2009 Sloan-Swartz Annual Meeting

On

Theoretical Neuroscience

25 – 28 July 2009

Harvard University

Center for Brain Science

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SCHEDULE

SATURDAY 25 JULY

19:30 Reception and registration

SUNDAY 26 JULY

8:00 Breakfast and registration

8:45 Welcoming remarks

Circuits Carlos Brody (Princeton), Chair

9:00 David McCormick (Yale): Functional properties of local cortical networks

9:30 Daniel Martí (NYU): A model of two interacting accumulators for reach and saccade reaction times

10:00 Tatjana Tchumatchenko (Bernstein): Correlations and synchrony in threshold neuron models

10:30 Paul Miller (Brandeis): Recall of word sequences via short-term plasticity in a temporal context model

11:00 Break and poster setup

11:30 *Guest speaker*—Mitya Chklovskii (Janelia): From neuronal circuit reconstructions to principles of brain design

12:30 Lunch and posters

Coding Larry Abbott (Columbia), Chair

14:15 Tatyana Sharpee (Salk): Information maximization across a synapse

14:45 *Special lecture*—Markus Meister (Harvard): Neural computations in the retina

15:45 Scott Makeig (UCSD): Linking brain, mind, and cognition

16:15 Break

16:45 *Guest speaker*—Andreas Herz (Munich): Simplicity in a complex world: subthreshold membrane-potential resonances shape spike-train statistics

17:45 Dinner on your own

20:00 Posters and drinks

MONDAY 27 JULY

8:15 Breakfast

Learning and Plasticity Robert Shapley (NYU), Chair

9:00 Stefano Fusi (Columbia): A multi-stage synaptic model of memory

9:30 David Sussillo (Columbia): Perception as Modeling: A neural network that extracts and models predictable elements from input

10:00 Tim Verstynen (UCSF): From synapse to BOLD: circuit plasticity and macroscopic responses in sensory-motor cortex

10:30 Michael Brainard (UCSF): Sources and function of variability in adult song production and plasticity

11:00 Break

11:30 *Guest speaker*—Jennifer Raymond (Stanford): The building blocks of cerebellum-dependent learning

12:30 Lunch, posters, and Directors' Lunch

Technologies and Structures Eve Marder (Brandeis), Chair

14:15 *Guest speaker*—Ed Boyden (MIT): Technologies for controlling neural circuit dynamics

15:15 Alexei Koulakov (CSHL): Disposable stem cell hypothesis: a new model for neurogenesis in adult hippocampus

15:45 Josh Dubnau (CSHL): Experimental evolution to probe gene networks underlying cognition in Drosophila

16:15 Break

16:45 *Guest speaker*—Jeff Lichtman (Harvard): Plumbing the Connectome

17:45 Break and lab tours

19:00 Banquet

20:30 Posters and drinks

TUESDAY 28 JULY

8:15 Breakfast

Decision-making Ken Miller (Columbia), Chair

9:00 Tatiana Engel (Yale): A neural circuit model for decision and categorization

9:30 Iain Couzin (Princeton): Collective motion and decision making in animal groups

10:00 Patrick Simen (Princeton): Real-time reward maximization in decision making: data and a neural circuit model

10:30 Chess Stetson (Caltech): Directionality of cross-cortical spike-field coherence during decision-making

11:00 Break

11:30 *Guest speaker*—Yael Niv (Princeton): Model-driven studies of learning and decision making

12:30 Lunch and posters

Sensory Xiao-Jing Wang (Yale), Chair

14:15 Rachel Wilson (Harvard): Neural processing in the fly olfactory system

14:45 Pietro Berkes (Brandeis): Neural evidence for statistical optimal inference and learning in primary visual cortex

15:15 Aaditya Rangan (NYU): Coding and reliability in the fly antennal lobe

15:45 Yoram Burak (Harvard): Image stabilization by Bayesian dynamics

16:15 Break

16:45 *Guest speaker*—Jim DiCarlo (MIT): Untangling object recognition in the ventral visual processing stream

17:45 Closing plus lab tours

Circuits

Sunday 26 July 2009
9AM – 12:30PM

Functional Properties of Local Cortical Networks

David McCormick
Yale University

Cortical networks operate through the interaction of a plethora of different cell types. Inhibitory neurons, in particular, consist of a broad range of different types of neurons. Presumably these various inhibitory cell types perform unique and important functions in the operation of the cerebral cortex. Here we have investigated the role of intracortical inhibitory systems through a variety of methods, from intracellular recording in vivo during visual stimulation, to recording of endogenous spontaneous Up and Down states in vitro in animals in which specific cell types are marked with GFP. To date, our results indicate that the cortex may use a relatively sparse code during natural activity, and that this sparse code depends upon the strong and precise activation of local inhibitory networks. Extracellular and intracellular recordings from identified cell types suggest that the fast-spiking inhibitory neurons are among the most responsive and active in the cerebral cortex and are highly involved in not only generating on-going spontaneous activities, such as gamma waves, but also the bulk of the inhibitory events observed during visually evoked responses. Other types of interneurons appear to have more specialized roles, discharging more rarely during spontaneous recurrent network activity. The role of these interneurons remains to be determined. Our results indicate that the cerebral cortex encodes information with a highly selective and relatively sparse code that depends upon the recursive interaction of local inhibitory and excitatory networks.

A model of two interacting accumulators for reach and saccade reaction times

Daniel Martí
Center for Neural Science, New York University

When primates make a coordinated eye-hand movement to a visual target, reach and saccade reaction times (RT) are correlated so that the eye arrives at the target just before the hand. In the first half of the talk I will present recent results from a psychophysical experiment showing how the mean RT for reaches and saccades, as well as the correlation between them, depend on the stimulus onset asynchrony (SOA) between the reach and the saccade go cues. Reach and saccade RTs are significantly correlated when the go cues for both movements are presented simultaneously, yet this correlation drops off as the SOA is increased beyond a few hundred milliseconds. The mean saccade RT decreases monotonically as the SOA is reduced. When the timing of the task is predictable (i.e., when the SOA is constant across blocks of trials), the mean reach RT generally increased with increasing SOA. This suggests that, when uncertainty about task timing is removed, both movements may be facilitated when made near simultaneously. In the second half of the talk I will present a model that accounts for the dependence on the SOA of mean RTs and correlations. The model consists of two nonlinear leaky accumulators mutually coupled that encode each the information available to the subject for the initiation of a particular movement. Each accumulator consists of a leaky nonlinear integrator that triggers a movement when it crosses a preset threshold of activity. The input to each accumulator unit is comprised of the noisy sensory signals induced by the corresponding go cue stimulus as well as recurrent excitatory contributions. Due to the excitatory coupling, the net input to both accumulators increases for short SOAs, giving rise to shorter mean RTs.

As SOA increases, each accumulator is less likely to be active as the other rises to threshold, so the facilitatory effect decreases and RTs increase. Similarly, for short SOAs, correlations between RTs are high for short SOAs because fluctuations in the input are more likely to determine threshold crossing-times when both units are active. Their mutual influence, and hence correlations, decrease as SOA increases. These results suggest that coordination can be seen as a result of interaction between two effector-specific representations.

Correlations and Synchrony in Threshold Neuron Models

Tatjana Tchumatchenko
Bernstein Center Göttingen, Germany

To understand the origin and computational properties of interneuronal spike correlations it is essential to analyze how neurons subject to correlated inputs coordinate their output spiking activity. We used a simple statistical framework to examine the synchronization acuity of a neuronal pair subject to correlated inputs [1]. We studied the cross conditional firing rates and analyzed their short and long time asymptotics. We computed the cross conditional firing rates for 1) low and 2) high common input fraction and 3) with firing rate heterogeneity and derived also 4) the population frequency response function. In the low correlation regime, we identified a rate dependence of spike correlations, corroborating previous findings [2], and predict that spike correlations in this regime reflect detailed properties of input correlations. However, as the correlation strength increases the synchronous rate gradually looses its firing rate dependence. For large cross correlations the synchronous spike correlations depend on the input correlation time and the coupling strength but are insensitive to firing rate and the detailed form of input correlations. For all correlation strengths the model predicts the appearance of a systematic delay of firing of the lower rate neuron relative to the higher rate neuron. We assessed our theoretical predictions in *in vitro* experiments in slices of rat visual cortex and injected in pyramidal neurons fluctuating currents with a varying degree of common input and different modulating frequencies. Conditional firing rates and frequency response functions, confirmed all basic theoretical predictions 1)-4) of our formalism.

[1] Tchumatchenko T, Malychev A, Geisel T, Volgushev MA, Wolf F: Correlations and Synchrony in Threshold Neuron Models. arXiv:0810.2901v2 [q-bio.NC](submitted).

[2] de la Rocha J, Doiron B, Shea-Brown E, Josic K, Reyes A: Correlation between neural spike trains increases with firing rate. Nature, 448:802-806, 2007.

Recall of word sequences via short-term plasticity in a temporal context model

Paul Miller
Brandeis University

Adults with hearing impairment, particularly the elderly, perform worse than controls with better hearing but otherwise equivalent memory abilities at recall of word sequences. Such a result is intriguing because the results hold when words are presented at a level of volume and clarity that allows the listener to recognize them correctly. If speech recognition is an “all-or-none” phenomenon as suggested by perception (we either correctly identify a word, or make a mistake) then these results give rise to the following conundrum: why is the distinct process of laying down a memory trace of an identified word affected by the difficulty of identification? That is to say, once a word is identified, should it not be as easily remembered as any other identified word?

