Workshop Network Synchronization: from dynamical systems to neuroscience

19-30 May 2008 Lorentz Center Leiden

Abstracts
in 3 groups, per group authors in alphabetical order

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Tutorial Lectures

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An overview of research on gamma-band synchronization
Pascal Fries

Neuronal gamma-band synchronization is a fundamental property of activated neuronal networks. It has been found in species ranging from honeybees to humans and in networks ranging from the retina to the prefrontal cortex. It has been implicated in several specific cognitive functions, especially perceptual binding, attentional selection, working memory maintenance and long-term memory encoding. I will critically review the experimental evidence that has been provided both in favor and against those functions.

Attentional selection through selective neuronal synchronization
Pascal Fries

Neuronal synchronization is pervasive in our nervous system and has been implicated in numerous functions. Yet to fulfill any function, it must have consequences for neuronal processing. I will demonstrate that synchronization profoundly modulates neuronal interactions, and that this mechanism sub serves attentional selection. While synchronization emerges from the interactions of neurons, it also affects those interactions, and thereby shapes our behavior.

Overview of recurrent network models
David Hansel

I will review several dynamical properties of recurrent neuronal networks in the context of a simplified model of a cortical circuit. Then I will focus on mechanisms underlying neural activity in the gamma frequency band (30-70 Hz) which have been observed in in the neocortex and in the hippocampus. It has been suggested that these oscillations are generated within local networks of GABAergic interneurons. This hypothesis is supported by in vivo and in vitro experiments as well as by previous modeling studies. Interestingly, gamma oscillatory episodes in vivo are short-lived and lose temporal coherence over the scale of several tenths of a millisecond. This decoherence could be the result of noisy fluctuating inputs extrinsic to the cortex. However this would require substantial spatial correlations in these fluctuations on the scale of the local circuits generating the rhythm. Another possibility is that the temporal decoherence is generated intrinsically within the local inhibitory circuits. I will present a simplified three dimensional model for a piece of cortex. In this model local inhibitory interactions between GABAergic interneurons generate gamma oscillations and I will show that interactions between cortical layers as well as long-range horizontal intra-layer interactions can induce temporal decoherence of the activity. In the context of visual cortex this model predicts that the temporal coherence of gamma activity in V1 can be controlled by spatial patterns of visual stimuli.

Synchronization through chemical and/or electrical coupling
David Hansel

In-vivo and in-vitro experimental studies have found that blocking electrical interactions connecting GABAergic interneurons reduces oscillatory activity in the gamma range in cortex. However, recent theoretical works have shown that the ability of electrical synapses to promote or impede synchrony, when alone, depends on their location on the dendritic tree of the neurons, the intrinsic properties of the neurons and the connectivity of the network. I will review these works and will then show that this versatility in the synchronizing ability of electrical synapses is greatly reduced when the neurons also interact via inhibition.

Analysis of neurons and synapses in the hippocampus: A view from the presynaptic terminal
Peter Jonas

Our knowledge about the mechanisms of synaptic transmission is based on the highly detailed analysis of a small number of model synapses, such as the squid giant synapse or the calyx of Held. However, our knowledge about glutamatergic synaptic transmission in cortical circuits including the hippocampus is much more limited. One of the reasons is that cortical presynaptic terminals are largely naccessible to direct recording, unlike the squid giant synapse or the calyx. We have iteratively improved patch-clamp techniques in brain slices, which finally allowed us to record from presynaptic terminals (mossy fiber terminals) and axonal processes (mossy fiber axon blebs). Direct analysis revealed several surprising properties of hippocampal mossy fiber terminals and axons. For example, we have found that presynaptic action potentials show substantial broadening during repetitive stimulation. Furthermore, capacitance measurements of mossy fiber terminals revealed that the size of the releasable pool is very large. This may explain the capability of mossy fiber synapses to undergo substantial changes in synaptic strength. Finally, we determined the locus of action potential initiation in mossy fiber axons. Our results show that action potentials are generated at a distance of 20 – 30 µm from the soma of the granule cells.

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Synchronization and oscillations in the hippocampus: The role of parvalbumin-expressing basket cells
Peter Jonas

Parvalbumin-expressing basket cells (BCs) play a key role in the function of neuronal networks. These cells operate as fast signaling devices, showing a fast excitatory input, a fast-spiking action potential phenotype, and a fast inhibitory output on their target cells. Parvalbumin-expressing BCs contribute to fast feedback and feedforward inhibition and also play a key role in the generation of network oscillations in the gamma frequency range. As inhibitory synapses between interneurons are thought to be particularly important for the generation of gamma oscillations, we studied the properties of BC-BC synapses, using paired recordings between synaptically connected neurons in slices. In contrast to previous views, which suggested that inhibition is slow, weak, and hyperpolarizing, we found that inhibition at BC-BC synapses was fast, strong, and shunting. Based on these experimental observations, we have developed a ‘reality-based’ interneuron network model and studied the ability of this model to generate coherent gamma oscillations when exposed to a tonic excitatory drive. Surprisingly, we found that fast, strong, and shunting synapses led to efficient synchronization if combined with a short synaptic delay. Realistic synaptic properties made the model more robust against heterogeneity in the excitatory drive.

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Emergence of collective behavior and synchronism in large networks of coupled phase oscillators
Edward Ott

Synchronization of large systems of coupled oscillators is a basic issue in settings ranging from brain function, to electrical circuits, to laser arrays, etc. This lecture will begin with a review of the paradigmatic Kuramoto model of globally coupled phase oscillators where each oscillator has a different intrinsic frequency drawn from some prescribed probability distribution function [Ott 2002]. We then introduce concepts of network connectivity and formulate the problem of phase oscillators coupled on a network. The problem is analyzed in three stages of approximation. It is found that the effect of network topology on synchronization is mainly charac- terized by the largest eigenvalue of the network adjacency matrix. Based on this, one can assess the influence upon synchronizability of such network attributes as di- versity in the number of connections to network nodes, spread in the link strengths, and the tendency for highly connected nodes to connect to other highly connected nodes (assortativity).

References

Section 6.6 of the book Chaos in Dynamical Systems by E. Ott (Cambridge Univ. Press, 2002) contains a review of the Kuramoto model.
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Emergence of collective behavior in networks of dynamical systems
Edward Ott

After a review and introduction of the sub ject, this lecture will be devoted to investigations of large systems of coupled heterogeneous dynamical systems. The first part of the lecture will deal with how interactions with external drivers influence the dynamics. Examples in this category include the interaction of the walking dynamics of pedestrians on Londonâ€™s Millennium Bridge that lead to unexpected violent oscillations of the bridge [Strogatz et al 2005, Eckhardt et al 2007] circadian rhythm governing the sleep-awake cycle of animalsthrough the coupling of many oscillatory neurons in the brainâ€™s superchiasmatic nucleus influenced by the daily 24 hour variation of sunlight [Antonsen et al], etc. The second part of the talk will be devoted to the study of systems of many coupled heterogeneous dynamical systems, including cases where the coupled systems can be chaotic. As the coupling strength is increased, a transition from incoherent to coherent collective behavior is typically observed. A general theory for this transition will be presented [Ott et al 2002, and Baek and Ott 2004]. An important point is that the macroscopic (i.e., averaged) system behavior is typically periodic even if the systems that are coupled behave chaotically. We present a treatment for the case of global coupling and then indicate how it can be generalized to situations with nontrivial network topology [Restrepo et al 2006].

