Research Results of the BCCN Freiburg
presented at:

FIFTEENTH ANNUAL
COMPUTATIONAL NEUROSCIENCE MEETING
CNS*2006

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Other current topics related to cortical map development, or neural maps in general, are also very welcome.

Format: Informal mini-symposium. An overview talk and informal research and discussion-oriented talks from a series of speakers are planned, with questions and comments encouraged throughout.

Cortical Microcircuitry

Recent years have brought a tremendous progress in unravelling anatomical and physiological properties of the cortical microcircuitry. Indeed, a large number of different cell-types is increasingly revealed to be engaged in the cortex into dense and complicatedly structured networks that span longitudinally through all cortical layers and extend laterally across distances of up to several millimetres in the cortical maps. Anatomical complexity is in addition paralleled by a rich intrinsic and stimulus-related dynamic repertoire. We are only at the beginning of an understanding of the observable complexity and its possible impact on cortical function. Still, there is the believe that despite its rich structure and dynamics, something like a "prototypical cortical microcircuit" can be isolated, that repeats throughout the cortical areas and provides a core functionality capable to adapt to different requirements in different areas.

The present workshop brings together experts from experimental and computational neuroscience in order to review some of the ongoing experimental research concerning cortical microcircuitry as well as related theoretical concepts.

The workshop will span both afternoon sessions at the 19th/20th of July.

Each of the speakers has a 45 minutes slot split between presentation and discussion at his/her convenience.

14:00-14:45 Alex Thomson Wiring diagrams and synaptic properties: What we know and what we don't know
14:45-15:30 Arnd Roth Predicting synaptic connectivity from neuronal morphology
15:30-15:45 break
15:45-16:30 tbc
16:30-17:15 Mike Denham Computational theories for the cortical microcircuit

20. July 2006
14:00-14:45 Rolf Koetter Mapping cortical microcircuitry by focal flash release of caged glutamate
14:45-15:30 Daniel Durstewitz NMDA-driven recurrent dynamics and its implications for active memory
15:30-15:45 break
15:45-16:30 Stefano Panzeri Stimulus specificity of cortico-cortical connections optimizes information transmission
16:30-17:15 Thomas Wennekers Operational cell assemblies in large-scale cortex models

This workshop has been funded in part by the Engineering and Physical Sciences Research Council / UK as part of the COLAMN project (EPSRC grant EP/C010841/1)

Synaptic plasticity and stability

Thursday 20, 9.00-12.00
Organizer: Mark van Rossum

Mark van Rossum. Introduction

Abigail Morrison
Spike-timing dependent plasticity in balanced random networks

The balanced random network model attracts considerable interest because it explains the irregular spiking activity at low rates and large membrane potential fluctuations exhibited by cortical neurons in vivo. Here, we investigate to what extent this model is also compatible with the experimentally observed phenomenon of spike-timing dependent plasticity (STDP). Confronted with the plethora of theoretical models for STDP available, we re-examine the experimental data. On this basis we propose a novel STDP update rule, with a multiplicative dependence on the synaptic weight for depression, and a power law dependence for potentiation. We show that this rule, when implemented in large (100,000 neurons) balanced networks of realistic connectivity and sparseness (10,000 synapses per neuron), is compatible with the asynchronous irregular activity regime. The resultant equilibrium weight distribution is unimodal with fluctuating individual weight trajectories, and does not exhibit spontaneous self-organisation of structure.

Stefano Fusi
Limits on the memory-storage capacity of bounded synapses

Memories, maintained in patterns of synaptic connectivity, can be over-written and destroyed by ongoing plasticity arising from the
Coding Communication Signals with Synchrony and Asynchrony

Jan Benda  
André Longtin, Len Maler

ITB, Humboldt University, Berlin, Germany

j.benda@biologie.hu-berlin.de, alongtin@physics.uottawa.ca

Synchronous spiking of neural populations is hypothesized to play important computational roles, like for example in solving the binding problem, attention, and cortical communication. We present an example where the opposite, i.e. the desynchronization of a neural population encodes a transient communication signal. During male-female interaction of weakly electric fish the superposition of the electric fields results in an ongoing high frequency beat of about 100 to 300 Hz. Our in vivo recordings of P-unit electroreceptor afferents in Apteronotus leptorhynchus (single unit, dual unit, and whole nerve recordings) clearly show a highly synchronous response to such beats. However, whenever a male emits a courtship signal, a so-called type-I or large chirp, the beat is interrupted for about 25 ms and the response of the electroreceptor population becomes desynchronized. The mean firing rate during the synchronous and asynchronous response is approximately the same. We conclude that desynchronization of the spike response can be as important as synchronous spikes. The situation is completely reversed during a male/female encounter where beat frequencies are lower than about 50 Hz and a different type of chirps, so called type-II or small chirps, are emitted as an aggression signal. Such low beats simply modulate the firing rate of the electroreceptors; the spike times of different electroreceptors are uncorrelated. A small chirp generates a sudden increase or decrease of the electric field amplitude that transiently boosts or reduces the electroreceptor's firing rate and thus causes a brief period of increased synchrony. In summary, depending on the social context, the spike response of the population of electroreceptor is either synchronized or desynchronized by a communication signal. This example clearly demonstrates that in general it is the change of the degree of synchrony that codes a signal and not synchrony as such.

A biophysical model to explore the effects of network activity on short-term synaptic depression

Jose Manuel Benita  
Antoni Guillamon  
Gustavo Deco  
Maria V. Sanchez-Vives

Universidad Politecnica de Catalunya, Barcelona, Spain

jose.maneul.benita@upc.edu  
antoni.guillamon@upc.edu

Short-term synaptic depression (STD) is a process that modifies the probability of transmitter release. Recent experiments show that the reduction of STD over time is related to the intensity of spontaneous rhythmic activity. In order to study the effect that network activity has on STD, we built a biophysical network model and measure STD in it (from EPSPs amplitude of hyperpolarized neurons) in two different stages that mimic  

Models of Correlated Poisson Processes: Rate Covariance and Spike Coordination

Staude Benjamin  
Stefan Rotter  
Sonja Gruen

Neuroinformatics, Freie University Berlin  
Bernstein Center Computational Neuroscience, Berlin, Germany

staude@neurobiologie.fu-berlin.de  
rotter@biologie.uni-freiburg.de

This study explores the statistical properties of correlated Poisson processes as models of the spiking activity of neurons recorded in parallel. As a new model, we introduce the 'covarying rate process' (CRP) that produces correlation due to jointly varying firing rates. This model will be compared to a 'jittered coincidence process' (JCP) (Gruen et al., 1999; Kuhn et al., 2003) that features temporally coordinated spiking activity with stationary firing rates. For both models, we provide explicit mathematical expressions that relate the model parameters to the mean firing rate, count correlation coefficient and temporal scale of correlation. This yields two models with identical biologically relevant parameters, whereas the mechanisms producing the correlation differ. Sample data generated by the two models are analyzed using cross-correlation techniques. The time scale of the correlation can easily be extracted by these tools, but the different origin of correlation cannot be revealed. Cross-correlations from data of both models look identical, even for a variety of predictors. The usage of the 'correct' predictor implies knowledge of the underlying process and has to be chosen accordingly. Only then data originating from the two types of model can be differentiated. We will discuss further analyses that, if applied additionally, help to obtain better knowledge about the underlying process. Acknowledgments. Funded by NaFoEg Berlin, the German Ministry for Education and Research (BMBF grants 01GQ01413 and 01GQ0420), and the Stifterverband fuer die Deutsche Wissenschaft. Support by the IGPP Freiburg is gratefully acknowledged.