We present a simplified computational model of word recognition and recall that includes some of the key underlying biological processes needed for sensory processing and memory. The simulations include groups of model neurons, some of which fire spikes in response to specific word stimuli. Synaptic connections between cells are altered by the patterns of spikes according to spike-timing dependent plasticity (STDP) rules. The model is based on attractor dynamics, such that stimuli of different quality can provoke network activity which is identical following stimulus offset, representing our ability to recognize a word correctly across a wide range of stimulus qualities.

Our model reproduces experimental findings that recall of one word can promote recall of a prior word as well as a following word in the sequence. We find it essential to include in our simulations "context" cells, which can be co-active with word-specific cells, and promote their recall in an implementation of the temporal context model of list-item retrieval. We note that for reverse-recall we must include spike triplet terms to produce a rate-dependence in the standard STDP rules. Such reverse recall is also produced when we use rules based on recent in vitro data demonstrating associative short-term plasticity in hippocampal synapses.

Importantly, in all cases the ability for the model to provide word recall is strongly dependent on the strength and speed with which prior word recognition occurred. That is, even though a weak stimulus can produce sufficient network activity to produce word recognition, the slow and weak process by which such recognition is reached produces less of the strengthening of connections to other cells that is needed for later memory recall. Our simulation results are supported by preliminary experimental data, suggesting that a single word in a list masked by noise can reduce a subject's ability to recall both the prior word and the following word.

From neuronal circuit reconstructions to principles of brain design

Mitya Chklovskii
Janelia Farm, Howard Hughes Medical Institute

Coding

Sunday 26 July 2009
2:15PM – 6:00PM

Information maximization across a synapse

Tatyana Sharpee
The Salk Institute

I will discuss a simple strategy for how to re-encode spike trains to convey the same information about stimuli using substantially fewer numbers of spikes. Analysis will be based on simultaneous recordings of neural responses in the visual thalamus and the retina carried out in collaboration with L. Sincich and J. Horton.

Neural computations in the retina

Markus Meister
Harvard University

Linking Mind, Brain, and Behavior

Scott Makeig
University of California San Diego

Human brain dynamics are inherently multiscale, at different spatial scales (e.g., whole brain, thalamocortical modules, columns, neurons, synapses, molecules) having different time constants, dynamics, and structural connectivity structure. One currently pressing basic research issue in brain dynamics concerns the active coordination of dynamics at multiple space and time scales, a subject long neglected during the experimental era dominated by single microelectrode data recording and analyses based on response averaging (event-related potential / ERP averages; spike rate and peri-stimulus spike time histogram (PSTH) averages). A second unresolved issue, and also a relic of the original psychophysics focus on passive linear systems analysis, is to develop mathematical models of the ways in which behavioral and brain dynamic variability implements 'embodied agency' by which the brain organizes behavior based on its perceived/projected impression of the 'challenge' of each moment.

Scalp EEG (or MEG, its near-complement) can only see the far-field projections of locally synchronized field activity, chiefly across cortical domains of poorly understood size, location, and dynamics. Ideal measures of cortical field dynamics therefore should be multi-resolution. A unique window of opportunity is afforded by the current clinical practice of invasive monitoring of cortical (and/or sub-cortical) activities in subjects with complex cases of intractable epilepsy for the purpose of planning remediative brain surgery. I and colleagues have begun analyzing first human multi-resolution electrophysiological data. Though adequate recording, joint analysis, and modeling of activity recorded simultaneously at multiple spatial scales is not simple, it is necessary to truly understand electrophysiological data recorded at any scale.

However, high-density imaging modalities that view brain activity from the greatest distance (e.g., from the scalp) may paradoxically also be better suited to studying its distributed dynamics. Our research into new methods for human EEG analysis suggests that high-density EEG is now becoming a true functional cortical imaging modality with high temporal and adequate spatial resolution. EEG is also the only lightweight, low cost, low energy, and therefore portable brain imaging modality. We are now exploiting this capability by pioneering the use of simultaneous high-density portable (even wearable) EEG, body motion capture, and eye tracking to image brain dynamics supporting our active behavior in the natural 3-D world, a new imaging modality, in effect, that I call Mobile Brain/Body Imaging (MoBI).

At least since the advent of response averaging computers in the early 1960s, electrophysiological research at the neuron and scalp scales has been separated into two camps (neurobiology and psychophysiology) with little to say to each other. More adequate analysis methods, applied to model the complexities of unaveraged data collected concurrently at multiple spatial scales, and of unaveraged data collected concurrently with detailed behavioral recordings in natural 3-D environments, should produce a reunification of brain electrophysiology as a single topic. In this process, public data resources including the new NIMH-funded public 'Human Electrophysiology, Anatomic Data, and Integrated Tools (HeadIT) resource that I and Jeff Grethe are beginning to build at UCSD may play a useful role.

Simplicity in a complex world: subthreshold membrane-potential resonances shape spike-train statistics

Andreas Herz
Ludwig-Maximilians-Universität, Munich

Learning and Plasticity

Monday 27 July 2009
9AM – 12:30PM

A multi-stage synaptic model of memory

Stefano Fusi
Columbia University

Over a century of experimental and clinical studies provide overwhelming evidence that declarative memory is a dynamical and spatially distributed process. Specifically, lesion studies have shown that the hippocampus is crucial for the formation of new memories but that its role decreases in importance over time; ablation of the hippocampus does not affect remote memories. This suggests that memory consolidation involves the transference of memory to extra-hippocampal areas, most likely the cerebral cortex. Despite the wealth of behavioral data from animals and humans on this consolidation process, relatively little theoretical work has been done to understand it, and no work has addressed the underlying physiological process which is presumably long-term synaptic plasticity. Here we present a model of memory consolidation explicitly based on the constraints imposed by a plausible rule for synaptic plasticity. The model consists of N plastic, binary synapses divided into n stages. Uncorrelated memories are encoded in the first stage with a rate r. Synapses in the second stage are potentiated or depressed with a fixed probability according to the state (potentiated or depressed) of synapses in stage 1. Synapses in downstream stages are updated in an analogous way with stage k directly influencing only stage k+1. Additionally, synapses become increasing less plastic the further downstream one goes, i.e. learning rates decrease with increasing stage number. Therefore we posit a feed-forward structure in which the memory trace in each stage is actively transferred to the next downstream stage. This is reminiscent of the physiological process of replay which has been recorded in cells of awake and sleeping rats. It is also consistent with the clinical and experimental findings showing that memory consolidation appears to involve memory transfer to areas outside of the hippocampus.

The model trivially reproduces power-law forgetting curves for the learned memories by virtue of the distribution of learning rates. Furthermore, through degradation or removal of early stages in our model we can easily account for the phenomena of anterograde and graded retrograde amnesia which are common in animals and humans having suffered damage to the hippocampus. In a similar vein we can qualitatively reproduce results from studies in which the administration of drugs has been found to selectively enhance or degrade memories in a temporally graded fashion. Finally, this model leads to vastly improved memory traces compared to uncoupled synapses; this holds especially when adjacent stages have nearly the same learning rate and the total number of stages is large. The work has been done in collaboration with Alex Roxin.

Internal Learning in Recurrent Neural Networks

David Sussillo
Columbia University

Neural circuits typically display a rich set of spontaneous activity patterns, and also exhibit complex activity when responding to a stimulus or generating a motor output. How are these two forms of activity related? We develop a procedure we call FORCE learning for modifying feedback loops either external to or within a model neural network to change chaotic spontaneous activity into a wide variety of desired activity patterns. FORCE learning, which involves error-directed modifications of synaptic strengths, works even though the networks we train are spontaneously chaotic and, in contrast to earlier proposals, we leave feedback loops intact and unclamped during learning.

In my talk I will explore the mathematical framework that allows FORCE learning to solve the spatial credit assignment problem, specifically, that of using the error defined for an output neuron to be used to modify the synaptic strengths of synapses that are pre-synaptic to internal (non-output) neurons. The success of our technique is a direct result of the Johnson Lindenstrauss theorem.

From synapse to BOLD: linking circuit plasticity to the macroscopic responses of sensorimotor cortex

Tim Verstynen
Keck Center for Integrative Neuroscience
University of California San Francisco

Simple network models, such as line attractors, can perform statistically-principled computations on noisy inputs, e.g., maximum likelihood estimation. We and others have shown that applying Hebbian learning to these networks allows them to use recent input histories to approximate adaptive Bayesian estimation. This learning process captures the experience-dependent changes in movement statistics that we have observed in both reaching and saccadic eye movements. Here we introduce our use of fMRI to begin to testing this model of adaptive retuning in sensorimotor circuits. We developed a novel model-based approach to studying experience-dependent changes in cortical activity, as reflected in the blood-oxygenation level dependent (BOLD) signal. Our approach assumes that changes in the BOLD signal recorded from a single voxel are dominated by changes in the synaptic inputs of a local, heterogeneously tuned neural network. This allows us to quantitatively predict the responses of both individual voxels and entire regions of interest under different behavioral conditions. According to the model, a sequence of repeated (or highly similar) inputs re-tunes the local lateral connections, biasing future computations towards the repeated inputs. This retuning process results in a predicted increase in BOLD response to inputs presented near the repeated input position. Indeed we observed these changes in BOLD, and they correlate across subjects with the magnitude of experience-dependent behavioral changes in a novel saccade task. Moreover, this effect was only observed in the frontal and parietal regions thought to mediate saccade planning. This general approach allows us to test the predictions of network-level models in a variety of behavioral contexts, bolstering the power of fMRI as a tool for studying network dynamics, beyond simple region identification and inter-region correlation analyses.

