temporal structure of the spiking activity of the neurons involved. Thus, cortical activity would be characterized by synchronous spike volleys, traveling through the sparsely firing cortical network (‘synfire chain’ hypothesis [Abeles 1982a, 1991]). In order to test this hypothesis, we analyzed multiple single-neuron recordings from various cortical areas for the presence of excessive coincident spike events among the recorded neurons. We refer to such conspicuous coincidences as ‘unitary events’, and define them as those joint spike constellations that occur more often than expected by chance [Grün et al. 1994, Grün 1996]. The functional significance of such unitary coincident events was tested by investigating their occurrence and composition in relation to sensory stimuli and behavioral events.

### 2.1 ‘Unitary Event’ Analysis

We developed a method that detects the presence of conspicuous spike coincidences and evaluates their statistical significance, taking into account the non-stationarities in the firing rates of the neurons involved (details and calibration are described in [Grün 1996]). Briefly, the detection algorithm works as follows: The simultaneous observation of spiking events from  $N$  neurons can be described mathematically by the joint process, composed of  $N$  parallel point processes. By appropriate binning,

this can be transformed to an  $N$ -fold (0,1)-process, the statistics of which is described by the set of activity vectors reflecting the various (0,1)-constellations that occurred across the recorded neurons. Under the null-hypothesis of independently firing neurons, the expected number of occurrences of any activity vector and its probability distribution can be calculated analytically on the basis of the single neuron firing rates. The ‘mutual dependence’ measures the degree of deviation from independence among the neurons by comparing these theoretically derived probabilities with their empirical values. Those activity vectors that violate the null-hypothesis of independence define potentially interesting occurrences of joint events; their composition defines the set of neurons which are momentarily engaged in synchronous activity.

In order to test the significance of such unitary events, we developed a new statistical measure: the ‘joint-p-value’. For any particular activity vector, this joint-p-value measures the cumulative probability of observing the actual number of coincidences or an even larger one by chance. Finally, in order to account for non-stationarities in the discharge rates of the observed neurons, modulations in spike rates and coincidence rates are determined on the basis of short data segments by sliding a fixed time window (typically 100 ms wide) along the data in steps of the coincidence binwidth. This timing segmentation is applied to each trial, and the data of corresponding segments in all trials are then analyzed as one quasi-stationary data set, using the appropriate rate approximation.

## 2.2 ‘Unitary Events’ in Motor Cortex

In collaboration with Alexa Riehle (CNRS, Marseille, France) we tested the hypothesis that such precise synchronization of individual action potentials among groups of neurons in the monkey motor cortex is involved in dynamically organizing the cortical network during the planning and execution of voluntary movements [Riehle et al. 1997].

We found that simultaneously recorded activities of neurons in monkey primary motor cortex indeed exhibited context-dependent, rapid changes in the patterns of coincident action potentials during performance of a delayed-pointing task. Accurate spike synchronization occurred in relation to external events (visual stimuli, hand movements), commonly accompanied by discharge rate modulations, however, without precise time-locking of the spikes to these external events. Accurate spike synchronization also occurred in relation to purely internal events (stimulus expectancy), where firing rate modulations were distinctly absent. These findings indicate that internally generated synchronization of individual spike discharges may subserve the cortical organization of cognitive motor processes. The systematic correlation of timing and composition of the spike coincidences with behavioral events presents a clear indication of their functional relevance [Riehle et al. 1997; see also Fetz 1997].

## 2.3 Summary and Conclusions

Taken together, these findings demonstrate the existence of precise ( $\sim 5$  ms) synchronization of individual spike discharges among selected groups of neurons in

the motor cortex. This synchronization is associated with distinct phases in the planning and execution of voluntary movements, indicating that it plays a functional role. Moreover, these findings suggest that under behavioral conditions as investigated in this study, the brain uses different strategies in different contextual situations: In order to process a purely cognitive, i.e. an internal and behaviorally relevant event, neurons preferentially synchronize their spike occurrences without changing, at the same time, their firing rates. By contrast, when processing an external, behaviorally relevant event, neurons tend to synchronize their spikes and modulate their firing rates at the same time. Thus, precise synchronization of spike events and modulation of discharge rate may serve different and complementary functions. They act in conjunction at some times, not at others, depending on the behavioral context [Riehle et al. 1997].