Storing sparse random patterns with cascade synapses

Daniel Ben Dayan-Rubin  
Stefano Fusi

INI-institute of neuroinformatics, Zurich, Switzerland

dbd@ini.phys.ethz.ch, fusi@ini.unizh.ch

New experiences can be memorized by modifying the synaptic efficacies. Old memories are partially overwritten and hence forgotten when new memories are stored. The forgetting rate depends on the number of synapses which are modified: networks in which many synapses are highly plastic and hence change following each experience, are good at storing new memories but bad at retaining old ones. On the contrary a small number of synaptic changes (rigid synapses) means good memory retention, but poor performance at storing new memories. Recently Fusi, Drew and Abbott (2005), introduced a model of a synapse which has a cascade of states, each characterized by a different degree of plasticity. Each stimulus can modify the synaptic efficacy or induce a transition to a different state (metaplasticity). Such a synapse combines the advantages of plastic synapses with those of more rigid synapses, outperforming the models in which each synapse is characterized by a single predefined degree of plasticity. In that work the authors assumed that each synapse was modified independently. Moreover, they estimated the memory capacity by measuring the correlation between the synaptic configuration right after a particular experience was stored, i.e. when the memory was still vivid, and the synaptic configuration obtained after the synapses were exposed to a certain number of new experiences. The problem of how this information is actually stored in a dynamic network of neurons was ignored. Here we consider a two layer network in which input neurons are connected to output neurons through cascade synapses. In our case and in the case of every network, different synapses turn out to be correlated even when storing random and uncorrelated input and the output patterns. We analyze how the memory performance depends on the statistics (sparseness) of the patterns to be memorized. Given that the sparseness of the pattern can significantly reduce the number of synapses which are needed to be modified to store new memories, is it still advantageous to have a cascade synapse with metaplasticity? We show that cascade synapses have always a better memory performance.

Coordination

Models of Correlated Poisson Processes: Rate Covariance and Spike Coordination

Staude Benjamin  
Stefan Rotter  
Sonja Gruen

Neuroinformatics, Freie University Berlin  
Bernstein Center Computational Neuroscience, Berlin, Germany

staude@neurobiologie.fu-berlin.de  
rotter@biologie.uni-freiburg.de

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A biophysical model to explore the effects of network activity on short-term synaptic depression

Jose Manuel Benita  
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Universidad Politecnica de Catalunya, Barcelona, Spain

jose.maneul.benita@upc.edu  
antoni.guillamon@upc.edu

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Staude Benjamin  
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Neuroinformatics, Freie University Berlin  
Bernstein Center Computational Neuroscience, Berlin, Germany

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Dendritic Morphology Influences Burst Firing  
Ronald Elburg  
Arjen vanOoyen
Experimental Neurophysiology, Vrije Universiteit Amsterdam  
Amsterdam, Netherlands
ronald@cnocr.vu.nl  
arjen.van.ooyen@falw.vu.nl

Burst firing, i.e., the occurrence of clusters of spikes with short interspike intervals, is a specific and important mode of neuronal signaling. Bursts can improve the signal-to-noise ratio of neuronal responses, while the fine structure of bursts may convey stimulus related information and can influence short- and long-term synaptic plasticity. Given the importance of bursts, it is crucial to understand how bursts are generated and what factors influence their occurrence and fine structure. Here we study in a systematic way how dendritic morphology influences the cell's propensity for burst firing. We distinguish between the effects of dendritic topology and dendritic length, and use both somatic and dendritic stimulation. We show that both the total length of the dendritic tree and its topology markedly influence the degree of bursting. Both under somatic and dendritic stimulation, burst firing can occur only for a particular range of tree lengths. Interestingly, this range depends on topology: asymmetric trees start and stop bursting at a lower total dendritic length than symmetric trees. This implies that a small change in the topology of a dendritic tree can change the firing pattern from bursting to non-bursting or vice versa.

Parallel and Distributed Simulation of Large Biological Neural Networks with NEST  
Jochen Eppler  
Abigail Morrison  
Markus Diesmann  
Hans Plesser  
Marc-Oliver Gewaltig
Honda Research Institute Europe GmbH  
Computational Neurophysics, Biology III, Offenbach, Germany
eppler@biologie.uni-freiburg.de  
abigail@biologie.uni-freiburg.de

The Neural Simulation Tool NEST is a simulation environment for large heterogeneous networks of point neurons or neurons with a small number of compartments. In this contribution, we describe two major developments: first, the combination of parallel and distributed simulation. Second, the introduction of a more flexible connection and communication framework. In a companion contribution, we present the main features of NEST from a user's perspective (Gewaltig et al., this volume) In order to combine multi-threaded and distributed simulation, we introduce a new network representation in NEST: in this scheme, the network is represented as list of nodes, which are either neuron models, devices or sub-networks. Device nodes are created for each thread on each computer in order to allow parallel data access and avoid bottlenecks during simulation. Neuron nodes are only instantiated on a single thread to achieve a distribution of the load across all computers. On all other threads a light-weight proxy node is created as representative and serves as a local anchor for a connection which would otherwise join neurons on two separate threads. In this way, from the perspective of an individual thread, all connections appear to be local, thus minimising cache problems. We also implemented a new connection framework which extends the scope of the simulation tool. In the new system, the connection information is stored separately from the nodes. This permits parallel event delivery on multi-processor computers. An A -> B connection in the new system is realized on the unique computer on which neuron B is instantiated; on all the other computers, where B is represented by a proxy node, the connection is ignored. Thus the distribution of the nodes leads to a distribution of the connection information in a natural way. The new connection framework can incorporate plasticity and the usage of heterogeneous synapse types to build a much wider range of networks. Preliminary results indicate that linear scaling of the simulation time with respect to the number of processors can be achieved.

A model of intention understanding based on learned chains of motor acts in the parietal lobe  
Wolfram Erlhagen  
Fabian Chersi, Albert Mukovskiy, Leonardo Fogassi, Pier Francesco Ferrari
Dep. of Mathematics for S&T, Univ. of Minho, Guimaraes, Portugal
wolfram.erlhagen@mct.uminho.pt, chersi@rocketmail.com

The understanding of other individuals' actions is a fundamental cognitive capacity for all species living in social groups. It is generally accepted that the mirror circuit is essentially involved in this capacity. Recently we have shown that mirror neurons in the monkey's inferior parietal lobe (IPL, areas PF/PFG), while coding a specific motor act like grasping an object, show markedly different activation patterns depending upon the final goal of the action sequence in which the act is embedded (placing vs. eating). The experimental data supports the hypothesis that neurons in the parietal cortex are organized in chains of motor acts dedicated to achieve certain action goals. Here we present a dynamic field model which aims at substantiating the idea that the mechanism for understanding intention may be based on an activation of specific motor chains in IPL. In its architecture, the model reflects the basic functionality of anatomically connected populations of neurons in the STS-PF/PFG-F5 mirror circuit and the prefrontal cortex (PFC). In the IPL layer, specific pools of neurons represent motor acts like reaching, grasping or placing by means of self-stabilized, transient activity patterns. The various subpopulations are coupled via synaptic links, thus establishing a chain toward a rewarded end state or goal represented in PFC. Important cues for triggering the motor chains are visual inputs representing object properties and observed motor acts (provided by STS). To validate the model, we have conducted an observation task we chose the grasping-placing paradigm used for the experiments with the monkeys. We show that the connectivity pattern between the various local pools of neurons can be established through training using a Hebbian rule, and that the resultant distributed network can exhibit a range of physiologically interesting behaviors during the process of action recognition.