References

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Low dimensional behavior of large systems of globally coupled oscillators: exact solution of the Kuramoto model and generalizations
Edward Ott

It is shown that, in the infinite size limit, certain systems of globally coupled phase oscillators display low dimensional dynamics. In particular, we derive an explicit finite set of nonlinear ordinary differential equations for the macroscopic evolution of the systems considered. For example, an exact, closed form solution for the nonlinear time evolution of the Kuramoto problem with a

Lorentzian oscillator frequency distribution function is obtained. Low dimensional behavior is also demonstrated for several extensions of the Kuramoto model.

Introduction to synchronization concepts
Arkady Pikovsky

I give a general introduction to synchronization phenomena and their theoretical description, intended as a preparational for other, more involved lectures. After a historical introduction, I focus on synchronization on periodic oscillators due to external forcing and to coupling. Then the phase and complete synchronization types of chaotic oscillators are described. Manifestations of these phenomena in distributed media and in large populations are outlined.

Data analysis of coupled oscillations
Arkady Pikovsky

In many cases one wants to infer an information on the structure and dynamics of a complex system solely from the observations. I discuss an approach in this direction based on an assumption that the dynamics which underlines the observed bivariate data is due to coupled active oscillators. I show how one can reconstruct the dynamics in an invariant, observable-independent way, and characterize coupling of the elements.

Neural Networks with Dynamic Synapses
Misha Tsodyks

Synaptic transmission in the cortex is characterized by the activity-dependent short-term plasticity (STP), which can be broadly classified as synaptic depression and synaptic facilitation. As recent experiments indicate, different cortical areas exhibit variable mixes of facilitation and depression, which are also specific for connections between different types of neurons. In the first half of my presentation, I will describe the basics of dynamic synaptic transmission, its biophysical underpinnings and the ways it can be captured in biophysically motivated phenomenological models. I will also discuss some immediate implications of STP on information transmission between ensembles of neocortical neurons. In the second half of the presentation, I will focus on the effects of STP on the dynamics of recurrent networks and resulting neural computation. I will introduce the 'population spikes' (PSs), which are brief epochs of highly synchronized activity that emerge in recurrent networks with dominating synaptic depression between excitatory neurons. PSs can underlie some of the response properties of neurons in the auditory cortex. I will then describe the recently introduced idea that synaptic facilitation could be utilized in order to maintain information about the incoming stimuli in the facilitation level of recurrent connections between the targeted neurons, thus providing an effective mechanism for short-term memory for a period of several seconds after the termination of the stimulus.

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Focus & Contributed Talks

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Characterization of time-dependent event-related directional couplings

Ralph G. Andrzejak

The framework of nonlinear time series analysis comprises a variety of measures that allow extracting different characteristic features from complex dynamical systems. In particular, nonlinear interdependence measures estimate the strength and direction of couplings between two dynamical systems from pairs of signals derived from them (e.g. [1, 2]). This aspect is of high relevance for neuroscience because often multivariate signals are measured from different parts of the brain, and a reliable detection of directional couplings can contribute to the understanding of physiological or pathological processes. In particular, neuronal activity is often measured time-locked to multiple repetitions of a task, and it can be hypothesized that such paradigms result in transient event-related directional couplings between the involved brain areas. We here present a novel technique which can detect such transient event-related directional couplings from multiple realizations of a measurement. For this purpose, we have introduced the general concept of time-resolved causal statistics derived from embeddings across multiple realizations of time-dependent dynamics. While in a first implementation [3] we adapted a well-established conventional nonlinear interdependence measure [1] to serve as a time-resolved causal statistic and constructed surrogates from an unconstrained permutation of the order of realizations, we here discuss two important improvements. On the one hand we introduce a new nonlinear interdependence measure which is based on distance-rank statistics rather than directly on distances in reconstructed state spaces. We show that, in comparison to distance based measures, this rank based measure is to a lesser extend influenced by properties of the individual dynamics and thereby more specific for directional couplings. As a second improvement we introduce surrogates which are constructed from permutations of the realizations which are constrained to maintain the linear correlation across realizations. The inclusion of these linear correlations across realizations into the surrogatesâ€™ null hypothesis further improves the specificity of our approach for event-related directional couplings. In applications to mathematical model systems we demonstrate that our approach allows one to detect event-related directional couplings based on only a few tens of realizations. Couplings as short as one oscillation period of the dynamics can be detected. We show that the performance of this approach degrades smoothly with increasing noise levels. Importantly, the new rank based nonlinear interdependence measure is not restricted to the detection of event-related couplings but can readily be applied to conventional time-continuous time series. Furthermore, the constrained surrogates are not restricted to the combination with measures derived from reconstructed state spaces but can also be combined with across realization statistics based on instantaneous phases (e.g. [4]). Thereby, both improvements designed originally for the characterization of time-dependent event-related directional couplings are of wider applicability.

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Coherence of theta local field potentials in hippocampus and prefrontal cortex modulates prefrontal network activity during learning.

Karim Benchenane

Coherence of oscillations of local field potentials (LFPs) could serve as a synchronizing mechanism coordinating the timing of neuronal firing in different areas of the brain. For example even though theta rhythm activity is primarily observed in the hippocampus (Hpc), it appears in its output regions such as amygdala, striatum and prefrontal cortex (Pfc). Here, we analysed the relation between Hpc-Pfc theta coherence and learning in a Y-maze task with cross-modal strategy shifts. Furthermore we investigated the neuronal activity correlates during Hpc-Pfc theta coherence in order to better understand the impact of coherence on local processing. We show here that Pfc and Hpc LFPs in the theta band were most coherent when rats made response selection decisions in the maze (p<. 05, ANOVA). Furthermore this coherence was greater in behavioral trials following learning than before (p<. 05, two-ways ANOVA). Interestingly, at the single cell level, a subpopulation of cells in the Pfc was modulated by Hpc-Pfc coherence. Of 1531 neurons, 147 (9.6%) had increases or decreases of firing rate exceeding 50% during periods of strong Hpc-Pfc coherence. To study the relation between Hpc-Pfc coherence and ensemble activity in the Pfc, we analyzed the correlation matrix of activity of all neurons recorded simultaneously each day. We found that the number of significant correlations between pairs of Hpc theta modulated neurons in the Pfc was significantly enhanced during high coherence periods as compared to low coherence periods (p<. 05, Student t test). Altogether our data provides evidence that Hpc-Pfc theta coherence is elevated during decision making and learning and also modulates firing rate and coactivation of prefrontal neurons. This is consistent with our functional binding hypothesis and suggests that theta coherence could be important in the transmission of signals from hippocampus to Pfc for learning and memory consolidation. Acknowledgements: Supported by EC-contracts FP6-IST-027140 (BACS), -027017 (NeuroProbes), and -027819 (ICEA).

Excitability mediated by localized structures
Pere Colet

Localized structures in dissipative media have been found in a variety of systems, such as chemical reactions, gas discharges, or fluids. We discuss the instabilities that such localized structures, also called dissipative solitons, may undergo. In particular these structures may show excitable behavior even if the system is not locally excitable, so that excitability is property that emerges from the spatial dependence. The interaction of two localized structures in the oscillatory regime induces the displacement of the structures until they lock by the interaction of the tails leading to in-phase or out of phase oscillations or even to the coexistence of both. We also study the interaction of two structures in the excitable regime. We finally address the influence of noise showing that a single structure can exhibit coherence resonance.