Sources and function of variability in adult song production and plasticity

Michael Brainard
University of California San Francisco

Adult birdsong is an example of a well-learned and highly stereotyped motor skill. Nevertheless, for adult song, as for all motor skills, there is subtle residual variation in performance from one iteration to the next. Such variation is often construed as biological noise, perhaps arising from the motor periphery, that is below threshold for behavioral relevance and not subject to central neural control. I will describe experiments that address an alternative hypothesis, that such behavioral variation, rather than meaningless noise, represents subtle, but active experimentation by the nervous system to optimize and maintain motor performance. I will first describe neurophysiological experiments that indicate a central neural origin for a component of observed variation in features of song such as the pitch of individual syllables. These experiments indicate that excess variation is actively introduced into song premotor circuitry from extrinsic sources, including avian basal ganglia structures know to be important for learning. I will then show that the subtle variation present in song can be used by the nervous system to enable rapid adaptive plasticity of 'crystallized', post-critical period song. Collectively, these experiments suggest that for birdsong, and perhaps other well-learned vertebrate skills, subtle behavioral variation may be purposefully introduced by the nervous system to enable continuous monitoring and optimization of performance.

The building blocks of cerebellum-dependent learning

Jennifer Raymond
Stanford University

The relatively simple circuit architecture of the cerebellum suggests that this brain structure may be one of the first to yield its computational principles. A key function of the cerebellum is motor learning. Results from my laboratory indicate that the cerebellum contains independent and molecularly-distinct building blocks from which motor memories can be constructed in a combinatorial fashion. We are now working to dissect cerebellum-dependent learning into its elemental components. To date, we have identified molecularly distinct mechanisms supporting: increases versus decreases in movement amplitude; changes in movement dynamics versus amplitude; changes in dynamics in one direction (phase advance) versus the other (phase lag), and the effects of low-frequency versus high-frequency training. Our results suggest that a single training experience can engage more than one plasticity mechanism. Moreover, subtle changes in the way the training is done can influence which molecular mechanisms are recruited or not recruited.

Technologies and Structures

Monday 27 July 2009
2:15PM – 6:00PM

Optical Control of Brain Dynamics: Empowering Computational Descriptions of Neural Circuits

Ed Boyden
Massachusetts Institute of Technology

Over the last few years, we and others have introduced optical molecular sensitizers (channelrhodopsins, halorhodopsins, and novel reagents to be described in this talk) and hardware for optical neural control, which have found use in studying the causal role of cell types and neural circuits in behavior, neural computation, and pathology, in a wide variety of species. We here describe the beginnings of a set of novel, powerful reagents, as well as new sophisticated optical hardware architectures, which we anticipate will open up new approaches to systematically resolving the contribution of specific neural circuit components to behavior. We also describe new data from non-human primates suggesting clinical and translational possibilities for cell-type specific optical neural control prosthetics.

Disposable stem cell hypothesis: A new model for neurogenesis in adult hippocampus

Alex Koulakov
Cold Spring Harbor Laboratories

Experimental evolution to probe gene networks underlying cognition in Drosophila

Josh Dubnau
Cold Spring Harbor Laboratory

One of the great challenges to understanding genetic impact on human cognitive diseases is that clinical outcomes often are influenced by interactions among groups of genes. A good example is schizophrenia, where no clear genetic mechanism has emerged. In some individuals, complex disorders such as schizophrenia likely derive from co-inheritance of multiple common gene variants each of which would have little clinical impact on their own. Despite its widespread relevance, mechanisms by which such multi-gene interactions modulate phenotype are ill understood. This is because almost all mechanistic genetic studies have been limited to analysis of pair-wise interactions.

To investigate this question, we have developed and implemented a novel approach in Drosophila, using the biologically important and clinically relevant cAMP signaling pathway as a model. Our approach uses the power of selective breeding to evolve combinations of gene variants that together are capable of suppressing the learning defect of mutations in the rutabaga adenylyl cyclase gene. This method is novel in several ways. First, unlike a classical suppressor screen, our use of experimental evolution has allowed us to explore the impact on the learning phenotype of higher order, non-linear gene interactions. Also, unlike a classical selective breeding experiment, we have constrained the initial genetic variability to a set of 23 identified and molecularly characterized gene loci with known involvement in memory. We then applied selective pressure by artificially choosing and breeding the highest performing animals from among a large heterogeneous population that varied only at these 23 genes. This strategy models non-linear multi-gene interactions that underlie natural evolution, and that influence naturally occurring variation in complex phenotypes such as learning. Because we have limited the genetic variation to known genes, this approach also made it feasible to fully genotype the causative loci across multiple animals. This has given us unprecedented access to the underlying molecular genetic mechanisms.

Over the course of 41 generations of breeding, we observe a robust response to selection, resulting in dramatic improvement in learning performance despite the fact that all animals remain null mutant for the adenylyl cyclase. We genotyped 288 animals from each replicate population at two different generation time-points. Multivariate analysis of the high dimensional genotype data set identified 8 alleles that explain much of the phenotypic effect. Using independent genetic experiments, we then verified that each of three enriched alleles partially improve the rutabaga learning defect on their own. Importantly, we now are in a position to systematically investigate both the molecular genetic mechanisms underlying the selection response, and the rules that govern higher order interaction of identified loci. This data set also provides an opportunity to test models from population genetics that have so far remained confined to a largely theoretical realm.

Plumbing the Connectome

Jeff W. Lichtman
Harvard University

Decision-making

Tuesday 28 July 2009
9AM – 12:30PM

A neural circuit model for categorization and decision making: computing with passive versus active short-term memory

Tatiana Engel
Yale University

Short-term memory is a crucial component to many decision processes, whereby information is maintained over time and interacts with incoming stimulation. Electrophysiological studies in behaving monkeys have identified two neural mechanisms of short-term memory. First, a repeated presentation of a stimulus results in attenuated response. This passive short-term memory in the form of ``repetition suppression'' was predominantly displayed by neurons in area IT of monkeys performing a standard delayed match-to-sample task. The monkeys had to respond to the repetition of a sample in a sequence of test stimuli and performed based on simple detection of any stimulus repetition. The second, active short-term memory was engaged in more complicated tasks, which could not be solved just relying on stimulus repetition, e.g. if distractors could repeat (e.g. in a sequence of stimuli ABBA) or if the match/nonmatch decision was based on abstract category membership of stimuli rather than on their physical similarity. Under these conditions, the sample identity was maintained in persistent firing of some neurons in the monkey's prefrontal cortex (PFC), while two other neural sub-populations showed suppression and enhancement of response to matching stimuli.

Based on these observations, we propose a neural circuit model for categorization and match versus nonmatch comparison. The model consists of several interconnected local circuits endowed with three key characteristics. First, spike rate adaptation of single neurons (with a time constant of up to 10s) leads to reduced response to repeated stimuli, i.e. passive repetition suppression. Second, a subpopulation of neurons shows match enhancement as a result of modulatory top-down inputs from a working memory circuit where the identity of a sample stimulus is actively maintained by self-sustained neural firing. Third, category selectivity of neurons is generated through reward-dependent learning. We demonstrate how learning can adjust synaptic weights from the neurons with repetition suppression to the readout network to generate correct match vs. nonmatch decisions using only the passive short-term memory in the standard task. In the ABBA and categorization tasks, the circuit model implements the match vs. nonmatch decision as the competition between two pools of neurons that show match enhancement and suppression. In this case, passive and active short-term memory act in parallel and produce single-cell response patterns that closely match experimental data from PFC. Our model suggests a mechanism of how two forms of short-term memory are used in decision processes in a flexible manner according to task demands.

Collective Motion and Decision-Making in Animal Groups

Iain Couzin
Princeton University

Grouping organisms, such as schooling fish, often have to make rapid decisions in uncertain and dangerous environments. Decision-making by individuals within such aggregates is so seamlessly integrated that it has been associated with the concept of a "collective mind". As each organism has relatively local sensing ability, coordinated animal groups have evolved collective strategies that allow individuals to access higher-order computational abilities at the collective level. Using a combined theoretical and experimental approach involving insect and vertebrate groups, I will address how, and why, individuals move in unison and investigate the principles of information transfer in these groups, particularly focusing on leadership and collective consensus decision-making. An integrated "hybrid swarm" technology is introduced in which multiple robot-controlled replica individuals interact within real groups allowing us new insights into group coordination. These results will be discussed in the context of the evolution of collective biological systems.

Real-time reward maximization in decision making: data and a neural circuit model

Patrick Simen
Princeton University

Bogacz et al. (2006) analyzed a reduced drift-diffusion model of two-alternative decision making to identify parameters (starting point and decision threshold) that maximize reward rate. Results of a motion discrimination experiment support quantitative optimal-performance predictions made by this model for tasks with fixed durations.
Qualitatively, these are: 1) as average response-stimulus interval (RSI) decreases, speed-accuracy tradeoff (SAT) shifts toward speed; 2) as one response becomes more likely or more rewarded, an RSI-dependent bias toward that response develops; 3) for a given stimulus probability, fast-guessing exclusively in favor of the biased response should occur at short, but not long, RSIs. Constrained fits of Ratcliff's diffusion model (in which the reduced model is nested) imply that performance was quantitatively optimal, while unconstrained fits imply a suboptimal accuracy emphasis. (Simulations suggest that non-uniform contaminant RTs may account for this discrepancy, suggesting general advantages to constrained fitting.) Simen et al. (2006) proposed a fast algorithm to learn these optimal parameterizations by accumulating reward feedback across trials with exponentially weighted moving averages. The distance between starting point and each threshold is a decreasing function of these averages, so that as reward rate increases, thresholds decrease. As predicted by this algorithm, RTs in the motion task were both autocorrelated and negatively correlated with estimated values of the moving average at the time of each response, and RT variance decreased as the reward average increased. Thus, optimal performance in a class of decision-making tasks appears both computationally feasible and empirically supported.