Contour detection from quasi-ideal contour integration  
Udo Ernst  
Nadja Schinkel, Pawelzik Klaus, Sunita Mandon, Simon Netzel, Kreiter Andreas
U Bremen, Bremen, Germany
udo@neuro.uni-bremen.de, nadja@neuro.uni-bremen.de

Psychophysical experiments have shown that humans and macaque monkeys are very good in grouping collinearly aligned contour elements which are embedded in a background of randomly oriented edges. However, the neural mechanisms of this process are still not well understood. During the past years, two main model classes have emerged which claim to explain contour integration in the brain: probabilistic models and standard neural network models. Both classes employ 'association fields' (AFs) which implement the Gestalt rule of good continuation to describe dependencies between edge detectors. In probabilistic models, AFs are interpreted as conditional link probabilities, whereas in neural networks, AFs are interpreted as horizontal interaction weights between neural orientation columns with non-overlapping receptive fields. Besides this similarity, there are several important differences between both model classes: Probabilistic models multiply visual input and input from uni-directional horizontal interactions. In contrast, in standard neural networks all inputs are summed up, and horizontal interactions extend bi-directionally in visual space. The conditional link probabilities or AFs can be used to generate contour ensembles with pre-defined statistical properties by means of a Markov process. Consequently, contours are integrated optimally when using the same AF. While this poses no problem in a probabilistic model, the brain can not readily adapt the structure of horizontal interactions to the statistics of the current stimulus. In order to identify plausible neural mechanisms of contour integration, we investigate the explanatory power of these model classes. In particular, we compare model predictions to human behaviour using identical stimuli in simulations and psychophysical experiments. For this purpose, we implement a novel method for a quantitative comparison between the individual decisions from different contour observers like humans or models. We first find that decisions between humans are systematically correlated, hereby establishing a benchmark for models which should reproduce not only the human performance, but also any systematic errors due to illusory contour configurations. Second, a comparison of different model classes with human observers basing on both, correlations and detection performance, strongly suggests the involvement of multiplicative interactions between neuronal feature detectors in contour integration. Finally, by taking into account the eccentricities of the contour elements, we show that a very good match between multiplicative models and empirical results can be achieved.
A model for adjustment of the retinotectal mapping, using Eph-dependent ephrin regulation

Marcus Frean

Victoria University of Wellington, Wellington, New Zealand
marcus@mcs.vuw.ac.nz

The formation of a topographically ordered map in the retinotectal system, independent of neural activity, has long been thought to rely on the matching of molecular cues between the innervating retinal ganglion cell axons and their targets in the tectum. In the last few years Eph-ephrin signalling has emerged as the likely substrate for this matching process. For example, Eph-A receptors are expressed in a decreasing gradient along the naso-temporal axis of the retina, while their ephrin A ligands increase along the caudal-rostral axis of the tectum. In principle this allows a retinal axon to be targeted to a particular termination zone within the tectum. There are several plausible mechanisms for how this targeting might occur. These models are able to account to varying degrees for recent key findings, but do not address a number of experiments carried out even before the discovery of Eph-ephrin signalling. The experiments involved recovery of the topographic projection following ablation of portions of the retina or tectum, in which the resulting mapping is seen to expand or contract appropriately, apparently making optimal use of the remaining areas. This paper describes a model for the formation of topographic mappings that incorporates the recent discoveries about Eph-ephrin signalling and is able to account for the expansion and contraction experiments. The model features (a) regulation of ephrin expression in cells that are innervated from the retina, with changes acting to match the current ephrin value to a target level, and (b) smoothing of ephrin levels in the tectum via a local diffusion process. It also incorporates a continuous tectum and ‘soft’ competition between RGC axons for tectal space, as well as a tendency - rather than a hard constraint - for those axons to terminate in the tectum. An appealing feature is that since the ephrin levels are being reset, an axon growing from the retina at a later time should still find the correct position in the tectum.

Roles of short-term synaptic plasticity in electroreception under competing sensory signals

Kazuhisa Fujita

Yoshihiko Kashimori

University of Electro-Communications, Chofu, Japan

Short-term synaptic plasticity is ubiquitous in sensory systems. There has been significant progress in understanding the mechanism underlying short-term synaptic plasticity. However, the functional roles of plasticity in sensory coding and behavior are not well understood. To investigate this issue, we studied the functional roles of short-term synaptic plasticity in electroreception under competing sensory signals. Weakly electric fish use amplitude modulations of their self-generated electric organ discharge (EOD) to detect objects near by the fish and communication signals from a neighboring fish. The electric fish receive simultaneously two kinds of EOD amplitude modulations (EOD AMs), each of which is elicited by an object or a neighboring fish. The EOD AM elicited by an object is spatially localized around the object and has a low temporal-frequency (< 10 Hz), whereas the EOD AM elicited by a neighboring fish is globally distributed over the fish body surface and has a high temporal-frequency (> 20 Hz). The former is used for electrolocation and the latter for electrocommunication. The fish must extract in hindbrain the sensory features relevant to the behavior and then bind them in midbrain, in order to know the situation of environment. To extract successfully the sensory information in the hindbrain and the midbrain, the neural activities needs to be modulated by short-term synaptic plasticity. The roles of short-term synaptic plasticity in the hindbrain and the midbrain have been reported at single cell level. However, it is not yet clear how the short-term synaptic plasticity is used in the hindbrain and midbrain networks to extract and bind the stimulus features relevant to the two types of behavior. We develop a model of fish body by which we calculate numerically the spatiotemporal patterns of electric field around the fish body, and made a model of electroreceptor system which consists of receptors, hindbrain, and midbrain. We show here that the short-term synaptic plasticity in the hindbrain neurons are used to extract efficiently the spatiotemporal features required for electrolocation and communication from the competing signals. We also show that the short-term synapses of midbrain neurons are needed to combine consistently the two different stimulus features of the two types of behavior.