From phase-locking to bursting in networks of gap junction coupled neurons
Stephen Coombes

The presence of gap junction coupling among inhibitory neurons of the neocortex has been appreciated for some time now. In recent years there has been an upsurge of interest from the mathematical community in understanding the contribution of these direct electrical connections between cells to large-scale brain rhythms. In this talk I will focus on a class of exactly soluble single neuron models, capable of producing realistic action potential shapes, that can be used to as the basis for understanding dynamics at the network level. In essence I will discuss planar piece-wise linear models that can mimic the firing response of both Type I and Type II cells. Under constant current injection periodic responses can be obtained in closed form, as indeed can the phase response curve (PRC), and conditions for stability (using Floquet theory). From the calculated PRC and the periodic orbit a phase interaction function can be constructed that allows the investigation of phase-locked network states using the theory of weakly coupled oscillators. For large networks with global connectivity I will also show how to develop a theory of strong coupling instabilities of the splay state. In this case an increase in the strength of gap junction coupling is shown to lead to large amplitude bursting oscillations in the mean membrane potential.

Absolute stability and complete synchronization in a class of neural fields models
Olivier Faugeras

Neural fields are an interesting option for modelling macroscopic parts of the cortex involving several populations of neurons, like cortical areas. Two classes of neural field equations are considered: voltage and activity based. The spatio-temporal behaviour of these fields is described by nonlinear integro-differential equations. The integral term, computed over a compact subset of $\mathbb{R}^q,\,q=1,2,3$, involves space and time varying, possibly non-symmetric, intra-cortical connectivity kernels. Contributions from white matter afferents are represented as external input. Sigmoidal nonlinearities arise from the relation between average membrane potentials and instantaneous firing rates. Using methods of functional analysis, we characterize the existence and uniqueness of a solution of these equations for general, homogeneous (i.e. independent of the spatial variable), and spatially locally homogeneous inputs. In all cases we give sufficient conditions on the connectivity functions for the solutions to be absolutely stable, that is to say asymptotically independent of the initial state of the field. These conditions bear on some compact operators defined from the connectivity kernels, the maximal slope of the sigmoids, and the time constants used in describing the temporal shape of the post-synaptic potentials. Numerical experiments are presented to illustrate the theory. To our knowledge this is the first time that such a complete analysis of the problem of the existence and uniqueness of a solution of these equations has been obtained. Another important contribution is the analysis of the absolute stability of these solutions, more difficult but more general than the linear stability analysis which it implies. The reason why we have been able to complete this work programme is our use of the functional analysis framework and the theory of compact operators in a Hilbert space which has allowed us to provide simple mathematical answers to some of the questions raised by modellers in neuroscience.

Emergent behavior of coupled non-linear oscillators
Prof. dr. C. Gielen

Oscillating activity is observed in many biological systems. Within living cells most oscillating mechanisms can be described by a Hodgkin-Huxley type mechanism, which typically includes a fast activation, followed by a slow inactivation. The dynamics of the excitable membrane is a good example of a non-linear (Hodgkin-Huxley type) oscillator. Coupling between spiking neurons can generate a broad range of oscillatory behaviour where neurons may fire in synchrony, 180 degrees out-of-phase, asynchronously, or even chaotically, depending on coupling strength and the range of oscillation frequencies of spiking. These phenomena have received much attention as they are thought to be important for intercellular communication and information transfer.
In addition to the Hodgkin-Huxley dynamics of the excitable membrane, which is responsible for action potentials, many cell-types also reveal intracellular calcium oscillations, which are due to intracellular Hodgkin-Huxley type oscillations of calcium stores. Like the spiking mechanism of two

neurons, which are electrically coupled by synapses, the non-linear oscillators of the excitable membrane and calcium stores are coupled by intracellular calcium.
In this presentation we will discuss the behaviour of coupled non-linear oscillators with special emphasis on i) intracellular communication and ii) intercellular communication, such as in coupled neurons and neuronal information processing. We will show that coupling of nonlinear oscillators causes multi-stability and hysteresis. This is highly important from a functional point of view.

A Coupled Oscillator Approach to Network and Single Cell Activity
Boris Gutkin

Synchrony of rhythmic neuronal firing has been of great interest in neuroscience for quite some time. To date, several mechanisms for the coherence and synchronization of oscillations in the various frequency band have been proposed. Some of these rely on local synaptic coupling, while others emphasize intrinsic cellular mechanisms. In this talk I will describe a mathematical framework for understanding the mechanisms leading to different phase-locked behaviors in networks of neuronal oscillators: the so-called weakly coupled oscillator approach. I will illustrate how this approach can be applied to understanding the influence the various biophysical phenomena on the mechanisms of synchrony (e.g. the spike generating dynamics and neuromodulation of there of, synaptic reversal potentials). Time permitting I will also describe our on-going efforts to understand dendritic oscillations using the coupled-oscillator framework.

Sparsely synchronized oscillations: theory and some experiments.
Vincent Hakim

Electrical recordings of brain activity show a diversity of neural rhythms. These neural oscillations reflect the synchronized discharge of a large number of neurons. They were first studied in the regime where neurons emit action potentials in a periodic fashion and behave as nonlinear oscillators. However, this classical synchronization regime is easily disrupted by noise and heterogeneity and, in several instances, it appears at odds with available experimental data on the discharge patterns of individual cells. Here, we discuss work performed in the past few years on a different mode of synchronization in which a fast collective oscillation is produced by neurons firing in a stochastic way and at a low rate compared to the oscillation period. We first show how these sparsely synchronized oscillations can be theoretically analyzed in the simple settings of rate models and networks of leaky integrate-and-fire neurons. We then show how various important neurophysiological features can be incorporated in this framework. We finally compare theory to available experimental results and especially focus on a recent study of 200Hz oscillation in the cerebellar Purkinje cell layer.

The influence of network oscillations on face responsive regions in the temporal lobe
Kari Hoffman

Neural oscillations are thought to play an important role in memory formation and attention to visual objects. Although oscillations appear in many types of neural circuits, and in numerous species, their presence in brain regions that process the faces of individuals is not well established. The gap in our understanding is striking given the prominent role of social stimuli in the content of our memories and as salient objects of our attention. I will describe neural population activity from the superior temporal sulcus (STS) of the macaque, in response to passively-viewed faces and objects and during rest. Time-frequency analysis of local field potentials reveals both stimulus-evoked and state-dependent changes in the frequency domain. Two behavioral factors that were associated with oscillatory activity in the STS were levels of arousal and saccadic eye movements. Decreasing levels of arousal led to consistent changes from high (>40Hz) to low (<4Hz) frequencies, as expected from the EEG literature. In contrast, the peri-saccadic modulations varied with electrode location, and included band-limited modulation from a variety of frequency ranges. Taken together, these results suggest that, rather than merely responding to preferred faces or objects, cells in the STS show a myriad of ongoing fluctuations in network activity that can modulate responses to preferred stimuli.

Oscillatory gamma activity in humans: from working memory to consolidation
Ole Jensen

While it has been proposed that feature binding is achieved by neuronal gamma band synchronization (30-100 Hz), the role of the gamma synchronization might extend beyond object representations. We employed a working memory paradigm in which subjects had to retain faces presented at various orientations. During the retention of faces orientations, we observed sustained gamma activity in the occipital cortex. This suggests that occipital gamma activity is important for maintenance of visual working memory. In a subsequent memory study we investigated gamma activity reflecting encoding and recall of pictures of landscapes and buildings. We found that occipital gamma activity predicted successful memory encoding. Finally, in a study on memory stabilization (consolidation) subjects learned to associate faces to specific locations on a screen. We later tested recall of the locations when only a face was presented. Stronger occipital gamma activity was observed for recall of recently but not remotely learned associations. In sum, occipital gamma activity can be induced not only by visual stimuli, but also by the recall or maintenance of memory representations. The gamma activity during long-term memory recall is possibly a consequence of a reconstructive process re-evoking the initial memory representation. Future work is required in order to elucidate the top-down mechanism responsible for evoking the occipital representations.