Bogacz, R., Brown, E., Moehlis, J., Holmes, P. and Cohen, J. D. (2006).
The physics of optimal decision-making: a formal analysis of models of performance in two-alternative forced choice tasks. Psychological Review, 113, 700-765.

Simen, P., Cohen, J. D. and Holmes, P. (2006). Rapid decision threshold modulation by reward rate in a neural network. Neural Networks, 19, 1013-1026.

Directionality of cross-cortical coherence during decision-making

Chess Stetson
California Institute of Technology

The parietal reach region (PRR) and dorsal premotor cortex (PMd) have been implicated in the planning of reach movements. These areas are monosynaptically connected, and they are thought to communicate with each other during a decision to move. Yet, as the decision evolves, it is not known in which direction the information flows depending on the task. Earlier data from our lab showed an increase in cross-cortical spike-field coherence as the animal decides where he will move in space, with somewhat greater coherence in the fronto-parietal direction (Pesaran et al. 2008). Spike-field coherence is the phase-locking of spikes with local field potentials (LFPs, thought to be related to the inputs of a brain region) at a certain frequency, and is thought to be involved with communication between cortical areas. Here we present data from a new experiment, in which the animal decides how to move -- whether to reach with his arm, or saccade with his eyes. During this "How" task, as the animal decides which effector to use, parietal cells in PRR show increased coherence with local fields in the PMd, more so than in the other direction. About 15% of spike-LFP pairs recorded in each of the two areas show evidence of significant cross-cortical coherence between 5-30Hz during "How" decision-making. Of these, 80% are parietal spikes cohering with frontal LFPs. These data add to the growing body of knowledge on coherence between single-units and local field potentials across different parts of cortex.

Model-driven studies of learning and decision making

Yael Niv
Princeton University

Sensory

Tuesday 28 July 2009
2:15PM – 6:00PM

Neural processing in the fly olfactory system

Rachel Wilson
Harvard University

Neural evidence for statistically optimal inference and learning in primary visual cortex

Pietro Berkes
Brandeis University

How do we infer from sensation the state of the external world? Human and animal subjects are able to take into account noise and uncertainty in behavioral task and perform statistically optimal inference and learning. Moreover, statistical models of natural images have been shown to reproduce many features of receptive field organization in primary visual cortex. However, there has been so far no evidence of optimal inference and learning at the neural level. In this talk, I will derive a general consequence of the statistical framework, predicting that the distribution of neural spontaneous activity and that of activity evoked by natural stimuli must become more and more similar with visual experience, and be identical in the ideal case, under the assumption that neural activity represents samples from an internal, probabilistic model of the environment. I will present data from multielectrode recording in awake ferrets a various stage of post-natal development that supports this prediction.

The increasing similarity between the two distributions is found to be due to an increasing match between the spatial and temporal correlational structure of the activity patterns, and is specific to activity evoked by natural stimuli, and not by noise or grating stimuli. These results provide support for the statistical framework at the neural level, and suggest a novel interpretation for neural variability and spontaneous activity.

Coding and reliability in the fly antennal lobe

Aaditya V. Rangan
New York University

Recent experiments have revealed the existence of excitatory and inhibitory local neurons within the fly antennal lobe (AL), as well as several other key architectural features, such as profound synaptic depression of the olfactory receptor neuron synapses. I will present a hypothesis concerning the functional role of these architectural features of the fly AL. Based on modeling and subnetwork analysis, I believe that the network mechanisms underlying synaptic depression of the olfactory receptor neurons serve to maintain a balance between (1) the AL's coding capacity and (2) the reliability of projection neurons within the AL.

Image Stabilization by Bayesian Dynamics

Yoram Burak
Harvard University

Bayesian models of neural computation imply that the brain represents probabilities, rather than a single value of an estimated quantity. In models suggested so far, this estimated quantity was typically a single time-independent variable such as the direction of motion in a random dots task. This leaves open an interesting question, whether the brain could apply the principles of Bayesian computation also to the inference of highly multi-dimensional quantities, which involve a large number of degrees of freedom and are possibly dynamic. An interesting example for an inference problem of this type arises in foveal vision, where fixational movements constantly shift the image projected on the retina relative to the photoreceptor array. To form an estimate of the image, an ideal decoder downstream of the retina would need to form a joint dynamic estimate of the eye's trajectory, together with its estimate of the image itself. I will propose an approximate probabilistic approach to this problem, which is based on a factorized representation of the multi-dimensional probability distribution. The decoding scheme that emerges from this approximation suggests a neural implementation that involves two neural populations, one that represents a Bayesian estimate for the position of the eye, and another that represents an estimate of the stabilized image. I will discuss the performance of this decoder under simplified assumptions on retinal coding, in comparison to an ideal optimal decoder, and suggest experimental implications.

Untangling object recognition in the ventral visual processing stream

Jim DiCarlo
Massachusetts Institute of Technology

Poster Abstracts

1. Towards an ecological approach to vision: wireless recordings from rat V1

Margarida Agrochao
Harvard University

The traditional approaches to studying V1 share a number of problems: biased sampling (e.g. neurons with high firing rates constitute a large percentage of the cells recorded), use of biased stimuli (e.g. gratings, spots), and biased theories (data-driven; simple/complex cells). We report a new approach with the potential to solve these problems.

At the core of this approach is a wireless system that allows neural signals to be recorded from an unconstrained animal. The system consists of a chronically implanted tetrode drive with 64 electrodes. It allows for the monitoring of many neurons simultaneously and addresses the problem of biased sampling of neurons. With this system we can record neural signals from freely roaming animals to study of the response properties of V1 neurons under natural, ecologically relevant visual stimulation.
In this poster we examine the firing properties of simultaneously recorded neurons with the intent of shedding light on Efficient Coding ideas. Our initial data suggests that behavior introduces statistical dependencies not predicted by this theory and that analyzing data recorded from freely behaving animals requires revisiting old spike train analysis tools and coming up with new ones.

2. Reconciling inter-areal gamma-range synchrony with neural irregular activity in selective attention

Salva Ardid
Yale University

Selective attention modulates firing rates and local gamma-range synchronization of neurons in the visual cortex. Synchronization is believed to be an important mechanism for enhancing attentional processing, but its functional consequences remain unknown. However, spike firing is highly irregular, and attentional modulations do not have an appreciable effect on such variability. An understanding of how these results can be reconciled is a prerequisite to evaluate the functional role of synchrony related to attention.

These attentional modulations have been hypothesized to be under control of top-down inputs coming from working memory circuits in PFC/PPC. Neurons in such circuits present sustained selective firing, which maintains behaviorally relevant information during the delay-period between cue and response. These neurons also provide top-down input to sensory circuits. Thus, attentional modulations, including synchrony modulations, might emerge from the interaction of a sensory circuit and a downstream area in PFC/PPC.

We integrate this phenomenology in a biophysical model of two cortical areas. Both interacting networks, MT and PFC/PPC, share the same 1-D ring architecture to code the stimulus feature (direction of motion), and are composed of 4:1 spiking excitatory to inhibitory neurons connected through conductance-based synaptic inputs (mediated by AMPARs, NMDARs and GABAARs).

Apart from the influence of the top-down signal onto rates, (biased competition, multiplicative scaling and selectivity enhancement, which we considered before: Ardid et al. J Neurosci 2007), the model matches synchronization and irregular firing. These measures offered conflicting views on the impact of temporal dynamics modulations in attentional processing. Our model provides a new perspective integrating these results and reconciling the dichotomy. We show that significant attentional modulation of local and long-range coherence is compatible with irregular Poisson-like statistics.

Our model produces specific predictions: Gamma-range coherence between sensory and executive areas occurs only between neurons of similar selectivity if the attended and test feature coincide with their neuronal preference. The footprint of top-down synaptic projections underlies this specificity. In addition, using a manipulation in the model, we assess the functional impact of synchronization by comparing attentional modulations of sensory neuron activity in the presence versus absence of synchronization across the sensory and executive circuits. We demonstrate that the temporal reorganization of top-down incoming spikes into MT is responsible of around 10-15% of the attentional modulations of firing rates.
In conclusion, our model reconciles the rate and synchronization effects, and suggests that coherence facilitates large-scale neuronal computation in the brain, in part through modest enhancement of rate modulations.

3. Central roles of bipolar cells in retinal neural circuits

Hiroki Asari
Harvard University

One key step in visual processing is the transmission of signals from photoreceptors to retinal ganglion cells by bipolar cells. There are about 10 types of bipolar cells in a vertebrate retina, and they form parallel channels where each bipolar cell type carries a distinct type of visual information from the outer to inner retina. The signals from these bipolar channels are then integrated by ganglion cells through intricate interactions with about 30 types of amacrine cells. Specific combinations of bipolar and amacrine inputs generate about 10 functional types of ganglion cells, and thus such interactions in the inner plexiform layer are the most interesting---but least understood---processings in the retinal circuitry.

By simultaneously recording from multiple ganglion cells while manipulating the bipolar cell activity intracellularly, here we explored how the signal from an individual bipolar cell is distributed to the various types of ganglion cells. We found that injecting current into an individual bipolar cell elicited significant effects on the visual responses of many ganglion cells. (1) The contribution of a single bipolar cell was generally excitatory at short distances (<0.3 mm) and inhibitory at longer distances (around 0.5 mm). This is consistent with the presumed role of amacrine cells as inhibitory interneurons. (2) Within the excitatory region, different ganglion cells showed distinct response patterns. A sustained depolarization of the bipolar cell produced a transient burst of spikes in some ganglion cells, but a sustained firing in others. Furthermore, some ganglion cells responded to the bipolar cell stimulation in a linear fashion, whereas others showed a highly rectifying nonlinearity. These results emphasize the diversity of neural circuits that distribute signals from the same bipolar cell to various ganglion cells. Specifically, the distinction between transient and sustained response dynamics in ganglion cells is not simply determined by what bipolar channels they receive, but in large part by differential circuitry in the inner plexiform layer.