Mechanisms for the formation of neural representations of abstract rules

Stefano Fusi

Curti Emanuele

Wang Xiaojing

Institute of Neuroinformatics, Zurich, Switzerland

fusi@ini.unizh.ch

In many circumstances primates' behavior cannot be described as a simple one-to-one mapping between a stimulus and a motor response. Every event or action can modify the animal's dispositions to behavior, and, for example, the same sensory stimulus might lead to different motor responses depending on the context, previously determined by a set of other cues. We propose a network model in which each inner mental state is represented by an attractor of the neural dynamics. Each state represents a rule encoding the prescriptions for going from one state to another or for expressing a decision about a motor response. We illustrate this theoretical framework with a simple example. We consider a task in which an animal has to respond with a saccadic movement (Left or Right) to two sensory stimuli (A and B). In one context A should lead to L and B to R. In another one the associations are reversed and A should lead to R and B to L. The two rules can be expressed in words as: 1) when A is associated with L, then B is associated with R 2) if A leads to R, then B leads to L. We address two issues: how are the rule representations built? How can the active representation of a rule lead to the decision about the motor response? We propose a network in which two populations of neurons compete to express a final decision about the motor response (L or R). These two populations are assumed to be highly structured due to heterogeneities. In particular we assume that within L there is a population AL which has a preference for A (i.e. before learning, A drives it to higher frequencies than other neurons within L). Analogously we can define populations BL, AR, BR. When the first rule (AL- BR) is in effect, the activation of AL is consistently followed by the activation of AL or BR. The rule representation then forms because of the temporal contiguity of AL-BR for rule 1, and AR-BL for rule 2. When rule 1 is active, then A favors L in the competition because AL receives a recurrent (from BR) and a sensory input, while BR receives only the recurrent input. Hence stimulus A steers the activity of the network towards a state which expresses the final decision about the motor response and it keeps in memory which rule is in effect.

NeuronRank for Mining Structure-Activity Relationships of Biological Neural Networks

Tayfun Gürel

Luc De Raedt

Stefan Rotter

Bernstein Center for Comp. Neuro., Freiburg

Machine Learning Lab., University of Freiburg, Freiburg, Germany

guerel@informatik.uni-freiburg.de

deraedt@informatik.uni-freiburg.de

It is a difficult task to relate the information of a cortical neural network to its dynamic activity analytically. In the present work, we employ machine learning and data mining algorithms to obtain these relations from example random recurrent cortical networks and corresponding simulations. Inspired by the Page-Rank and hubs & authorities, we introduce the NeuronRank algorithm, which assigns a source value and a sink value to each neuron in the network. We show its usage to extract features from a network for a successful prediction of its activity. Our results show that NeuronRank features are successful to predict average firing rates in the network, and the firing rate of output neurons reading the network.
During speech production, two different areas of the brain become simultaneously active: primary motor cortex (responsible for sound articulation) and auditory cortex (stimulated by the produced sounds). We postulate that during language acquisition, the repeated simultaneous activation of these two areas leads, through Hebbian learning, to the formation of strongly-associated neural assemblies. The formation of these assemblies facilitates our understanding of the underlying biomechanical principles as well as their neural control. The goal of this study is to specifically demonstrate that stable biped walking can be achieved by combining the physical properties of the walking robot with a small, reflex-based neuronal network, which is governed mainly by local sensor signals. Here we will show that human-like gaits emerge without specific position or trajectory control and that the walker is able to compensate for small disturbances in a way that follows normal human walking patterns.

Exploring large-scale models of neural systems with the Neural Simulation Tool NEST

Marc-Oliver Gewaltig  
Markus Diesmann

Honda Research Institute Europe GmbH
Offenbach, Germany

marc-oliver.gewaltig@honda-ri.de

diesmann@biologie.uni-freiburg.de

The Neural Simulation Tool NEST is a simulation environment for large heterogeneous networks of point neurons or neurons with a small number of compartments. In this contribution, we present the main features of NEST from a user's perspective. Through a number of examples, we illustrate how large-scale simulations of neural systems can be constructed and executed. We also present results which demonstrate the capabilities and performance of NEST in large-scale simulations, using multiple processors or cores. In a companion contribution, we describe our latest technological advances in integrating parallel and distributed simulation (Eppler et al.) A network simulation in NEST is set up in a number of steps: First, a network model is constructed by creating neurons from a set of different models and connecting them in the desired way. It is possible to combine model neurons of different types, thereby constructing heterogeneous networks. Sub-networks help to hierarchically organize large networks. A simulation follows the analogy of an electrophysiological experiment. Measurement and simulation of network dynamics are made possible by special network elements, called devices. After the network is set-up, it can be executed for a given amount of time, and results may be analyzed either online or offline. A powerful and flexible simulation language supports the user in tasks which require the combination of simulation and data analysis such as scanning the parameter space of a model, or interfacing with packages like Matlab, Mathematica, or Python, for online analysis or visualization. Moreover, the modularized and extensible architecture allows NEST to be tailored to a wide range of applications. NEST is developed and maintained by the NEST Initiative (see www.nest-initiative.org), which also provides public releases under an open-source type license. Our current research focuses on the integration of parallel and distributed simulation strategies into a common framework (Morrison et al. 2005, Neuronal Computation).
Population synchrony generation in a layered network of the cat visual cortex

Jens Kremkow  Tuesday Poster – T69
Arvind Kumar, Stefan Rotter, Ad Aertsen
Neurobiology and Biophysics, INCM/UMR6193/CNRS, Freiburg, Germany
kremkow@biologie.uni-freiburg.de, kumar@biologie.uni-freiburg.de

Recently a quantitative wiring diagram of the local neuronal network of cat visual cortex was described (Binzegger et al. 2004), which gives the first realistic estimate of synaptic connections among various neuron types in different cortical layers. Here we numerically studied the dynamics of the resulting heterogeneous layered network of leaky-integrate-and-fire neurons, connected with conductance-based synapses. Binzegger et al. (2004) specified the total number of neurons in cat area 17 to be ~ 31x10^6. We downscaled the network of area 17 of cat to a size of 10,000 or 50,000 neurons such that the proportion of neurons and the ratio of excitatory (NE) and inhibitory (NI) neurons across the layers were conserved. The number of synapses within a layer was restricted to have a maximum sparsity p = 0.10% (p = K/N = 100, K is the number of synapses each neuron receives and N is the number of neurons). The layered network elicited an interesting asynchronous activity intermitted by population wide synchronizations, among other states. These population bursts [PB] were initiated by a network hot spot and spread into the whole network. The cause of this PB is the correlation amplifying nature of the recurrent network, which becomes significant in densely coupled network. The layer of origin was dependent on the level of excitatory recurrent connections, which was highest in layer 2/3. PBs occurred for all the network sizes studied (up to 50,000), including the possibility that a PB occurs because the correlation originated due to shared presynaptic pools. However, the characteristics of the PBs (e.g. the probability of their occurrence) were susceptible to changes in the network architecture. So we conclude that in a heterogeneous structured network, the region with highest degree of recurrence and high out-degree may become a hot-spot to initiate a population wide synchronization.