Multiscale dynamics of sensory processing
Andre Longtin

The senses must process a vast amount of environmental information and package it in a form that is accessible to a variety of target neurons. Main challenges for deciphering the principles of this coding and decoding are the presence of multiple scales of time and space and the influence of plasticity. One advantage of working at the sensory periphery is that one has a better intuition as to significance of the signals being processed at each stage, which can guide the analysis. This talk will present dynamical models for a few select combinations of space and time, inspired from experiments in electrosensory processing (a mix of the senses of touch and hearing). We will show two parallel schemes that enable the animal to simultaneously process high and low frequencies. One relies on â€œenvelopeâ€ coding, and the other on synchronous afferent spikes â€“ both nonlinear phenomena. We will also discuss how spatial correlations of stimuli interact with feedback in the sensory pathway to modulate gamma-range oscillations. Finally we present results on short-term plasticity, showing how it conveys broadband response properties regardless of the mixture of facilitation and depression.

How gamma-band oscillatory activity participates in encoding of naturalistic stimuli in random networks of excitatory and inhibitory neurons
Alberto Mazzoni

Recent experiments suggest that in V1 information about natural scenes is encoded in gamma band and low frequency Local Field Potentials (LFPs). To understand which features of the stimuli are encoded in these frequency bands and how they are encoded, we analyzed how a model of cortical network responded to various types of simulated stimuli.
The network was a randomly connected network of excitatory and inhibitory neurons, that can exhibit both asynchronous and synchronous irregular activity, in which the global activity oscillates in time with a frequency that depends both on synaptic time constants and on the excitation/inhibition balance. The LFP was modeled as a linear combination of excitatory and inhibitory currents. This choice allows to reproduce the dependence of the LFP spectrum on frequency and contrast as recorded in vivo. We first considered the responses of the network to Poisson random inputs with various levels of time-independent intensity. We found that the intensity modulates the power of the gamma band of LFPs, in agreement with experimental results [3]. When we used input stimuli characterized by a sinusoidally varying firing rate low frequency (< 20 Hz), modulations in the input were transformed into LFP modulations with the same frequency and with a power inversely proportional to the frequency itself. Thus, low frequency LFPs encoded the information about input low frequency modulations. In contrast, the gamma band LFPs encoded information about the overall spike rate of the input. We then considered the network responses to a dynamic 'naturalistic' stimulus based on real spike trains from LGN neurons recorded from anesthetized monkeys watching movies. We found that the mutual information conveyed by the LFP power about the different movie scenes has two pronounced peaks, at low frequency and in the high gamma band, with approximately the same peak height. As expected from the analysis with simple stimuli, we found a correlation between low frequencies power in each input interval and the power of the same frequencies in the corresponding output interval, and between the input intensity and the output gamma power. This suggests that, under naturalistic stimulation, low frequency cortical LFPs encode slow variation in the input, whereas gamma LFPs encode the total input spike count. Since stimulus-to-stimulus variations of input spike count and input slow oscillations are only very weakly related under natural viewing, low-frequency and high-frequency LFPS encoded largely independent information.

Perceptual binding by neuronal synchronization: a critical review
Sergio Neuenschwander

A major challenge in understanding perceptual organization is to explain how the visual system dynamically constructs stable relationships from local features. Given the distributed nature of cortical networks, approaching this problem is bound to identify the mechanisms by which selective neuronal interactions enable large-scale coordination of brain activity. Theoretical and experimental work suggest that neuronal synchronization may serve as a linking mechanism for grouping operations of visual inputs. To validate this hypothesis, a general experimental goal has been to find correlations between synchronously firing neuronal ensembles and perceptually coherent visual objects. Numerous studies in anesthetized animals have shown an increase in power for the gamma frequency band in response to coherent stimuli, such as moving bars, dots and gratings. Recently, these observations were extended to behavioral studies, which specifically addressed the role of gamma activity in cognitive processes demanding selective attention. In studies in the behaving monkey, we have investigated oscillatory responses in V1 to sequences of single and superimposed moving gratings (plaids). Strong oscillatory activity was evoked by the gratings, both at the single cell and population level. Adding a second component (plaids configuration) led to a redistribution of frequencies with the appearance of components at higher frequencies. In a second series of experiments we used a cueing paradigm to study the effects of expectancy on gamma activity. Expecting a behaviorally relevant stimulus event led to enhancement of gamma oscillations in the local field potential (LFP) and occasionally in the spiking activity, and it was typically associated with an alpha suppression, as generally seen in studies on selective attention. Phase-locking between spiking activity and LFP also increased for gamma components as estimated from spike-field coherence measurements. Gamma enhancement occurred in a frequency-specific, stimulus-dependent manner. Our findings support the existence of a gain mechanism capable of widespread, spatially non-selective modulation of gamma activity. It is possible that internal states, such as expectancy, are capable of gain-controlling the frequency-specific rhythms induced by features of the stimulus. These results will be presented followed by a more general critical discussion on the role of gamma oscillations in cognitive processes, such as surface segmentation and perceptual binding.

Synchronisation properties of electrically coupled networks of neurons in presence of noise and heterogeneities
Srdjan Ostojic

Electrical synapses are believed to enhance synchronous firing between neurons, yet their effect in large networks has not been fullye lucidated. To address this issue, we studied analytically the onset of synchrony in networks of electrically coupled integrate-and-fire neurons subject to noisy and heterogeneous inputs. We find that electrical coupling can lead to synchronization even for large input noise and strong heterogeneities. The behavior of the networks is found to depend critically on the amount of after-hyperpolarization (AHP) following a spike. If the AHP is weak, electrical coupling leads qualitatively to the same effects as excitatory coupling. If the AHP is strong, a novel behavior appears: for moderate values of noise, the network exhibits bistability between an asynchronous state and an oscillatory state where all the neurons fire in synchrony. The network switches between these two states depending on the synchrony of inputs. We conclude that electrically coupled neurons might lead to generation of multiple attractors with a diversity of temporal structures of activity.

Synaptic plasticity during synchronised network oscillations: spike timing-dependent plasticity and phase response curves
Ole Paulsen

The hippocampus is necessary for spatial learning and memory. When an animal actively explores an environment, the hippocampal network enters a rhythmic state with synchronised oscillations at theta (~5 Hz) and gamma (~40 Hz) frequencies. Synchronised network oscillations naturally organise firing of the relevant neuronal elements in a manner conducive to spike timing-dependent plasticity (STDP). In STDP, the precise relative spike timing of presynaptic and postsynaptic neurons governs both the sign and magnitude of synaptic change. This presentation will highlight some computationally interesting findings from our work on STDP. Moreover, I will discuss how spike timing in individual neurons can be controlled in a spontaneously active, oscillating network by external tonic and phasic synaptic inputs. These experimental results may have implications for how information is stored into and retrieved from the hippocampus.

Oscillation patterns in biological networks
Simone Pigolotti

Many biological systems can be modeled as network of units activating or repressing each other. The dynamics of these networks often shows oscillations, either regular or chaotic. I will show that, given the structure of the network, it is possible to restrict the possible dynamical patterns of these oscillations. The maxima and the minima of the variables on the nodes must follow a unique pattern when the network is composed by a single negative feedback loop, while there are more possibilities in more complex networks. I'll show applications of these techniques to data analysis of gene regulatory networks.