4. Intrinsic Stability of Temporally Shifted Spike-Timing Dependent Plasticity

Baktash Babadi
Columbia University

Spike-timing dependent plasticity (STDP), a wide-spread synaptic modification mechanism, is sensitive to correlations between presynaptic spike trains, and it generates competition among synapses. However, STDP has an inherent instability because strong synapses are more likely to be strengthened than weak ones, causing them to grow in strength until some biophysical limit is reached. Through numerical simulations and analytic calculations, we show that a slight temporal shift in the STDP window can stabilize synaptic strengths. Shifted STDP also stabilizes the postsynaptic firing rate and can implement both Hebbian and anti-Hebbian forms of competitive synaptic plasticity. Interestingly, the overall level of inhibition determines whether plasticity is Hebbian or anti-Hebbian. Even a random symmetric jitter of a few milliseconds in the STDP window can stabilize synaptic strengths while retaining these features. Our results indicate that the detailed shape of the STDP window function near the transition from depression to potentiation is of the utmost importance in determining the consequences of STDP, suggesting that this region warrants further experimental study.

5. A likelihood framework to decode the timing of information in spiking and LFP activity

Arpan Banerjee
New York University

Movement plans are formed after sensory stimuli have been discriminated and before movements are executed to cued target locations in space. Here, we present a unifying framework for the analysis of simultaneously recorded spiking and LFP activity and apply it to identify target selection times, the onset of movement planning stage of information processing when subjects perform look-reach movements. The key idea in this framework is to develop statistical models of spiking and LFP activity and use these models to obtain time varying likelihood ratios for selection of each movement direction. Accumulation of the likelihood ratios leads to a probabilistic decoding of target selection times from the neural activity on individual trials. We illustrate this approach by comparing the results from modeling spiking and LFP activity with or without history dependence. We apply this framework to detect target selection times in the posterior parietal cortex of awake, behaving monkeys performing reaches and saccades to an instructed location.

6. Artificial Networks with Exponential Representational Power

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Attractor neural networks constitute a well established paradigm for the modeling of associative memory, as well as for the implementation of algorithms for pattern restoration, retrieval and classification. We introduce here a novel approach to the problem of associative representation and categorization. We consider first a simple warning propagation dynamics over the graphical models associated to instances of hard Constraint Satisfaction Problems (CSPs). Statistical Physics analyses have shown that, in certain phases, these network dynamics exhibit an exponentially large number of selectively addressable clusters of attracting states. This feature allows these states to be used for associating an exponentially large set of arbitrary new inputs to clusters of attractors in a reliable way. In contrast with an ordinary Hopfield network approach, in which associations are performed by learning a small (i.e. linear in the network size) number of attractors highly adapted to the stimulus statistics, in a CSP-based network approach associations are performed using an exponentially large number of fair quality unlearned attractors. The fine quantization grid provided naturally by these exponentially many states will ensure general classification capabilities, since a tabula rasa state of the network.

We then exhibit a class of artificial neural networks, assembled out of randomly interconnected stereotyped motifs of binary neurons, whose dynamics emulate the evolution of CSP networks (CSP-like neural networks). We show how such CSP-like neural networks can be used to store and retrieve patterns corresponding to combinations of patterns stored by Q ancillary Hopfield networks, each one of size N. Although the number of such combinations of patterns is growing exponentially with Q, a single CSP-like network of size NQ can be used to represent all these compound patterns, whereas the size of a Hopfield network of analogous capacity would be exponentially larger (i.e. of the order of N to the power Q). The exponential representational power of CSP-like networks is used to build a toy-model for the generation of hierarchic internal symbolic representations, in which "codewords" associated to object described by multiple features have the same length of the "codewords" describing the values of any single of its distinct features. To conclude, we also discuss how effects akin to priming might occur naturally within such a network modeling framework.

7. Stationarity of intracranial field potentials in human cortex during visual object recognition

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We typically gather information from the human brain on a time scale of minutes to hours. However, subdural electrodes recording intracranial field potentials (IFPs) in epileptic subjects undergoing electrophysiological monitoring for potential surgical resection can remain implanted for a week or longer. We investigated how stable the representations of visual input are over a scale of days in eight subjects. In order to address this question, we compared the elicited responses to passive viewing of greyscale images. These images belonged to five different categories (faces, fruits, chairs, animals and vehicles) shown at five different rotations and scales and presented in pseudo-random order. Each subject performed two to five recording sessions with identical stimuli (in different order) with gaps between sessions of six hours to four days. As a measure of selectivity we classified the visual responses at each electrode using a support vector machine classifier and compared classification performance for different days. To evaluate the stationarity of the responses, we trained classifiers using data from one recording session and evaluated performance on independent test data from other recording sessions. To take into account the temporal properties of the signal we calculated the cross-correlation between different categories, both within and between sessions.

The results suggest that the selectivity of IFP responses to object categories is maintained over the course of several days. A classifier trained to recognize the object categories within one recording session could extrapolate to subsequent sessions. The cross-correlation analysis also revealed no significant decrease in selectivity over days. These findings indicate that intracranial field potentials provide a stable measure of visual selectivity at least over the course of several days. Characterizing the stability of visual selectivity over days constitutes an important aspect of deciphering the neural code for visual information. In addition, understanding the degree of stationarity of neural signals may have a crucial impact on the development of prosthetic devices to read out information from the human brain.

8. Generating Specificity in random network models of paired-stimulus learning

Mark Bourjaily
Brandeis University

In the delay pair-association task a monkey learns to associate specific pairs of cues, for example, A with B and C with D. The monkey is presented with one cue (A or C) followed by either a distractor (e.g. D after A or B after C) for which the monkey holds a lever or a stimulus that belongs to the stimulus-pair (e.g. B after A or D after C) for which the monkey must release the lever to obtain reward. Single-cell recordings demonstrate that neurons responsive to the specific paired associations needed to solve the task (e.g. A with B) arise over the course of training.

In this computational study based on spiking neurons, we investigate the requirements on network structure and synaptic plasticity for the formation of cells responsive only to such specific pairings of inputs. We begin with an initially randomly connected network with randomly projecting inputs (Associative layer), using a similar task (biconditional discrimination) without memory.

We find that neither spike-timing-dependent plasticity (STDP) nor triplet STDP (3-STDP) alone generates specificity in the Associative layer. Long-term potentiation of inhibition (LTPi) must be present to generate the strong cross-inhibition that is essential to produce and maintain specificity in the circuitry. The combination of triplet STDP with LTPi generates specificity and the strong self-excitatory connections necessary for persistent activity (memory). In all studies, multiplicative synaptic scaling is necessary to maintain homeostasis in the network.

We train a decision-making network, which simulates a binary behavioral choice (e.g. hold/release), to readout information in the Associative layer using a reward-based dopaminergic plasticity rule. Reward is dependent on the decision-making network's output matching the instructive cue (e.g. release decision for stimulus pair A&B leads to reward). We find that stimulus-pair selective cells in the Associative layer are necessary for optimal decisions.

9. When can rates be reliably transmitted in feedforward networks?

Kendra Burbank
Harvard University

Under what conditions can firing rate information be quickly and reliably transmitted from layer to layer in a feedforward network? Information transmission in the brain requires transforming inputs across many layers of computation without pathological synchrony (where all/most neurons in a given layer fire in unison), firing rate explosion (a monotonic increase in firing rates from layer to layer), or exponential decays in firing rates. Several authors have argued that such transmission is feasible whereby the neurons in a given layer can be made to fire at the desired rate but at random, uncorrelated times [1,2]. The averaged firing rate of many such unsynchronized neurons will accurately reflect the correct rate on timescales significantly shorter than the average inter-spike interval. Shadlen and Newsome claimed that a feedforward network with balanced excitation and inhibition could transmit rate information without the buildup of synchrony [3]. However, Litvak et al disputed this claim, using computer simulations to show that, over as few as 6 to 7 layers, this network would either tend towards synchronous firing or asynchronous firing at a rate which was independent of the initial rate [4]. Van Rossum et al proposed combating the buildup of synchrony by introducing noise into the system through the addition of a noisy background current [5].

We propose an alternative solution, using a feedforward network where inhibition outweighs excitation. We use analytical expressions for the mean and variance of a neuron's firing given the statistics of its inputs [6,7]. We propose network parameters which produce a gain close to unity, that is, that allow reliable transmission of rates over multiple layers. Furthermore, the network maintains a high variance in the distribution of rates across neurons within a layer. We find such parameters both for models of current-based integrate-and-fire neurons and for models of conductance-based neurons.

Two additional constraints should be imposed in the development of theoretical models for information transmission in feedforward networks: biological plausibility and robustness of the simulations to parameter changes. We therefore examine the biological plausibility of the proposed network, we ask whether weights need to be fine-tuned and evaluate the robustness to noise sources. Finally, we use simulations to confirm that networks with these parameters are capable of robustly transmitting rate information over many layers without the buildup of synchrony.