Effects of multiple spike-initiation zones on signal integration properties of leech touch cells

Jutta Kretzberg  Monday Poster – M23
Friedrich Kretschmer, Antonia Marin-Burgin
University of Oldenburg, IBU, Oldenburg, Germany
jutta.kretzberg@uni-oldenburg.de, friedrich.kretschmer@mail.uni-oldenburg.de

Information processing is not for all neurons consistent with the classical picture of a neuron that transforms integrated input signal to sequences of action potentials at the axon hillock. Particularly in sensory cells and in invertebrate neurons, spikes can be generated far away from the soma. Several neuronal types were found to have multiple spike-initiation zones. Moreover, the site of spike initiation can vary depending on neuronal excitation. These findings can have severe impacts on neuronal information processing. The aim of this combined experimental and modeling study is to analyze the effects of multiple spike-initiation zones in T-cells (touch sensors) of the leech. The soma of these mechanosensory neurons is located in a ganglion of the central nervous system, while the touch sensitive dendritic endings are located in the skin. Based on experimental results, Burgin & Szczupak (2003) proposed that leech T-cells have two separate spike initiation zones, a peripheral one to signal touch stimuli and a central one to signal synaptic input within the ganglion. To test this hypothesis, we implemented a compartmental model of a leech T-cell in NEURON, using modified versions of the cell morphology shown by Cataldo et al. (2005) and Hodgkin-Huxley type conductances developed by Baccus (1998). This model reproduces the experimental finding that spike responses to somatic current injection cease during inhibitory synaptic input, while responses to skin stimulation are not altered. Comparing a model with homogenous channel distribution and a model with separate spike initiation zones for peripheral and central information processing, we found that both models show this effect. Hence, the experimentally observed difference in the integration of inputs could be explained by the electric isolation of spatially distant parts of the cell. By specifically analyzing I. How does the spatial distribution of active zones influence the integration of central and peripheral inputs? 2. How is information processing influenced by the ratio of the maximum conductances in strongly active and weakly active regions of the cell? 3. Does the site of spike initiation vary depending on the level of excitation? 4. Can the location of the inhibitory synapse be predicted? We hope to find universal principles of neuronal information processing, showing how inputs interact and influence the final output of a neuron. References: Burgin & Szczupak (2003) J Comp Physiol A 189:59-67. Cataldo et al. (2005) J Computat Neurosci 18:5-24. Baccus (1998) Proc. Natl. Acad. Sci. USA 95:8345-8350.

Population synchrony generation in a layered network of the cat visual cortex

Jens Kremkow  Tuesday Poster – T69
Arvind Kumar, Stefan Rotter, Ad Aertsen
Neurobiology and Biophysics, INCM/UMR6193/CNRS, Freiburg, Germany
kremkow@biologie.uni-freiburg.de, kumar@biologie.uni-freiburg.de

Recently a quantitative wiring diagram of the local neuronal network of cat visual cortex was described (Binzegger et al. 2004), which gives the first realistic estimate of synaptic connections among various neuron types in different cortical layers. Here we numerically studied the dynamics of the resulting heterogeneous layered network of leaky-integrate-and-fire neurons, connected with conductance-based synapses. Binzegger et al. (2004) specified the total number of neurons in cat area 17 to be ~ 31x10^6. We downscaled the network of area 17 of cat to a size of 10,000 or 50,000 neurons such that the proportion of neurons and the ratio of excitatory (NE) and inhibitory (NI) neurons across the layers were conserved. The number of synapses within a layer was restricted to have a maximum sparsity p = 0.10% (p = K/N = 100, K is the number of synapses each neuron receives and N is the number of neurons). The layered network elicited an interesting asynchronous activity intermixed by population wide synchronizations, among other states. These population bursts [PB] were initiated by a network hot spot and spread into the whole network. The cause of this PB is the correlation amplifying nature of the recurrent network, which becomes significant in densely coupled network. The layer of origin was dependent on the level of excitatory recurrent connections, which was highest in layer 2/3. PBs occurred for all the network sizes studied (up to 50,000), including the possibility that a PB occurs because the correlation originated due to shared presynaptic pools. However, the characteristics of the PBs (e.g. the probability of their occurrence) were susceptible to changes in the network architecture. So we conclude that in a heterogeneous structured network, the region with highest degree of recurrence and high out-degree may become a hot-spot to initiate a population wide synchronization. Binzegger, T., Douglas, R. J., & Martin, K. A. C. (2004). A quantitative map of the circuit of the cat primary visual cortex. [J. Neurosci.] 39 (24), 8441-8453.

Dale's principle and the formation of spatio-temporal activity patterns

Birgit Kriener  Tuesday Poster – T37
Ad Aertsen
Stefan Rotter
BCCN Freiburg (Germany), Albert-Ludwigs-University Freiburg (Germany)
kriener@biologie.uni-freiburg.de aertsen@biologie.uni-freiburg.de

Cortical networks are assumed to respect Dale's principle, according to which neurons are either inhibitory or excitatory for all their synaptic projections. Here we demonstrate the crucial impact of Dale's principle on the ongoing activity dynamics in networks of different topologies, ranging from regular and 'small-world' to random coupling topologies in 1- and 2-dimensional space. We find that in simulated networks of integrate-and-fire neurons, which do not regard Dale's principle the inhibition dominated regime is nearly independent of the underlying network topology, while Dale-conform networks show a broad range of synchronization phenomena and formation of spatio-temporal activity patterns (e.g. 'activity bumps') according to their respective coupling scheme.

Dynamics of latching in Potts models of large scale cortical networks

Emilio Kropff  Tuesday Poster – T72
Alessandro Treves
SISSA,Trieste, Italy
kropff@sissa.it, ale@sissa.it

Multi-modal Potts networks have been introduced as simplified models of large scale cortical networks that store and retrieve semantic memories. We study a version of these networks which includes two important ingredients: neural adaptation and correlation in the stored patterns. It has been shown that under these conditions Potts networks present latching: the capacity to hop spontaneously from one attractor state to another following a structured set of complex transition probabilities. Latching is a mechanism for recursion, and thus a candidate to explain the emergence of language in human beings, following the proposal by Chomsky et al, 2002. We develop the mean field equations that govern the dynamics of latching for networks storing 1 and 2 global patterns. This is enough to study 'noiseless' latching, which we show to be the result of a finite-size effect for low levels of correlation. Only for very high correlation between patterns the numerical solutions of the dynamical equations have a latching behavior. Important parameters that govern dynamics (other than the size of the network) are the threshold U, mimicking a global inhibition system, and the self-weight of Potts units J, accounting for the complexity of local networks to sustain their activity within a given basin of attraction. An equilibrium between these parameters is necessary for latching, while small variations of U can control the complexity of latching transitions for a given set of correlated patterns, spanning all the range from completely random to deterministic, and including the intermediate -- rich in complexity -- case.
Pyramidal cells in the electrosensory lateral line lobe (ELL) of the electric fish Apteronotus leptorhynchos display a characteristic mode of burst discharge that has been shown to have important implications for sensory coding. This mode of burst discharge involves a coupling of active dendritic and somatic compartments by a depolarizing afterpotential (DAP) caused by the generation of a dendritic spike. Recent work has involved characterization of synaptic mechanisms for modulation of the burst dynamics. A diffuse inhibitory feedback projection creates GABAergic contacts with pyramidal cells on their proximal dendrites, activating GABA receptors. Pharmacological activation of GABA receptors in ELL pyramidal cells by focal application of baclofen in vitro leads to a shift in both firing and burst threshold. However, activation of these conductances has a greater effect on tonic firing threshold than on burst threshold, causing a decrease in tonic firing, and a relative increase in burst firing. A reduced model of burst dynamics in our cells was able to replicate these effects, and suggests that the shift to burst firing mode requires a dendritic locus of inhibition. A two parameter bifurcation analysis of our reduced model shows the shift to burst firing requires GABA type synaptic conductances (Erev=-90), but fails to function with GABAa type conductances (Erev=-70). This is consistent with previous results showing no switch to bursting mode after dendritic activation of GABAa receptors by muscimol. We suggest that this shift to burst firing mode after activation of dendritic inhibitory conductances is due to a change in the relative coupling between somatic and dendritic voltages. The increased delay increases the effectiveness of the DAP on the somatic membrane voltage, leading to an immediate burst discharge. In ELL pyramidal cells, dendritic inhibition has non-linear effects due to the inherent dynamics of the cell, which may be able to drastically influence the coding properties of the cell.