Ref. S. Pigolotti, S. Krishna and M. H. Jensen,
Proc. Natl. Acad. Sci. 104(16):6533-6537, 2007.

Stability properties of asynchronous regimes
Antonio Politi

A rigorous method is introduced to analyze splay states in networks of globally coupled identical units. As a result, we show that the stability may crucially depend on the ratio between the interspike interval and the single pulse-width. The implications on the requirements for performing accurate numerical simulations is also discussed.

Grandmother cells in the human brain?
Rodrigo Quian Quiroga

We can easily recognize a person or an object in a fraction of a second even when seen from different angles, with different sizes, colors, contrasts and under strikingly different conditions. How neurons in the brain are capable of creating such an invariant representation has been a hot topic of debate in Neuroscience for decades. In epileptic patients candidates to surgery we analyzed the responses of neurons in the human medial temporal lobe to picture presentations. Several technical improvements allowed us to start recording simultaneously from up 100 neurons simultaneously, what led to the finding of a remarkable type of neurons that fired selectively to different views of familiar individuals or objects. Given the extremely sparse, explicit and abstract representation by these neurons, can they be considered grandmother cells?

A linear path toward synchronization
David C. Roberts

I will present a linear reformulation of the Kuramoto model describing a self-synchronizing phase transition in a system of globally coupled oscillators that in general have different characteristic frequencies.
The discussion of this reformulated model will focus on the continuum limit, the regime of validity of the Kuramoto solution, but one of the advantages of the linear model is that it is also solvable for systems with a finite number of oscillators. This linear approach allows one to solve explicitly for the synchronization order parameter and the critical point for a new class of continuum systems that have no solution through the traditional approach to the Kuramoto model. Furthermore, the synchronization order parameter will be shown to exhibit anomalous scaling in the vicinity of the critical point. While the discussion will be restricted to systems with nonuniform time-independent global coupling, I will argue that this reformulation is a powerful method to further generalize solutions to the Kuramoto synchronization model.

Synchrony in the primary visual cortex is unrelated to binding
Pieter R. Roelfsema

The visual system imposes structure onto incoming information, by grouping image elements of a single object together, and by segregating them from elements that belong to other objects and the background. One influential theory holds that the code for grouping and segmentation is carried by the synchrony of neuronal discharges on a millisecond time scale. We tested this theory by recording neuronal activity in the primary visual cortex (area V1) of monkeys engaged in a contour-grouping task. We found that synchrony was unrelated to contour grouping. Instead, neurons coding the contour elements to be grouped in perception enhance their response, which provides a neurophysiological correlate of object-based attention.

Theta and gamma oscillation in layer II of the medial entorhinal cortex:
A modeling study
Horacio G. Rotstein

Stellate cells (SCs) play an important pacemaker role in the generation of rhythmic activity at theta frequencies (4-12 Hz) in layer II of the medial EC (MEC-II). They are principal neurons that give rise to the main afferent fiber system to the hippocampus. In addition, in MEC-II the recently discovered grid cells are putative SCs. Grid cells are principal neurons that fire at multiple ``place fields'', located at the vertices of equilateral triangles. Grid cells show phase precession with respect to a local ``fixed'' theta rhythm that they contribute to generate.
SCs 'in vitro' develop mixed-mode oscillations (MMOs) in their membrane potential when they are depolarized by a constant (DC) current. These temporal patterns consist of a combination of subthreshold membrane potential oscillations (STOs) and spikes which occur at the peak of an STO. These findings are correlated with 'in vivo' electrophysiological results. In a different set of

experiments SCs have been shown to become hyperexcitable in epileptic pilocarpine-treated rats as the result of a reduction of recurrent inhibition as compared to control ones. In these experiments, both the level of recurrent excitation and the electrophysiological intrinsic properties of SCs were similar in the control and epileptic cases.
This presentation concerns the mechanisms of generation of MMOs at theta frequencies in SCs and the transition from theta to ``epileptic'', gamma (30 - 80 Hz), activity in networks that include SCs and interneurons (ICs). We use a biophysical (conductance-based) model that includes these cells. This model consists of a multiscale, high-dimensional system of nonlinear ordinary differential equations describing the evolution of voltage and other biophysical variables. Parameters have been taken from experimental measurements. Both cell types have the standard spiking currents (transient sodium and delayed-rectifier potassium). In addition, the SC model includes a persistent sodium (Ip) and a hyperpolarization-activated (Ih)currents whose interaction has been shown to be responsible for the generation of STOs in SCs. Cells in the network are synaptically connected. SCs are excitatory (AMPA) and ICs are inhibitory (GABA_A). By numerically simulating this model we reproduce the experimental findings described above. Using reduction of dimensions ideas and dynamical systems arguments we provide a mechanism for the generation of STOs and the onset of spikes in SCs. This mechanism is based on the so called three-dimensional canard henomenon. We show that, in the biophysically plausible range of parameters considered, the STO phenomenon is intrinsically nonlinear and three-dimensional, involving the participation of both (Ip) and (Ih). Recurrently connected SCs synchronize in phase even in the absence of inhibition. The resulting MMO network patterns are qualitatively similar to the ones found for single isolated SCs. The firing frequency depends on the maximal synaptic conductance. This coupling parameter has a threshold above which the SCs fire at gamma. The transition from theta to gamma activity is very abrupt. We demonstrate that this behavior depends on the presence of phasic excitation but no abrupt transitions can be achieved by only changing the tonic (constant) drive to SCs. Consistently with experimental results, we also show that the recurrently connected SCs undergo an abrupt transition from the theta to the gamma regimes by decreasing (slightly) the amount of synaptic inhibition to the recurrently connected SCs.
This project is in collaboration with {\bf Nancy Kopell} (BU), {\bf John White} (Univ. of Utah), {\bf Martin Wechselberger} (Univ. of Sidney) and {\bf Tilman Kispersky} (Univ. of Utah).

Local and global oscillations as a means for neocortico-hippocampal communication
Anton Sirota

Brain systems communicate by means of neuronal oscillations at multiple temporal and spatial scales. The exact mechanisms by which information is represented locally and transferred between different structures of the brain are of great importance. We use large-scale recordings of local field potentials (LFP) and multiple single units in rats to explore the potential mechanisms of communication between hippocampus and neocortex during different states. Exploratory behavior and REM sleep are associated with synchronous theta rhythm in hippocampal complex. Firing of neurons in different neocortical areas, including the primary somatosensory area and the prefrontal cortex, as well as local transient gamma oscillations, are phase-locked to hippocampal theta oscillations. Slow wave sleep is associated with synchronous transitions of network activity from silence to bursting (DOWN-UP) recurring with ~1 Hz periodicity of the slow oscillation. The onset of the UP state in the neocortex is associated with gamma and spindle oscillations that organize local activity in the neocortex which sequentially spreads to the hippocampus via the entorhinal cortex. Analysis of the membrane potential, unit activity and local gamma/ripple oscillations in the hippocampal network reveals activation of "extrinsic" EC-CA1/DG circuits during UP states and "intrinsic" CA3-CA1 circuit during DOWN state. Based on these results we propose the following mechanism of information transfer between the two structures. During learning, the transfer of neocortical information to the hippocampus is actively initiated by the hippocampus via theta-phase biasing of neocortical networks. Conversely, during memory consolidation, the transfer of hippocampal information to the neocortex during slow wave sleep is initiated by neocortical cell assemblies activated by the down-up transition of the slow oscillation, triggering the self-organized activity in the hippocampal network.