### **3 Conditions for Stable Propagation of Synchronous Spiking Activity in Cortical Networks**

In a complementary, model-oriented study we explored the mechanisms underlying the rapid synchronizations of cortical spiking activity observed in simultaneous multiple single-neuron recordings. Specifically we focused on the explanation for the excessive occurrences of highly accurate ( $\pm 1-3$  ms) spike patterns [Abeles et al. 1993a,b, Riehle et al. 1997, Prut et al. 1998]. Such patterns were observed both in frontal cortex and in motor cortex neurons of awake behaving monkeys; in both cases their occurrence was systematically related to behavior.

#### *3.1 Synfire Chains and Pulse Packets*

On the basis of the characteristic anatomy and physiology of the cortex, Abeles [1982a, 1991] proposed that ‘synfire’ activity, which propagates in volleys through the sparsely firing cortical neural network, presents a natural explanation for the occurrence of precise spike patterns. We have investigated the conditions under which such synchronous volleys of action potentials can propagate reliably through the cortical network [Aertsen et al. 1996]. The theoretical approach we adopted combined analytical calculations with extensive network simulations [Diesmann et al. 1995].

Existing measures for the efficacy of synaptic transmission concentrate on two limiting cases: full synchrony and random arrival of spikes. Intermediate cases with a realistic degree of temporal dispersion are hardly addressed. To overcome these restrictions and to quantify the degree of temporal synchrony in propagating volleys of spike activity we introduced the concept of ‘pulse packets’ [Diesmann et al. 1996]. A pulse packet is a probabilistic description of the spiking activity of a group of neurons, represented by a pulse density function. This density function is characterized by two parameters: the ‘activity’, defining the number of spikes in the volley, and the ‘width’, defining their temporal dispersion. For a single realisation of a pulse packet, the activity is measured by simply counting the number of spikes, the width is measured by the standard deviation of the pulse distribution.

### 3.2 *Neural Transfer Function and Synchronization Dynamics*

Adopting this approach, we studied the response behavior of a model cortical neuron to input activity with varying degrees of synchrony by presenting stimulation pulse packets with different choices of the ‘activity’ and ‘width’ parameters. From the model neuron we recorded the response (time of first spike), collected in a PST-histogram over many trials. After normalization for the number of trials, the resulting output distribution was again described as a pulse packet, and the associated pulse density, along with the values of the activity and width were determined. The resulting neural transfer function which describes the input-output relation between incoming and outgoing pulse packets were visualized in a so-called iterative map. This map yields a compact characterization of the neuron’s response to transient input. In contrast to earlier approaches where the neuron’s firing probability is measured quasi-statically as a function of DC-current, this new transmission function takes full account of the dynamic properties of the input distribution [Aertsen et al. 1996].

The temporal evolution of a pulse packet as it travels through the network can be traced by iterating the transfer function. Keeping the width of the chain fixed at a value in the order of 100 neurons, the dynamics of the two-dimensional iterated system is characterized by two fixed points: an attractor and a saddle point. Accordingly, the state space has two separate domains. Within one of these domains, there is stable propagation of pulse packets towards the attractor, which represents a very narrow packet of invariant shape. The parameters of this stable pulse packet are independent of the initial pulse packet provided the latter is taken from a certain range of parameters. For all other initial configurations, the result is eventual extinction of activity [Diesmann et al. 1997]. By contrast, for a too small number of neurons per group, both fixed points disappear and all trajectories lead to extinction. Synchronous spiking then is no longer a viable option for the network. Important aspects of these synchronization dynamics can be dissected and understood with the help of an analytical model [Gewaltig et al. 1997].