Comparison of Dynamical States of Random Networks with Human EEG
Ralph Meier
Arvind Kumar, Andreas Schulze-Bonhage, Ad Aertsen
Inst. Biol. III, A. L. University Freiburg, Freiburg, Germany
meier@biologie.uni-freiburg.de, kumar@biologie.uni-freiburg.de

Certain activity states of random neural network models have been found to resemble ongoing cortical activity in vivo in terms of spike statistics. While there are promising approaches, there is currently no standard procedure to relate network model dynamics to experimental population activity measures such as LFP, EEG or ECoG. Here, we try to bridge the gap between network activity states and relevant states in electrophysiological signals (EEG) recorded from humans. We simulated randomly connected networks of 50,000 leaky-integrate-and-fire type neurons (80% excitatory, 20% inhibitory neurons), representing a 0.5mm2 slice of cortex using the NEST simulation environment. In the first network type (referred to as homogeneous) all neurons had identical passive properties, in the second (referred to as heterogeneous) the passive properties were chosen from a normal distribution. We obtained a network population (Npop) activity signal by binning the spikes of all neurons. The spectral bandwidth of Npop was much wider than the EEG bandwidth. To draw a comparison between Npop and EEG, we first transformed Npop, using an alpha-function shaped kernel, to a signal (Sim-EEG) closely resembling the human EEG. We compared the resulting power spectral density (PSD) characteristics to those of the human EEG from awake, behaving subjects. We found that Sim-EEG for asynchronous irregular (AI) and synchronous irregular (SI) network states showed a good match with the human EEG - especially in the theta and delta bands. The Sim-EEG for the heterogeneous network model resembled the human EEG better, even in alpha and beta frequency bands. The small mismatch between Sim-EEG and human EEG could be due to an inappropriate choice of the convolution kernel. Therefore, we empirically estimated the kernel by assuming a linear mapping between Npop and human EEG. We found that convolving Npop with either the empirically estimated kernel or a gamma-function approximation gave a better fit, as measured by correlation of PSD-bands with the human EEG. In summary, we found that AI-type network activity is closely related to the human EEG in the awake state. Currently, we are studying the relation between other dynamic network states and clinically or behaviorally relevant EEG states. While there is good hope for bridging the gap between network simulations and human population activity recordings, further improvements in both, network models and conversion procedures may be needed.
In this communication we study both the stationary and transient response properties of a large population of independent neurons with conductance based synapses subject to an intense background mimicking conditions found \( \{ \text{vem in vivo} \} \). In the steady state, we compare the predictions of a solution of a computational model (R Moreno-Bote and N Parga, 2005) with the predictions of more standard models. In the transient regime, we show that this solution can reproduce some aspects of recent findings in auditory cortex (Wehr and Zador, 2003 and Tan et al 2004). Besides, we compare our prediction of the bimodality of the firing probability with its experimental observation in V1 neurons (Carandini, 2004).

### Spike-timing dependent plasticity in balanced random networks

Abigail Morrison  
Ad Aertsen, Markus Diesmann  
Bernstein Center for Computational Neuroscience, Freiburg, Germany  
abigail@biologie.uni-freiburg.de, aertsen@biologie.uni-freiburg.de

The balanced random network model attracts considerable interest because it explains the irregular spiking activity at low rates and large membrane potential fluctuations exhibited by cortical neurons in vivo. Here, we investigate to what extent this model is also compatible with the experimentally observed phenomenon of spike-timing dependent plasticity (STDP). Confronted with the plethora of theoretical models for STDP available, we re-examine the experimental data. On this basis we propose a novel STDP update rule, with a multiplicative dependence on the synaptic weight for depression, and a power law dependence for potentiation. We show that this rule, when implemented in large (\( 10^5 \) synapses per neuron), is compatible with the asynchronous irregular activity regime. The resultant equilibrium weight distribution is unimodal with fluctuations exhibited by cortical neurons in vivo. Here, we investigate to what extent this model is compatible with the experimentally observed phenomenon of spike-timing dependent plasticity (STDP).

### Modeling Spike-Frequency Adaptation in an Awake Cortical Network

Elif Muller  
Johannes Schemmel  
Karheinz Meier  
Kirchhoff Institute of Physics, Heidelberg, Germany  
emueller@kip.uni-heidelberg.de, schemmel@kip.uni-heidelberg.de

We show that the five-dimensional master equation for conductance-based integrate-and-fire neurons with spike-frequency adaptation and refractory mechanisms recieving a sufficiently strong but balanced barrage of Poisson inputs can be well approximated by a two-dimensional master equation by essentially neglecting membrane potential dynamics. Negative inter-spike interval correlations and transient population responses for the simplified model are shown to be in excellent agreement with the full system. These models exhibit filtering properties similar to a high-pass filter and transient responses at step stimuli which contribute to the evocation of synchronous bursts for weak changes in stimulation in balanced sparse coupled networks of inhibitory and spike-frequency adapting excitatory integrate-and-fire neurons characterizing a local circuit of cortical layer IV.

### Population Codes for Natural Dynamic Stimuli

Rama Natarajan, Quentin Huys, Peter Dayan, Richard Zemel  
Department of Computer Science, University of Toronto, Toronto, Canada  
rama@cs.toronto.edu, qhuys@gatsby.ucl.ac.uk

We propose a theoretical framework for efficient representation of time-varying sensory information using dynamic population codes. Our approach is based on the hypothesis that for accurate perception and computation, it must be possible for downstream neurons to readily extract correct estimates of stimulus states from the sensory input. Intuitively, optimal computational decoding must recover most of the encoded information. However, we have recently shown that even in a fairly constrained and analytically tractable formulation of a dynamic setting, decoding correct estimates can be a difficult computational problem. Information carried by the spikes is only temporally relevant, and when the inputs are noisy or sparse it becomes necessary to maintain a spike history to perform accurate inference at any given time. We posit a recurrently connected population of neurons that recodes the input representation such that each spike can be decoded independently in a causal manner, without referring to any spiking history. Decoding is carried out by a computationally simple, biologically reasonable scheme that interprets spiking activity as representing a probability distribution over stimulus states. Coding then involves learning to generate an apposite representation that optimizes the fidelity of decoding. We evaluate the efficacy of the proposed coding scheme by assessing the capability of the simple decoder in extracting the available information.

### Resonance as an effective mechanism of dynamical stability in large microcircuits of spiking neurons

Raul Muresan  
Cristina Savin, Iosif Ignat  
Frankfurt Institute For Advanced Studies, Center for Cognitive and Neural Studies, Frankfurt am Main, Germany  
raulmuresan@yahoo.com, csevin@gmail.com

The dynamical stability of large networks of spiking neurons is still an important issue in computational neurosciences. Here we investigate the behavior of a recently proposed model of spiking neurons, namely the resonator neuron put forward by E.M. Izhikevich. We show that the model prefers low frequency stimuli, while it is being less sensitive to high input bombardment. Furthermore, we show that large microcircuits of resonating neurons can easily get self-sustained in the absence of any external stimulation. Such a self-sustained regime proves to be very stable and robust for a wide range of network parameters.