Gamma oscillations in visual cognition
Catherine Tallon-Baudry

Oscillatory synchrony in the gamma (30-120 Hz) range has initially been related both theoretically and experimentally to visual grouping. Its functional role in human visual cognition turns out to be much broader, especially when attention, memory or awareness are concerned. Induced gamma oscillations are thus not related to a single cognitive function. They are probably better understood in terms of a population mechanism taking advantage of the neuron's fine temporal tuning: the 10-30 ms time precision imposed by gamma-band rhythms could favor the selective transmission of synchronized information (attention) and foster synaptic plasticity (memory). Besides, there is now experimental evidence in humans that gamma oscillatory synchrony is related to the emergence of visual awareness. The recent discovery that gamma oscillations could appear simultaneously in distinct areas at distinct frequencies and with different functional correlates further suggests the existence of a flexible multiplexing schema, integrating frequency bands within the gamma range but also at lower frequency bands. Understanding how and when oscillations at different frequencies interact has become a major challenge for the years to come.

Chaotic synchronization in extended systems as out-of-equilibrium phase transitions
Claudio J Tessone

We first briefly review the analogies between out-of-equilibrium phase transitions and chaotic synchronization in spatially extended systems with short range interactions [1]. Then, we will present recent developments concerning synchronization in systems with long-ranged (power-law decaying) coupling [2-3].
In this framework, the transitions are found to be always continuous, with the critical indexes varying continuously with the power-law exponent characterizing the interaction. For discontinuous local dynamics, numerical evidences indicate that synchronization transitions observed belong to the "anomalous directed percolation" family of universality classes found for Levy-flight spreading of epidemic processes [4]. On the other hand, for continuous local dynamics it is not possible to associate the transitions to previously studied crtitical phenomena.

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Which Network Connectivities Generate a Given (Neural) Dynamics?
Marc Timme

We present two alternative perspectives that may aid our understanding of structure-dynamics relations of complex (neural) networks. First, can we design a network, e.g. by modifying the features of units or interactions, such that it exhibits a desired dynamics? Here we positively answer this question analytically for a class of networks of spiking neural oscillators [1, 2], by finding the set of all networks that exhibit a given arbitrary periodic spike pattern as an invariant dynamics. We illustrate the applicability of the method by designing networks that exhibit a predefined dynamics and simultaneously minimize the networks? wiring costs, i.e. are structurally optimal. Second, we present a method to infer the connectivity of a given network from its response dynamics to external driving signals. For a given driving condition, measuring how the collective state changes reveals information about how the units are interconnected [3]. Sufficiently many repetitions for different driving conditions yield the entire network connectivity from measuring the response dynamics only [4].

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How is this: â€œVery fast (>80 Hz) network oscillations, gap junctions, and the initiation of seizures
Roger D. Traub

Very fast oscillations (VFO) occur in a number of contexts: prior to seizures, superimposed upon synchronized burst discharges, and intermixed with persistent gamma oscillations (30 - 70 Hz). The fact that VFO can be generated in low-calcium media, in pyramidal neurons, suggests that VFO is generated by electrical coupling via gap junctions. Electrophysiological evidence suggested that the requisite gap junctions were located between axons, and dye-coupling and (more recently) ultrastructural data support such a location. For gap junctions to lead to oscillations in this system, functional coupling must be strong, i.e. sufficient to allow an action potential to cross from axon to axon: the system is not one of coupled oscillators.

On patterns of synchrony and asynchrony in lattices of phase oscillators
Misha Zaks

I discuss phase dynamics in lattices of diffusively coupled non-identical phase oscillators. It is well-known that a sufficiently strong coupling enables a regime in which all units in the ensemble rotate with the same rate. This stable synchronous state is not necessarily a global attractor: I show that it may coexist with other, less trivial dynamical states. Take a lattice with weakly disordered distribution of individual frequencies and fix the coupling strength slightly (but distinctly) above the threshold value, required for the onset of global synchrony. Temporal evolution for most of the initial conditions leads to the synchronous state. Certain trajectories, however, never reach complete synchrony. I report on stable states in which nearly the whole ensemble is synchronized whereas a few adjacent elements do not conform to common dynamics and rotate with different frequencies. Phase differences between such oscillators and the rest of the ensemble grow linearly in time. In spite of unbounded temporal growth, these phase defects do not propagate along the lattice: they stay (exponentially) localized. On sufficiently long lattices, several growing defects can coexist. A closer look at them shows that their dynamics - periodic, quasiperiodic or chaotic - is related to bifurcations of periodic orbits which lie on toroidal surfaces in the phase space of the ensemble.

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Posters

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Two independent cortical subnetworks control spike timing in layer 5 pyramidal neurons during dynamic oscillation shifts
Karlijn I. van Aerde

Brain oscillations in different frequency bands have been linked to different behaviors and cognitive processes. During ongoing behavior, oscillations fluctuate in frequency and amplitude even within specific frequency bands. How these non-harmonic frequency and amplitude fluctuations in brain oscillations are generated has not been investigated. Here, we find that in EEG of humans and in intracranial EEG of awake, freely moving rats at rest, episodes of high (~23 Hz) and low (~18 Hz) oscillation frequency in the beta band (15-30 Hz) last 100 to 400 ms and occur independently. By recording from individual cortical neurons during oscillations, we show that frequency and amplitude fluctuations are generated by two distinct cortical subnetworks within the same cortical column. Networks of layer 2/3 show an intrinsic higher oscillation frequency than networks in layer 6, both in prefrontal and visual cortex. Layer 5 pyramidal neurons experience both low and high oscillations frequencies. We asked whether spike timing in layer 5 pyramidal neurons is controlled by both networks. Layer 5 pyramidal neurons alter their spike timing upon shifts between episodes of low and high oscillation frequencies. Layer 6 pyramidal neurons do not show these shifts in spike timing. Frequency and phase information is encoded and relayed to layer 5 neurons by superficial and deep cortical networks through timed excitatory and inhibitory synaptic transmission. Our data show that frequency fluctuations in brain oscillations reflect synchronized activity in distinct neuronal networks, and suggest that cortical subnetworks can process information in a parallel fashion within a single column.

Identification of cellular network hubs driving oscillations in the developing hippocampus
Paolo Bonifazi, PhD

Spontaneous activity synchronized over a large population of neurons is a common feature of brain development and plays a major role in the construction of neuronal circuits. Based on theoretical and experimental studies in complex systems and networks, it has been proposed that neuronal networks are organized with a small-world topology. This hypothesis predicts the existence of network “hubs”, i.e. rare neurons with much more spread and/or larger number of connections capable of strongly influencing the network dynamic. In this work, we tested this hypothesis in the developing hippocampus and we looked for hub neurons playing a key role in the initiation of synchronous network events. The activity of neuronal circuits was measured with single-cell resolution using fast multibeam two-photon calcium imaging and online pair-wise correlation was used to describe network dynamics. Neurons active before the onset of synchronous network events were identified and recorded in current-clamp mode while imaging network activity. Post-hoc morphological analysis and Neurolucida reconstruction of patched neurons was also performed. We describe the morpho-functional properties of neurons capable of significantly influencing the occurrence of synchronous events in the network when intracellularly stimulated. Altogether, our data provides experimental evidence supporting the existence of network hubs, single neurons with a critical role in the initiation of synchronous network events.