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10. Measuring the intrinsic autocoherent time-scale of gamma-band oscillations in V1 local field potentials

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Local field potentials (LFP) recorded in V1 during visual stimulation contain elevated power in the gamma-band (20-90Hz). The time series of this stimulated LFP signal is characterized by bursts of activity in the gamma-band in a background of 1/f type noise. In this study we determine the intrinsic time-scale over which the LFP bursts conserve their phase. Or equivalently, we measure the length of time over which the LFP oscillations show deterministic behavior, as knowledge of the phase at one point in a phase conserving oscillation gives information about the oscillation at a later time. The autocoherent time-scale of a neuronal network is an important parameter for the theoretical modeling of LFP oscillations. It is also essential for studies of the possible synchronization of different regions of the brain by gamma oscillations in the LFP.

To measure the time period over which the phase is conserved, the autocoherent time-scale, we developed a new method of time-frequency analysis involving the complex Gabor transform to track over time the local-in-time phase of the LFP gamma-band signal. Analysis of LFP data recorded from macaque V1 allowed us to estimate the distribution of time-scales and the mean autcoherent time-scale.

11. Population Decoding from Visual Area MT

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We are interested in decoding the response of a population of cells to some stimulus variable, for example, the response of motion cells in visual area MT to a coherently moving target. The initiation of smooth pursuit requires an estimate of the target velocity from the population response in a ~100 ms window. We suggest a sampling-based approach in which the aggregate population response is approximated via supralinear spike integration, which provides a gain-independent estimate without divisive normaliztion. We verify with a model population, which replicates key features found in neural data, that this yields an estimate of target motion of comparable quality to traditional center of mass (``vector averaging") calculations. We study the correlation between single neuron activity variation and the output of various decoding models as a function of the neuron's tuning; these curves are experimental signatures of different (encoding and) decoding algorithms. Our decoding approach can be tweaked in various ways to change its curve's shape, providing building blocks that might be useful in understanding different experimental results.

12. From grid cells to place cells: a generic and robust solution

Sen Cheng
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Despite intense modeling efforts it is still unclear how spatial representations (i.e. place cells) in the hippocampus arise. Since the discovery of grid cells in the main inputs to the hippocampus, several models have been proposed for the transformation from spatially periodic spiking of grid cells into punctate spiking of place cells. Here we show that a number of disparate models yield solutions that share the same underlying structure. Namely, a place cell has a place field at a given location, if there is a monotonic relationship between the synaptic weight from grid to place cell and the "normalized offset" of the grid cell. The normalized offset is defined as the distance between the spatial location and the closest center of a grid firing field normalized by the grid spacing.

We found this structure in the solutions generated by several models:

* A new local synaptic learning rule that we propose here. This rules learns the feedforward weights between grid cells and a single place cell and, thus, does not require competition among place cells like previous models do.
* The Tempotron, a powerful supervised learning algorithm.

13. Interactions between sensory, emotional, and executive brain regions during tasting

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Taste perception involves the integration of “bottom-up” information about the sensory stimulus with the “top-down” information about the current reward values of the stimuli. Therefore self-administration of tastes should evoke complex patterns of information transmission between orbito-frontal cortex(ofc), amygdala(am) and gustatory cortex(gc). In this study, we present an investigation of these system dynamics using spectral Granger’s causality analysis. Awake rats are trained to press a lever for 40-µl aliquots of one of the four taste (sucrose, NaCl, citric acid, quinine), with an 8 kHz tone signaling the availability of the tastes. Local field potentials (LFP) were recorded from each brain region(ofc, am, and gc) before, during and after trials. The LFPs are digitalized at 1000Hz, and down-sampled to 100Hz for Granger’s causality analysis. The spectral Granger’s causality analysis extracts the magnitude and direction of information flow from one brain area to another, at each frequency band. Our analysis shows a systematic pattern of information flow during self-administrated taste event. After the tone, the change in the information flow are immediately observed from gc to am, followed by that from am to ofc. The analysis also reveals a late feedback flow of information from ofc to gc at about 4 seconds after the tone. Our study quantitatively demonstrates a hierarchical and dynamical pattern of information processing and utilization during self-administrated tasting. Especially, the top-down information flow suggests that, rather than directly representing the taste, the gustatory cortex might have role in interpreting the taste, which could be task dependent.

14. Odor Coding Based on Spike Timing

Kevin Cury
Harvard University

Odors are first encoded by a pattern of activation across an array of ~1,000 odorant receptors. Therefore, the problem of odor discrimination can be regarded as the recognition of an “olfactory image” whose “pixels” correspond to the analog input from each odorant receptor type. To achieve rapid and robust odor recognition, Hopfield (1995) proposed a model in which the timing of spikes with respect to an ongoing population oscillation encodes “pixel” intensity.

It is important to note that the sense of smell is an active process, with volatile molecules being drawn periodically into the nose via inhalation. Furthermore, rodents and many mammals exhibit a diversity of respiration behavior, including stereotyped high frequency respiration (7-9 Hz), known as “sniffing”. Although it has been proposed that respiration-coupled activity might provide a basis for temporal coding, its relevance in awake animals remains controversial, especially during rapid sniffing. To address this, we monitored the activity of single neurons in the olfactory bulb – the first relay center of the olfactory processing stream – simultaneously with measurements of respiration behavior while rats performed an odor discrimination task.

First, we found that inhalation induces a stereotypical pattern of spikes in a cohort of neurons, following the respiration rhythm like a clock. Although respiration frequency varies dramatically during natural behavior, this clock-like activity is consistent across the broad range of respiration frequencies: 45% of neurons show inhalation locked activity during passive breathing, while 77% do so during rapid sniffing (chi-square test, $p < 0.01$). Second, upon odor stimulation, neurons responded with odor-specific temporal patterns precisely locked to the inhalation. These responses often appeared as temporal shifts of the activity observed at baseline, occurring without a change in overall firing rate. In order to estimate how much information such temporal patterns contain, we quantified how accurately an observer can classify six odors based on inhalation-coupled neural activity with or without taking into account fine scale activity (five 32ms bins versus one 160ms bin). Classification success was greatly improved (by ~50%) when considering fine temporal patterns. Finally, the same analysis in the piriform cortex suggested that output from the olfactory bulb is transformed into a more general rate-based code in the cortex. In sum, we show that the timing of spikes with respect to the onset of inhalation can play a substantial role in odor information coding during active sampling in the early olfactory circuit.

15. A theory of efficient coding in neural population with application to the optimality of retinal receptive fields

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Introduction: Efficient coding has long been suggested as a fundamental principle underlying the structure and functional properties of sensory systems [Barlow, 1961], and the basic response properties of mammalian retinal ganglion cells (RGCs) appear to be consistent with this [Atick and Redlich, 1990; van Hateren, 1992]. These earlier comparisons studies, however, relied on a number of simplifications. In particular, the theory was developed assuming a one-to-one ratio between input and output cells. This does not hold in practice, and thus has prevented direct comparison of theory to physiological measurements. Moreover, these earlier works assume that all RGCs have the same receptive field (RF) structure (i.e., they perform a convolution). Recent measurements [Gauthier et al., 2009] indicate that individual RF organizations exhibit significant irregularities, which appear to be coordinated so as to collectively tile the visual space like the pieces of a jigsaw puzzle.

Results: We develop a more general theory of efficient coding. It enables computation of an exact upper-bound for information that can be sent using linear neurons of an arbitrary population size, given that input is Gaussian and that input and output noise is white Gaussian. We also characterize the complete family of solutions, not just the convolutional solution. This extended theory can be used to evaluate the optimality of a population of idiosyncratic RFs.

We compare this theory with physiological data obtained from a patch of macaque retina. The data consists of RFs of 145 RGCs (ON/OFF, Parasol/Midget types) that receive input from 665 cone photoreceptors. We simulate the responses of these photoreceptors to natural images and derive the optimal RFs for the population of 145 model neurons. This is the theoretically optimal linear transform and can transmit 45.5 bits of information. We find the actual RFs can transmit 40.5 bits, close to the theoretical limit (89.1% to the limit). Also, the theory can explain as much as 65.7% of the RFs data variance, including the jigsaw-puzzle like organization.

Conclusions: We show quantitatively that the precise shape and size of individual RGC RFs, the tiling behaviors of the population, and the amount of information transmitted by the population, are in good agreement with the efficient coding hypothesis. The theory is general and may be applied to evaluating the optimality of population coding with linear neurons in any modalities.

16. Local field potential guides neocortical network activity

Flavio Frohlich
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Structured neuronal network activity causes endogenous electric fields that are routinely measured as changes in local field potentials. Previously, we have shown that active neocortical networks that exhibit the slow oscillation are susceptible to weak external fields with amplitudes similar to the endogenous electric fields in vivo (Frohlich et al, 2008). In these experiments, we characterized the response of active cortical networks to fundamental but artificial electric field waveforms. Here, we now show enhancement and entrainment of physiological neocortical network activity in presence of two classes of more realistic electric fields. First, we used electric fields with waveforms recorded in vivo during slow oscillation. The application of these more “natural” field waveforms to spontaneously active cortical slices successfully entrained network activity with a susceptibility threshold of below 1 mV/mm. Second, we directly studied the effect of feedback interaction between endogenous electric field and network activity. For this purpose, we used a hybrid system that consisted of an acute cortical slice that exhibited slow oscillation and an analog electronic circuit that applied an activity-dependent electric field in real-time based on the ongoing multiunit activity. We found that such a feedback interaction enhanced the ongoing network oscillation. Together with computer simulations of cortical networks, our results suggest that the feedback interaction between the endogenous electric field and neuronal activity guides physiological neocortical network activity.

17. Deciding without remembering

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In many decision making processes [1,2], evidence for and against multiple choices is distributed across time, imposing stringent memory requirements [3] on any neural circuitry that optimally implements such decisions. Furthermore, in many sensory circuits [4,5,6], stimulus information is stored in extended spatiotemporal spike patterns, requiring perceptual decision making circuits to integrate and remember not only spike counts, but also spike times. How well can neural circuits with limited memory make decisions about stimuli encoded in temporally extended, multineuronal spike time patterns [7]? What are the limits of performance under a memory constraint, and what kinds of neuronal computations can achieve these performance limits?