### Serial correlation of inter-spike intervals in cortical neurons

Martin Nawrot  
Clemens Boucsein, Victor Rodriguez-Molina, Sonja Gruen, Stefan Rotter  
Neuroinformatics, Free University Berlin  
Bernstein Center Computational Neuroscience, Berlin, Germany  
nawrot@neurobiologie.fu-berlin.de, boucsein@biologie.uni-freiburg.de

We investigated serial interval statistics of spike trains recorded from cortical neurons in two different experimental settings under stationary conditions, and tested the mutual independence of ISIs. First, we performed a set of in vitro whole-cell patch clamp experiments in layer 5 pyramidal neurons of neocortex, which were continuously stimulated by means of somatic noise current \( i_{\text{noise}} \). Input currents were designed to mimic stationary and uncorrelated input from large pools of excitatory and inhibitory neurons. Second, we analyzed in vivo intracellular recordings of spontaneous activity in neocortical neurons of the anesthetized rat. We found a general tendency for weak and negative first order serial interval correlations in all neurons. The correlations of neighboring intervals were small with an average of approx. \(-0.05\) in vitro and of \(-0.2\) in vivo, and significantly different from zero in about 50% of all tested spike trains. No significant serial correlation of higher order was found. Our results indicate that cortical pyramidal neurons are not compliant with a simple renewal model. We suggest an abstract point process model in which the spike probability at any given time takes into account the previous spike train history up to the penultimate spike to account for the negative 1st order serial correlation. This model provides a more accurate description of spontaneous spiking in cortical neurons than the simple renewal model. We discuss the effect of serial correlations on statistical quantities such as interval and count variability. Supported by the German Federal Ministry of Education and Research (BMBF, grants 01GQ0413 to BCCN Berlin and 01GQ0420 to BCCN Freiburg).
Modulation of excitability in CA1 pyramidal neurons via the interplay of EC and CA3 inputs

Eleftheria Kyriaki Pissadaki, Panayiota Poirazi
IMBB-FORTH, Vasilika Vouton, Hellas
ekpissad@imbb.forth.gr, poirazi@imbb.forth.gr

Hippocampal CA1 pyramidal neurons receive extrahippocampal and intrahippocampal inputs. EC projections converge at Stratum Lacunosum Moleculare (SLM) via the Temporopammonic Pathway (TA) while the Schaffer Collateral Pathway (SC) from CA3 projects to the Stratum Radiatum (SR) of the CA1 field. CA1 neurons in turn project to the Subiculum and to the deeper layers of EC. The SC pathway serves as the primary excitatory input to CA1 cells whereas the TA pathway provides a potent inhibitory modulation. The interplay between the two pathways can trigger different patterns of neuronal responses. The relative temporal placement of the stimuli conveyed by the two pathways seems to efficiently modulate the excitability of CA1 pyramidal neurons. Specifically, the excitatory effect of SC inputs is greatly attenuated when preceded by SLM stimulation within a well defined time-window. This phenomenon is referred to as the Spike Blocking effect. Dvorak-Carbone and Schuman, 1999 found that spike blocking efficacy has a temporal relation with the GABA signalling pathway, whereas in the presence of GABA antagonist spike blocking was almost abolished. In this work, we investigate the contribution of the GABA receptor on the aforementioned phenomenon using a refined version of a previously published multicompartmental model of a CA1 pyramidal cell. We also investigate to what extend spike blocking is affected by the clustering of synaptic inputs within the dendrites of the model cell. We find that in addition to a temporal regulation, the arrangement of synaptic contacts provides a location-dependent modulation of excitability by the EC input, which can selectively induce spike blocking or spike enhancement. This form of modulation could provide a cellular mechanism for switching between encoding and retrieval processes. Alternatively, this excitability modulation could subserve the consolidation of strong, TA-mediated stimuli. Experimental data support the notion that strong, patterned synaptic input from the TA pathway in initiating the transport of new mRNA transcripts to the synapse and propagating the response to higher brain regions.
Correlation analysis at these different levels is used to investigate the interplay between different neurons or neuron populations. Recent studies have utilized correlation measures to discover how different signal types relate to each other, and to the spiking activity mediating the fundamental interaction of the elements constituting the system. It has also been argued that the neuronal dynamics itself depends on the spatial and temporal correlations of input signals at different levels (e.g., spikes, synaptic currents). In this study we focus on signals which are derived from spike data by linear filtering. We investigate how correlation measures such as the standard correlation function, the joint PSTH, or the correlation coefficient are altered by the filtering procedure and highlight the consequences for the measurement and interpretation of correlations on the one hand, and for neural dynamics on the other. By generalizing shot-noise theory to joint (non-stationary, non-Poissonian) point processes, we show that filtering of spike signals by some linear kernel is accompanied by linear filtering of their correlation functions. To illustrate the effects, we construct common-input models which simultaneously enable us to generate correlated spike processes in a simple but realistic manner and describe the resulting correlation functions analytically. Surprisingly, the deformation of spike train auto- and cross-correlation functions by linear filtering generally leads to a dependence of the correlation coefficients on the properties of the filter kernel. In particular this holds for spike count signals, where correlations exhibit a clear bin-size dependence. We point out that in common-input systems, classical pairwise correlation measures are determined by the marginal second-order statistics of the presynaptic sources represented by their auto-correlations. We present methods which eliminate these auto-correlation effects for specific examples, thereby allowing an interpretation of measured correlations in terms of anatomical structure. Moreover, we demonstrate how features of the filter kernel can be reconstructed from auto- and cross-correlations of the filtered signals. In order to emphasize the relevance of our findings for biological systems, we consider a network model of a small cortical area with realistic anatomical and electrophysiological parameters. This example shows how global network oscillations as observed both experimentally and theoretically can effectively control the strength of correlations at different signal levels.

Branched dendritic tree with active spines

Yulia Timofeeva
Stephen Coombes
Gabriel Lord

University of Nottingham, Nottingham, UK

yulia.timofeeva@nottingham.ac.uk
stephen.coombes@nottingham.ac.uk

The dendrites of many nerve cells are complex branching structures that receive and process thousands of synaptic inputs from other neurons. Dendritic spines can be present in large densities on the dendrites. They are equipped with excitatory channels and loci for receiving excitatory synaptic input. Here we introduce a mathematical model of a branched dendritic tree based upon a generalisation of the analytically tractable Spike-Diffuse-Spike model. The active membrane dynamics of spines are modelled by an integrate-and-fire process. The spines are assumed to be discretely distributed along a passive branched dendritic structure. We obtain a quasi-analytical solution using the ësum-over-pathsí approach formulated by Abbott et.al. (Biol. Cybern., 1991, vol.66, pp. 49-60). The model supports salutary travelling wave propagation and wave scattering amongst branched dendritic trees. It is ideally suited for the study of spatio-temporal filtering properties and neural responses to different patterns of synaptic input.
Signal Propagation and Switching in Networks