### 3.3 *Summary and Conclusions*

Assuming realistic values for the architectural and physiological parameters, our model predicts that the cortical network is able to sustain stable propagation of synchronous spike volleys consisting of spikes from 50-100 neurons with a temporal precision of about 1 ms. Preliminary evidence from additional computer simulations suggests that this synchronization dynamics is strongly influenced by the activity climate in the surrounding network. In particular, the robustness and the propagation velocity of the synchronous spike volleys exhibit a non-monotonic dependence on the level of background activity. This result has interesting consequences in view of recent findings regarding the relation between ongoing network activity and the variability of evoked responses, both in cortical activity and in behavioral responses [Arieli et al. 1996a,b].

## 4 Synchronization Dynamics in Recurrent Networks

We also studied the spatio-temporal dynamics of spiking activity in cortical network models with recurrent synaptic architecture. The dynamics in such networks give clues to the interplay that might result from the simultaneous activity of many pulse packets traveling through the cortical network [Rotter and Aertsen 1998].

### 4.1 *Spatio-Temporal Patterns of Precisely Timed Spikes*

We used a network model, which is based on interacting stochastic point processes [Rotter 1994, 1996]. Such systems can be formally described in terms of a Markov process, the dynamic state of which at a given point in time is the spatio-temporal pattern of previously generated spikes. The transition probabilities specify how the pattern gradually evolves in time. A generalized type of integrate-and-fire dynamics thereby emerges as a mathematical consequence of the assumption that neurons communicate by action potentials. Assuming the existence of infinitesimal spike probabilities, which is in fact a very mild condition for physical systems, the corresponding dynamic equations could be completely solved [Rotter 1996].

The solutions for special cases have been used to identify some important model parameters from electrophysiological recordings of real neurons. A simple parametric characterization of single neuron function is in fact achieved by fitting the model to the discharge behavior of various types of cortical pyramidal cells. Several fundamental properties of recurrent cortex-like networks assembled from such neurons can be readily predicted, most notably their ability to maintain stable low rates of activity without the help of inhibitory neurons [Rotter and Aertsen 1997]. Furthermore, computer simulations of random-topology, but otherwise realistic cortical networks indicate that high precision spatio-temporal patterns, embedded in periods of enhanced cooperative group activity, may play a role for coding and computation in such networks. This is true, even if neither the anatomy of the network nor the physiology of its neurons are in any sense specifically designed for that purpose [Rotter 1996].

### 4.2 *Plasticity of Precise Time Structure*

Plasticity of the temporal structure of patterns of precisely timed spikes is achieved by introducing Hebb-like synaptic plasticity into the network. The phenomena observed in a number of experiments concerning the influence of local synaptic modification on the spatio-temporal dynamics in recurrent networks allow a number of conclusions [Rotter and Aertsen 1995, Rotter 1996]. Consistent with recent experimental findings [Markram and Tsodyks 1996, Markram et al. 1997], learning rules can be formulated which only use local information, without the necessity for explicit renormalization of total synaptic transmission. Rapid convergence of synaptic strengths can be achieved while stable global activity is maintained. Convergence can be extremely fast, within a few presynaptic action potentials. The reason is that the pre-existing (random) patterns of activity are ‘re-used’ or only slightly modified until the correlation structure of the stimulus input is matched. Learning affects only the microscopic time scale, i.e., there is plasticity of time struc-

ture in the millisecond range. In fact, the Hebbian time window defining temporal coherence is determined both by the dynamics of after-hyperpolarization in the post-synaptic neuron and by the lowpass properties of the synapse. Modification of a synapse can be enabled and disabled by controlling the rate of the presynaptic neuron. Thereby, a more global strategy of supervised learning is achieved by letting pools of dedicated instructor neurons control firing rates within the network, depending on some reward condition. The learning of input-output association may take place in terms of a stochastic exploration of error gradients. Again, this amounts to a completely local processing of global information.

### 4.3 Summary and Conclusions

Our findings indicate that the degree of irregularity of neuronal spike trains is primarily a reflection of the network dynamics. Spatio-temporal patterns of precisely timed spikes are a consequence of these network dynamics. The introduction of Hebb-like synaptic plasticity induces a plasticity of the precise spike patterns. A scenario for the functional relevance of these spatio-temporal spike patterns and their plasticity is subject of current investigation.

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