Synchronization based neural network model of perceptual multi-stability

David Chik

Perceptual multi-stability can be induced by either using some ambiguous figures (such as Neckar Cube or Face/Vase figure) or showing different images to left and right eyes (binocular rivalry). The observer will experience an irregular switching between different perceptions. The underlying neural mechanism is unclear, but EEG recordings showed that the perception of ambiguous figures seems to correlate with gamma band activity and transient synchrony of some distant brain areas (Keil et al. 1999; Klemm et al. 2000; Nakatani and van Leeuwen 2006; Melloni et al. 2007). Therefore in the present study, we propose a new model that is based on the idea of partial synchronization between a central element and some peripheral elements. This model does not involve a direct reciprocal inhibition as in all previous models (such as Lehky 1988; Bialek and DeWeese 1995; Dayan 1998; Lumer 1998; Ogawa et al. 2000; Laing and Chow 2002; Freeman 2005; Moreno-Bote et al. 2007). Instead, this model utilizes the mechanism of stochastic synchronization. Numerical simulations of the model successfully reproduce a skewed Gaussian distribution of dominance durations and the Levelt's second proposition, in agreement with psychological experiments.

Attentional modulation of coherence between monkey areas V1 and V4

Iris Grothe[1,2], Katja Taylor[1], Yulia Smiyukha[1], David Rotermund[1,2,3], Simon D. Neitzel[1,2], Udo A. Ernst[1,2,3], Sunita Mandon[1], Klaus R. Pawelzik[1,2,3], and Andreas K. Kreiter[1,2]

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Attention allows for selection and enhanced processing of behavioral relevant stimuli, out of a complex visual scene. The question remains, how selective processing through attention is achieved at the neuronal level. Previous experimental work has shown that attention increases gamma-band synchronization in areas V1 and V4. Interestingly, these modulations closely followed the behavioral demands of the task. Additionally, errors in directing attention were reflected by specific modulations in the strength of the gamma-band synchronization. This tight relation between synchronization and behavior provides evidence for a functional role of gamma-band synchronization as a mechanism of attentional modulation (Taylor et al., 2005a; Taylor et al., 2005b). Furthermore, these gamma-band signals contain a surprising amount of stimulus-specific information, which is enhanced in V4 if the stimulus is attended: with a support vector machine (SVM) we could distinguish between several stimulus shapes based on stimulus-specific changes in the patterns of gamma amplitudes (Rotermund et al., 2007). We expect that attention not only modulates synchronization within a neuronal population to enhance the effectiveness of its signals; we hypothesize that it also differentially modulates the coherence between multiple populations of afferent neurons and their common target neurons, in order to effectively select and process the relevant stimulus (Kreiter, 2006). To investigate the dynamic coupling of neurons in V4 with its afferent neurons, we plan simultaneous recordings with multiple electrodes from macaque monkeys' areas V1 and V4. The monkeys have to direct sustained attention to one of two stimuli, which are both changing shape continuously. Reoccurrence of its initial shape has to be reported. We predict that the population of V1 neurons representing the attentionally selected object will be stronger coupled to the V4 neuron than the V1 population representing the irrelevant object. Preliminary results suggest that differential synchronization indeed may serve as a mechanism to switch between different patterns of effective connectivity.

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Acknowledgements: We thank Anja Besuch, Katrin Toss, Ramazani Hakizimana and Michael Borisov for technical assistance. Financial support for this work was provided by the E.U. Grants BIND MECT-CT-20095-024831 and BACS FP6-IST-027140, BMBF grant DIP-METACOMP and the Bernstein Initiative, DFG SFB 517 'Neurocognition', the CAI Bremen, and the ZKW Bremen.

Oscillatory brain activity during human somatosensory working memory maintenance

Saskia Haegens

We used magnetoencephalography (MEG) to investigate oscillatory brain activity involved in somatosensory working memory maintenance. Subjects performed a delayed-match-to-sample task, with stimuli consisting of pulse trains delivered using median nerve stimulation. Time-frequency representations of power were calculated for the retention period. The maintenance of somatosensory working memory representations was reflected by sustained gamma band activity over bilateral somatosensory regions. Additionally, we observed an increase in alpha band activity over posterior areas and ipsilateral somatosensory cortex. Previous studies in the visual and auditory domains found a similar engagement of gamma activity during working memory maintenance, in the respective sensory areas. Our findings extend the notion that sustained gamma band activity reflects the mechanism of working memory maintenance to the somatosensory system. We interpret the alpha activity to reflect a functional inhibitory mechanism, since it was identified in brain regions not required for the task. We propose that the ipsilateral alpha activity plays a similar role for the somatosensory system as posterior alpha plays for the visual system. This study suggests that findings from other modalities, such as the visual system, can be extended to the somatosensory system.

Time-driven simulation with fully asynchronous pulse coupling

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Artificial synchrony can be introduced by discrete time simulation of neuronal networks, since they typically constrain spike times to a grid determined by the computational step size [1]. Event-driven algorithms avoid this problem but are computationally demanding, both with respect to calculating future spike times and to event management, particularly for large network sizes. We therefore investigate a third alternative: hybrid algorithms, in which the global scheduling algorithm is formulated in discrete time, but the handling and generation of spikes at the neuron level is formulated in continuous time [2]. We compare the efficiency of two different approaches with exact subthreshold integration, which attain the same precision as event-driven algorithms, limited only by the accuracy of the double representation of floating point numbers. Morrison et al. [2] showed that by combining an interpolation method to detect threshold crossings with exact integration [3] of the sub threshold dynamics, artificial synchrony is avoided and machine precision can be obtained at moderate computation step sizes. In the framework of event-driven simulations, Brette [4] presented an elegant method of calculating spike times of integrate-and-fire neurons with exponentially decaying currents. Here, we show that this scheme can also be implemented in a time-driven environment with exact spike time handling. The prediction of the next threshold crossing of the neuron membrane potential is reformulated into a root finding problem of the equivalent polynomial. To minimize the computational costs, standard numerical methods such as Sturm's theorem and Descartes' rule can be applied to determine whether a root of the polynomial exists; if it does, the root is calculated by a hybrid bisectioning and Newton-Raphson method. By constraining the relationships of the time constants involved the polynomial structure can be controlled in order to achieve an optimal algorithmic efficacy. A comparison between the interpolation and polynomial methods in the time-driven environment NEST [5] shows that both yield the same precision in single neuron simulations. The major difference is that in the former case the computation step size is the factor determining both the precision of the result and the computation time, whereas in the latter case machine precision is always reached. However, in order to choose which approach is more suitable for a given application, it is necessary to consider the efficiency of the methods, i.e. the simulation time required to achieve a prescribed accuracy [2]. We measure the simulation times for both approaches in a random network of around 12,000 neurons [6] whilst systematically varying the input and output spike rates; the corresponding accuracy is determined in single neuron simulations. For small input and output rates the polynomial method is more efficient than the interpolated method. The simulation times of both approaches increase with increasing input rate. However, the interpolation method is essentially independent of the output rate, whereas the simulation time of the polynomial method increases with increasing output rate. For high input rates such as can be expected in networks with cortical levels of connectivity (10^4 synapse per neuron) or for high output rates, the interpolated method is more efficient. All implementations discussed here will be made available in the next release of NEST.

Acknowledgments
Partially funded by DIP F1.2, BMBF Grant 01GQ0420 to the Bernstein Center
for Computational Neuroscience Freiburg, and EU Grant 15879 (FACETS).