Tim Vogels
Larry Abbott

Brandeis University, Columbia University
New York, New York, United States

vogels@brandeis.edu
lf2103@columbia.edu

Signaling between different brain areas is essential for cognitive function, but reliable target-specific signal propagation without large-scale synchronization is difficult to achieve in network models. We build and study randomly connected, sparse networks of integrate-and-fire neurons and show that they generate sufficient background activity to support signal transmission. We characterize the fidelity and range of signal propagation in such networks as a function of the magnitude and variability of synaptic weights, connectivity patterns, and other relevant parameters. Cognitive function and motor action also require mechanisms that gate and control the flow of information. We introduce gating mechanisms in both local and long-range connections, and special features like patchy projections or cell-type specific couplings. In this study we investigated and compared several alternative network architectures which may eventually lead to more realistic cortical network models. First, in order to enable distance dependent connectivity, we assumed an embedding of all neurons in space, reflecting the geometry of dendrites and axons. To assess the influence of the spatial embedding on network topology we considered both randomly positioned nodes and regular lattices. The wiring comprised local and non-local connections in various compositions. The parameters of all models were arranged to span the full continuum from local/regular to completely random connectivity. Second, we employed the framework of stochastic graph theory to define a set of characteristic network properties. For example, we analyzed the degree distribution, clustering coefficient and average shortest path length of our networks, as well as the spectrum of eigenvalues and the locality of the eigenvectors of the corresponding adjacency matrices. This enabled us to quantitatively study the impact of structural neuro-anatomical knowledge, and to compare our enriched cortical network models to other well-known types of abstract graphs, e.g. small-world networks. In a comparative study of these models we show that the global graph-theoretic properties of the resulting networks may be vastly different. Especially, the abundance of non-local connections is a crucial point, potentially leading to dynamic changes in network topology. In addition, the modalities of the spatial embedding are important as they strongly influence the variance of degrees across the network. In conclusion, we began to identify a set of parameters that characterize large networks like the neocortex as an integrated system, helping to better interpret neuro-anatomical data, and to develop new network models sub-serving the understanding of cortical function.

Anatomy-based network models of cortex and their statistical analysis

Nicole Voges
Ad Aertsen
Stefan Rotter

Inst. Bio III, A.-L. Universitèt Freiburg, Freiburg, Germany
nicole.voges@biologie.uni-freiburg.de
aertsen@biologie.uni-freiburg.de

Sensitivity analysis of neuronal firing to morphologic and spatially extended intrinsic properties

Christina Weaver
Susan Wearne

Mount Sinai School of Medicine, New York, New York, USA
christina.weaver@mssm.edu
susan.wearne@mssm.edu

Mathematical models are used frequently to elucidate the physiological mechanisms underlying experimentally observed behavior. Towards that end, it is valuable to know which model parameters contribute most to model output in some quantitative way. Our interest lies in understanding how dendritic morphology and spatially extended intrinsic properties contribute to the firing behavior of compartmental models. Various interactions between the parameters describing these properties makes it difficult to determine which parameters are most important. To investigate such parameters simultaneously, local sensitivity analysis techniques are used within a parameter space defined by both morphologic features and spatially extended intrinsic properties. These methods allow comparison of the sensitivity of neuronal model output to various parameters, regardless of parameter unit and magnitude. These sensitivity analysis techniques are demonstrated on a compartmental model composed of a soma and a single equivalent dendrite. Perturbations are made to the surface area, length, and diameter of the dendrite while controlling for associated changes in active channel distributions and numbers. For comparison, spatially distributed dendritic ion channel densities and parameters describing calcium dynamics are also perturbed, while dendritic morphology is held constant. The normalized sensitivity of action potential (AP) and afterhyperpolarization (AHP) shape and firing rate to each parameter is computed at several points in parameter space. The data indicate that some parameters consistently have a strong effect on AHP shape and firing rate while others have little effect, regardless of where the point lies in parameter space. Importantly, our data show that there are regions in parameter space in which morphologic parameters have a greater effect on model output than spatially extended properties that are purely conductance-related. Analysis of the effects of dendritic length, diameter, and surface area shows that these three parameters combine to influence AHP shape and firing rate in different ways. These findings lead to a greater understanding of how morphologic and spatially extended intrinsic properties might interact to generate the rich dynamics of neurons observed experimentally.

Astrocyte modulation of synaptic transmission - autapse as a case study

Vladislav Volman
Eshel Ben-Jacob
Herbert Levine

School of Physics & Astronomy, Tel-Aviv Univ., Tel-Aviv, Israel
hamlet@tamar.tau.ac.il
eshel@tamar.tau.ac.il

We present a simple biophysically tractable model for the coupling between synaptic transmission and the local calcium concentration on an enveloping astrocytic domain. This interaction enables the astrocyte to modulate the information flow from pre-synaptic to post-synaptic cells in a manner dependent on previous activity at this and other nearby synapses. We explored the possible consequences of this modulation for an astrocyte-gated autaptic oscillator, arguably the simplest possible neuro-glia circuit. For this apparently simple model system, we found that astrocyte modulation of autaptic transmission results in the irregular burst-like spiking statistics of a model neuron, manifested in the shape of the distribution tail and in an increase in firing rate when compared to the distribution consisting of calcium oscillations in the adjacent astrocyte. Our model suggests a novel, testable hypothesis for the spike timing statistics measured for rapidly-firing cells in culture experiments.

Sensitivity analysis of neuronal firing to morphologic and spatially extended intrinsic properties

Christina Weaver
Susan Wearne

Mount Sinai School of Medicine, New York, New York, USA
christina.weaver@mssm.edu
susan.wearne@mssm.edu

Mathematical models are used frequently to elucidate the physiological mechanisms underlying experimentally observed behavior. Towards that end, it is valuable to know which model parameters contribute most to model output in some quantitative way. Our interest lies in understanding how dendritic morphology and spatially extended intrinsic properties contribute to the firing behavior of compartmental models. Various interactions between the parameters describing these properties makes it difficult to determine which parameters are most important. To investigate such parameters simultaneously, local sensitivity analysis techniques are used within a parameter space defined by both morphologic features and spatially extended intrinsic properties. These methods allow comparison of the sensitivity of neuronal model output to various parameters, regardless of parameter unit and magnitude. These sensitivity analysis techniques are demonstrated on a compartmental model composed of a soma and a single equivalent dendrite. Perturbations are made to the surface area, length, and diameter of the dendrite while controlling for associated changes in active channel distributions and numbers. For comparison, spatially distributed dendritic ion channel densities and parameters describing calcium dynamics are also perturbed, while dendritic morphology is held constant. The normalized sensitivity of action potential (AP) and afterhyperpolarization (AHP) shape and firing rate to each parameter is computed at several points in parameter space. The data indicate that some parameters consistently have a strong effect on AHP shape and firing rate while others have little effect, regardless of where the point lies in parameter space. Importantly, our data show that there are regions in parameter space in which morphologic parameters have a greater effect on model output than spatially extended properties that are purely conductance-related. Analysis of the effects of dendritic length, diameter, and surface area shows that these three parameters combine to influence AHP shape and firing rate in different ways. These findings lead to a greater understanding of how morphologic and spatially extended intrinsic properties might interact to generate the rich dynamics of neurons observed experimentally.