We address these questions by developing a new statistical decision framework, which we term "forgetful" ideal observer models. These models perform optimal decision making given a limited memory of incoming spike times across a pool of sensory neurons. The simplest such model has access to only the most recent spike times within a short temporal window. We analyze the performance of this model in a sensory discrimination task in which two stimuli are encoded in two different, noisy spike time patterns which last much longer than the temporal window and are impossible to discriminate using only spike counts. The forgetful ideal observer computes a running log likelihood ratio of the most recent spike times and compares this to an optimized threshold. We find that performance degrades as the integration window shortens, but more slowly than naively expected. Even though the integration time decreases, leading to a smaller SNR in the log likelihood ratio between the two stimuli at any given time, the number of independent samples of this ratio increases, partially compensating for the reduced memory. For example, we find that forgetful ideal observers with a window of 30ms can, remarkably, discriminate between patterns lasting 1 second with spike timing jitters as large as 300ms.

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18. Sensory adaptation as optimal redistribution of neural resources

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Sensory adaptation is expected to optimize perceptual performance in the current environment (e.g., Sakitt and Barlow, 1982; Wainwright, 1999). But experimental studies of adaptation seemed to defy the expectation: Sensitivity to adapting conditions was found to sometimes increase and sometimes decrease in comparison to previous conditions. Sensitivity was also found to change at conditions very different from the adapting ones (e.g., Krekelberg *et al*., 2006).

We presently show that the view of sensory adaptation as optimization to new environment is consistent with the results of adaptation studies. We take into account the basic facts that sensory resources are limited and that every resource (such as receptive field) has intrinsic computational limitations. In particular, receptive fields of different sizes are best suited for measuring either signal location or signal content, due to the uncertainty principle of measurement (Gabor, 1946). Elements of our approach have been presented in Gepshtein *et al*. (2007; www.journalofvision.org/7/8/8/).

We tested our theory in speed adaptation experiments, by measuring human contrast sensitivity over a large range of spatial and temporal frequencies of drifting luminance gratings. We varied the statistics of stimulation: in some blocks of trials low speeds were more common than high speeds, and in other blocks high speeds were more common than low speeds. Using a novel adaptive procedure (Lesmes *et al*., 2008; www.journalofvision.org/8/6/939/) we rapidly estimated human sensitivity in every statistical context. We found that the distribution of sensitivity across the conditions of stimulation changed similar to our predictions. The changes were global. They formed foci of increased and decreased sensitivity, such that the map of observed changes was similar to the map of predicted changes.

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19. What kind of information can be provided by Optical Imaging?

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How much information can be extracted from cortical Voltage Sensitive Dye (VSD) recordings of the living brain? Typically, changes of the VSD imaging signal evoked by in vivo visual stimulation are global, extending over the entire recording frame. In most VSDI studies, stimulus dependent changes at each image pixel are normalized to fluorescence levels during blank conditions (deltaF/F) in which no stimulus was present. On one hand, the procedure allows a straightforward removal of noise artifacts resulting from heartbeat pulsations and irregular staining. On the other hand, such a simple signal-to-noise separation falls short in cases where the data structure is more complex, e.g. when there is no simple relationship between visual input and the dye signal.

Here we introduce several approaches to systematically derive objective criteria to interpret neuronal responses captured by VSD recordings. We used cortical responses (cat visual area 18) to stimulation with natural scene movies taken from a head-mounted camera displaying at 25 Hz the natural input of a strolling cat. We chose these movies, as they provide high-dimensional input of rich spatio-temporal structure, suitable for testing the richness of the VSD imaging output.

In a first step, we used spike-triggered averaging to confirm that VSD signals carry information about the electrode’s position of parallel electrophysiological recordings. Although the observed excitation field around the electrode was wide, it was constrained to an area surrounding the electrode and smaller than the extent of the global signal.

Next we analyzed the spectral properties of the imaging signal (200 Hz). The recording frequency of the movies (25 Hz) as well as the frequency of the excitation light (46 Hz) was detected. However, higher range gamma frequency could not be found. To conclude, either the signal-to-noise ratio in our recordings was not sufficiently high or the nature of the VSD signal is fundamentally different from LFP signals conventionally used for deriving power spectra.

Finally, we analyzed linear components of the VSD signal using PCA. We found that the first few components were sufficient to explain most of the signal variance. For a proper comparison of the input and output signals, additional assumptions about the structure of the artifact and neuronal signals have to be made. We discuss these, our results and provide directions for further investigations of information content of VSD imaging data.

20. Decoding eye position and movement from neuronal populations

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21. Continuous attractors for working memory are stabilized by short-term facilitation

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Persistent activity observed in cortex is thought to be the neuronal correlate of working memory. For example, a substantial fraction of neurons in the prefrontal cortex elevate their activity persistently during the delay period of spatial working memory tasks in which a monkey has to remember the direction of a visual cue for several seconds. This delay activity is selective to the direction to be memorized.

A common model for spatial working memory is a recurrent network with a ring connectivity, in which the connection strength between two neurons is fine-tuned to depend only on their distance on the ring, and is therefore rotationally invariant. With sufficiently strong and spatially modulated recurrent excitation the network dynamics possess an infinite and continuous set (ring) of attractors. In an attractor the activity is persistent and its profile has the shape of a "bump" localized at an arbitrary location. A transient external stimulus tuned to a specific location, corresponding to the direction to be memorized, selects one of these attractors. After the stimulus is withdrawn, the network remains in this attractor. If the fine-tuning of the interactions is perturbed however, even slightly, the invariance to rotation is broken, and the number of attractors becomes finite and small. Subsequently, after stimulus removal, the persistent bump drifts to the nearest attractor. If this drift is too fast, the network is inappropriate for working memory.

Here we show that short-term synaptic facilitation may be correcting this inherent structural instability. We consider a rate model with "ring architecture" for which we derive analytical one-dimensional approximations of the "bump" dynamics in the presence of weak randomness in the connectivity. We conclude that without facilitation, the drift is too fast and the number of attractors is too small for the memory trace to be accurate over the typical duration of a delay period, which is of several seconds. Synaptic facilitation temporarily modifies effective connection strengths on the ring, selectively amplifying connections between neurons that are activated by the cue. We demonstrate that this amplification tends to "pin down" the bump at its initial position. We show analytically that this slows down the drift dramatically (up to a factor of 100). Numerical simulations show that similar behavior occurs if the network is made of spiking neurons. We conclude that short-term facilitation may be essential to the stability of memory of continuous variables over delay duration up to a few tens of seconds.

22. The role of auditory cortex in mediating attention to moments in time

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When events occur at predictable instants in time, anticipation of their occurrence improves the speed and accuracy with which we respond to them.

We have developed a novel behavioral paradigm for rats in which we could study the effect of attention to moments in time on both performance and the electrophysiological responses of single cells in sensory cortex. Using this paradigm we found that: (1) attention to moments in time leads to improved performance on a two-alternative choice auditory detection/discrimination task in rats; (2) the auditory cortex plays a causal role in the performance of this auditory attention task; (3) neuronal activity in the primary auditory cortex is correlated with the behavioral performance of subjects on a trial by trial basis; and (4) the neuronal response of cells in the primary auditory cortex is enhanced by attention to moments in time.

These results suggest that the behavioral improvements observed when valid temporal expectation cues are available are due not only to motor preparation, but to changes in the processing of stimuli as early as primary sensory cortex.

23. Robust decoding of visual information from the human visual cortex

Gabriel Kreiman
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24. Extensive chaotic dynamics in neural networks in the balanced state

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Neurons embedded in operational cortical networks fire action potentials in highly irregular sequences [1]. The balanced state of cortical networks provides an attractive explanation of this temporally irregular behaviour [2]. In this state neurons are driven by large input fluctuations, resulting from a dynamically achieved balance of excitation and inhibition. It has been shown that the balanced state can robustly emerge from the collective dynamics of spiking neuron networks [2]. The detailed dynamics of the balanced state, however, is not well understood. Initially, Vreeswijk and Sompolinsky [2] found a kind of “hyper”-chaotic dynamics in networks of binary neurons, characterized by an infinite positive Lyapunov exponent, which is hard to reconcile with classical notions of nonlinear dynamics. More recently, Zillmer et al. [3] and Jahnke et al. [4] reported stable dynamics in networks of leaky integrate and fire neurons. Notably, all of these previous works neglect a major cellular mechanism of dynamic instability, the instability of the membrane voltage near the spike threshold.

To clarify which kind of balanced state dynamics is expected in networks of neuron models describing such dynamic spike generation, we analyzed networks of pulse-coupled theta neurons in sparse, random networks in the balanced state. The theta neuron model is a standard model of type I neuronal excitability [5]. Based on the analytic solution of the single neuron dynamics, we derived a map that was used for event based simulations and obtained the exact single spike Jacobian matrix for the entire network. This Jacobian was used to calculate the whole set of Lyapunov exponents, following the standard procedure [6]. From the Lyapunov exponents we acquired the entropy production via Pesin's formula and the attractor dimension via the Kaplan Yorke conjecture. In general, the studied networks in the balanced state exhibited chaotic dynamics. The largest Lyapunov exponent was positive and finite, giving evidence to conventional chaos. The entropy production and dimension of the chaotic attractor both scaled linearly with the number of neurons in the networks, hence chaos in the balanced state appears to be extensive spatio-temporal. Furthermore, we found a high attractor dimension, corresponding to many effective degrees of freedom that may potentially encode information in the network. Yet, this is accompanied by a rapid loss of information of 0.5 bits per spike. We conclude that extensive chaos should be expected in general for networks of type I neurons in the balanced state. If information loss in cortical networks is as high as in our model, information could hardly be encoded in detailed spiking patterns beyond the immediate stimulus response.