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**Desynchronizing the abnormally synchronized neuronal activity
in the subthalamic nucleus; a modeling study**

Christian Hauptmann

Preliminary abstract: In a modeling study, we show that synaptic connectivity can effectively be reshaped by an appropriate modulation of neuronal dynamics. The neuronal network models the behavior of the subthalamic nucleus, a common target area for deep brain stimulation, and incorporates activity dependent changes of the inter-neuronal connectivity's. Due to this we observe states characterized either by pathological synchrony or by uncorrelated activity. Suitably designed stimulation protocols enable to shift the neuronal population from one dynamical state to another. Due to low-frequency periodic pulse train stimulation, the population learns pathologically strong interactions, as known from the kindling phenomenon. In contrast, desynchronizing stimulation, e.g., multi-site coordinated reset stimulation enables the network to unlearn pathologically strong synaptic interactions, so that a powerful long-term anti-kindling is achieved. Our results show that desynchronizing stimulation may serve as a novel curative approach for the therapy of neurological diseases connected with pathological cerebral synchrony.

Measuring spike train reliability

Thomas Kreuz

Measuring the degree of synchrony between two or more neuronal spike trains is an important tool in order to address issues such as neuronal coding, information transmission and model validation.

Another prominent application is to measure the reliability of the response of individual neurons upon repeated presentations of the same stimulus. A number of both multivariate and bivariate measures have been proposed to address this issue. Multivariate approaches include the reliability measures by Hunter and Milton and by Tiesinga, while bivariate approaches comprise the Victor-Purpura and the van Rossum distance, as well as the similarity measure proposed by Schreiber et al., and, the most recent proposal, the ISI-distance, a method based on relative instantaneous firing rates. These approaches can be applied to multivariate data in a pairwise fashion, e.g., reliability can be defined as the average over all pairwise similarities. Here, we extend the bivariate ISI-distance to a truly multivariate measure. This extension inherits the distinct properties of the ISI-distance, in particular, it is parameter free and time scale adaptive. In an application to in vitro recordings of cortical cells from rats we show that the multivariate ISI-distance serves as an excellent means to track relative firing patterns in the spike trains. The instantaneous degree of synchrony can be visualized easily, thus rendering this method a good choice for moving window applications on non-stationary neuronal dynamics. In particular, when estimating reliability this property allows the analyst to correlate intervals of high or low synchrony to the respective local stimulus features, which is desirable in many application. Furthermore, we use a simulated network of Hindemarsh-Rose neurons with predefined clustering as a controlled setting to evaluate the performance of the multivariate ISI-distance in distinguishing different sets consisting of a variable number of spike trains from different clusters. In a comparison with other multivariate approaches, as well as generalizations of several bivariate methods, the method presented here proves to be a very reliable indicator of set balance.

Burst-field locking as a neurophysiological mechanism for attentional selection
Eric Maris

Attentional selection is the mechanism by which our brain selects the behaviorally relevant part of the complete sensory input. Only this selected part is transmitted from lower to higher sensory areas and ultimately to the brain areas that control motor output. One of the plausible mechanisms for attentional selection is a selective increase of the number of spike bursts in the sensory areas that process the attended information. This is because spike bursts have a much larger probability of triggering downstream neurons than spike trains with larger inter-spike time intervals. In this presentation, I will show how gamma oscillations contribute to the emergence of spike bursts. The empirical part of this project is based on a reanalysis of the data of the study by Fries, Reynolds, Rorie, and Desimone (Modulation of Oscillatory Neuronal Synchronization by Selective Visual Attention, Science, 2001).

Time course of reactivation of cell ensembles in the rat medial prefrontal cortex during sleep after training
A. Peyrache

The prefrontal cortex is implicated in the flexible learning of stimulus-outcome associations, which would be consolidated in memory during offline periods. Reactivation of memory traces, in the form of the reinstatement of experience-related activity in prefrontal cell assemblies during sleep could be the basis for such a consolidation process. To study this, we developed a novel analytical technique which tracks the time course of task-related reactivation. The correlation matrix of binned spike trains from multiple cells is decomposed into its principal components (PCs), the largest of which represents groups of cells whose activity was highly correlated. The instantaneous cell pair co-activation matrix during slow-wave sleep (SWS), weighted by the coefficients in a given PC, and averaged over all cell pairs, can then be taken as a measure of the reactivation of the cell assembly corresponding to that PC at a given time. We analyzed medial prefrontal ensembles recorded from five rats learning a set-switching task on a Y-maze, as well as in preceding and following sleep sessions. Hippocampal ripples triggered these reactivations during post-task but not pre-task SWS. Indeed, in the deep prefrontal layers a significant fraction of cells (15%, or 93/616) had significant firing rate changes during hippocampal ripples, compared to control periods (500ms prior). Hippocampal neuronal assemblies are known to be reactivated during ripples, and this corresponds to Pfc neuron assemblies reactivation. This could play a role in consolidation of memory from hippocampus to prefrontal cortex.

Interacting dendritic oscillators form a biophysical framework for grid cells

Michiel Remme

The dendritic tree, both by its intricate morpholgy and its composition of active conductances, contributes significantly to the elementary computations a neuron can perform. Recent data indicates that active dendritic conductances can support ongoing membrane potential oscillations. Often, the distributions of active conductances in the dendritic tree are nonuniform. This, together with the fact that the morphology of the dendritic tree is nonuniform, suggests that there may be multiple oscillators embedded in the cellâ€™s dendritic tree. Here we analyze, through mathematical analyses and numerical simulations of detailed biophysical models, the dynamics of such interacting dendritic oscillators and their impact on signal propagation in single neurons. Combining weakly coupled oscillator methods with cable theoretic arguments, we derived interaction functions for multiple oscillating dendritic compartments separated by less excitable membrane segments. In particular, we characterized how their phase locking properties depend on the intrinsic properties of the oscillators and the membrane properties of the segment connecting them. As a direct consequence, we show how the conductance load on the dendrite can modulate phase locking behavior. This suggests a new role for synaptic conductances impinging on the dendrites, particularly shunting inhibition, in controlling the coherence of ongoing dendritic activity. In turn, dendritic coherence is able to gate the integration and propagation of synaptic signals to the soma, ultimately leading to an effective control of somatic spike generation. We use our analysis to study the subthreshold oscillations in layer II entorhinal stellate cells. A recent model for the grid field firing properties of these cells is based on interfering dendritic oscillators (Burgess and Oâ€™Keefe, 2007; Hasselmo, 2007). We examine how this idealized sinusoid-interference framework can be implemented in a biophysically realistic model. Our preliminary results suggest predictions on the distribution of the active dendritic conductances.

Stability analysis of pulse-coupled oscillators with delay

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Mirollo and Strogatz (1990) have shown mathematically that two excitatory pulse-coupled oscillators will synchronize if the state variables are described by a smooth, monotonic increasing function that is concave down (1.e. $f'<0$ and $f''>0$). In a more realistic model also the finite propagation time of signals and the role of excitatory (phase advance) and also inhibitory (phase delay) synaptic connections should be included. Ernst et al. (1995) reported that a finite propagation time of t-delay results in a t-delay out-of-phase relation between the two excitatory oscillators. Furthermore they showed that the finite delay between two inhibitory oscillators can lead to anti-phase and to in-phase synchronization. These models were developed for the case of symmetric coupling which is equally strong for both neurons. However, in the real brain connectivity is not symmetric. Often the feedforward projections of a neuronal population to another population of neurons are much stronger than the feedback connections. Therefore, we investigate the role of asymmetric couplings between two pulse-coupled neuronal oscillators with delays in the coupling. We do this for purely excitatory and purely inhibitory coupling, as well as for a mixture of excitatory and inhibitory, like in the well-known PING-models, presented by Kopell and co-workers. By using the Mirollo-Strogatz model we find analytical expressions for the stable states of the dynamical system of two interacting (groups of) neurons.