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25. Contrast influences the pattern direction selectivity of macaque MT neurons

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Neurons in extrastriate visual area MT can signal the direction of motion of complex 2D patterns by integrating information about the motion of their 1D components. This pattern direction selectivity is typically studied using plaids made by adding two identical high-contrast gratings, and we wondered whether the computation of pattern motion would prove robust when the contrast of one or both of the plaid components was reduced. We recorded from 73 MT neurons in anesthetized, paralyzed macaques while presenting drifting gratings and plaids at multiple component contrasts, and quantified their pattern direction selectivity and preferred direction.

Recent models of pattern direction selectivity emphasize the role of contrast gain control mechanisms, so we explored the effect of reducing overall contrast on direction tuning. While direction selectivity to gratings was unaffected by contrast, the pattern index fell at lower contrasts. This effect cannot be explained by a simple decrease in the signal/noise ratio of the weakened responses, supporting the conjecture that gain controls are important in creating pattern selectivity. Next, we examined the effect of reducing the contrast of only one component of the plaid. MT neurons are typically very sensitive to contrast; their responses saturate in the range of contrasts typically tested. Thus, reducing contrast does not strongly reduce responses to a single grating. Surprisingly, we observed that reducing the contrast of one of the plaid's component gratings by as little as a factor of 2 had a profound impact on direction tuning - the response became dominated by the component of higher contrast. At higher contrast ratios, the influence of the weaker grating was barely detectable in the response, even though the weaker grating evoked a reliable response when presented alone. A linear prediction based on the plaid's component responses was insufficient to explain this effect. A model incorporating contrast gain control at the level of V1 (e.g. cross-orientation suppression) captured the change in direction selectivity, but not the change in response magnitude.

We compared these data to psychophysical measures of the change in perceived direction to plaids of different component contrasts and found a similar trend. Five subjects robustly indicated the veridical direction of motion even when the plaid's component contrasts differed by a ratio of 4:1. At higher ratios, subjects showed a strong direction bias towards the higher contrast component.

We conclude that the pattern motion computation depends strongly on stimulus contrast, apparently more than the firing rate evoked by simple stimuli. Some aspects of this contrast-dependence are predicted by current models, but the strong dominance of a weaker grating by a stronger one suggests that additional neural machinery may be involved. The changes in direction selectivity seen at the level of MT may contribute to the perceived direction of plaids composed of unequal contrast.

26. Are Motor Neurons in ALS running out of energy? A computational approach to a motor neuron disease

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Amyotrophic Lateral Sclerosis (ALS) is a devastating adult-onset disease characterized by the selective degeneration of motor neuron and resulting in progressive palsy and death within 2 to 3 years. ALS affects about 4 out of 100,000 people per year and has no cure.
Amongst the causal factors, many are linked to the energy metabolism of motor neuron, supported by the identification of many defects in mitochondria morphology and function. This may lead to a restriction in ATP production and a reduced $Ca2+$ buffering capacity. Moreover, these mitochondrial defects are likely to be compartment dependent, as alteration of mitochondrial transport is also altered in ALS, leading to a redistribution of mitochondria with fewer in axons and accumulation in cell body.
An intriguing hypothesis would be that motor neuron in ALS have a persistent reduction in ATP availability, specifically in the axon and its distal end. This defect could initiate the dying back process, could be responsible for a local and sustained depolarization due to the failure of the ionic pump and could lead to a loss of calcium homeostasis.
To address these questions, we have built a detailed model of a motor neuron that includes the entire cell morphology, the known voltage gated ionic channels as well as a detailed description of intra cellular metabolic pathways for ATP production and consumption.

Using this model, we ask the following questions
- What is the energy budget of a firing motor neuron?
- What could be the consequences of a persistent reduction in ATP availability?
- Can we optimize the ATP consumption to avoid those consequences?
- Can the selective vulnerability of motor neurons be explained by their specific energy requirement?

27. Genetic noise and decision-making in the assembly of sensory-motor circuits

Victor Luria
Columbia University

The assembly of sensory-motor circuits is a serial decision-making process. Neurons, whose axons project to muscle targets and ultimately control movement, execute discrete, local and binary decisions at sequential trajectory selection points. Motor axon trajectory selection is controlled by guidance cues composed of ephrin ligands and Eph receptors, whose expression levels are variable, or noisy. Some cues direct axons to opposite trajectories. Genetic inactivation of cues encoded by ephrin and Eph genes results in inaccurate trajectory decisions and incorrect neural circuit topology. In ephrin and Eph mutants, these decisions are not only inaccurate but also abnormally variable, suggesting genetic variability is translated into phenotypic variability (1). Quantitative modeling shows that trajectory decision accuracy is enhanced by having repellent and competing cues, and is decreased by cue genetic noise. Thus the total number of informative guidance cues is limited by gene expression noise and energetic cost constraints. I propose this model applies to trajectory choices in neural circuit assembly, and generally to discrete decisions controlled by noisy and competing cues.

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28. Robust state sequence and oscillatory state in different model of cortical sensory processing

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A recent study of the cortical neuronal response to taste information suggests that cortical neurons process information through stimulus-specific sequences [1]. Another study finds 7-12Hz (μ) oscillations in the LFP during periods of inattentiveness before stimulus onset [2]. In this work, we suggest a model neural circuit to explain these electrophysiological data. We adapt a simple model [3] that has rich dynamical behavior and has been shown to progress through chaotic state sequences. Our adaptation includes addition of cross-excitation between cells and varying noise in the circuitry within levels appropriate for cortical activity. We implement versions of the network with spiking neurons that have biophysically realistic parameters. We find that by adding a stimulus-dependent input, the network with noise can switch to a mode that has sharp transition between several different states which specific firing pattern across neurons. We investigate the robustness of these stimulus-dependent state sequences by implementing Hidden Markov Modeling (HMM). HMM demonstrates that our model generates a reproducible sequence of states with a large trial-to-trial variance in the transition times between states, in accordance with the experimental data. We find that by varying background input, the network can switch to a mode with strong μ oscillations before adding the stimulus input. Such behavior is similar to the cortical response during periods of inattentiveness. We assess networks of different sizes and complexity and determine the minimal requirements for production of non-periodic state sequences in the presence of a stimulus with the possibility of μ oscillations in the absence of a stimulus.

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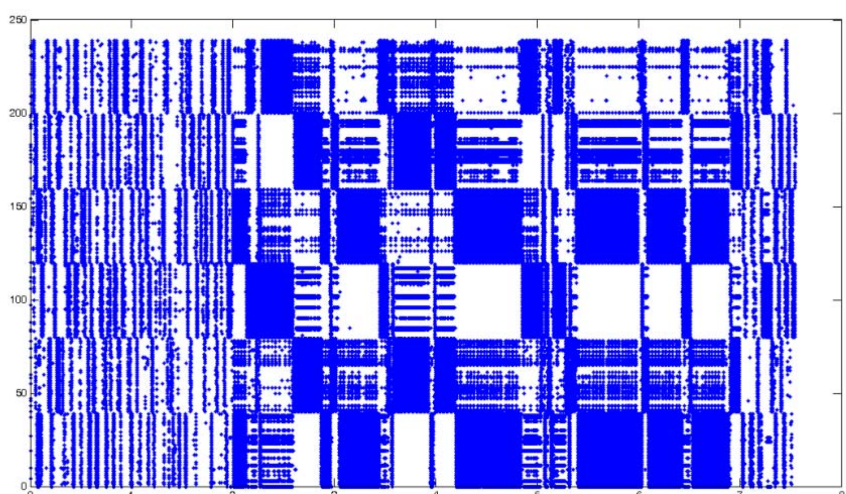
Figure: Raster plot of 6 groups of neurons respond to stimulus. Stimulus arrives at 2s-7s.



29. Recording a large population of retinal ganglion cells with a 252 electrode array and automated spike sorting

Authors: Marre, O., Amedei, D., Soo, F., and Berry II, M.
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Recent theoretical work has suggested that recording the activity of more than 100 neurons in the retina simultaneously might uncover non-trivial collective behavior [1]. Furthermore, understanding the neural code of the retina requires access to the information sent to the brain about a large region of the visual space.

For that purpose, we used a dense array of 252 electrodes to record activity in the ganglion cell layer of the salamander retina. Electrodes were spaced by 30 μm, and this density, which is close to the cell density, has been shown to be high enough to record from nearly all the ganglion cells in a patch of retina for smaller arrays [2]. Our preliminary results showed that the 252 electrode arrays gave a similar quality of recording as previous data with smaller arrays, suggesting that we will have electrical access to nearly all the ganglion cells over this large region.

The large number of electrodes precludes doing spike sorting by hand. We thus designed a highly automated algorithm to extract spikes from these raw data. The algorithm was composed of two main steps: 1) a "template-finding" phase to extract the cell's templates, i.e. the pattern of activity evoked over many electrodes when one ganglion cell fires an action potential; 2) a "fitting" phase where the templates were matched to the raw data to find the location of the spikes.

For the template-finding phase, we started by detecting all the possible times in the raw data that could contain a spike. Using the minima and maxima values in the neighborhood of the spike on each electrode, spikes were clustered into groups. We then extracted the template corresponding to each group by a least-square fitting method.

In the fitting phase, we matched the templates to the raw data with a method that allowed amplitude variation for each template. For that purpose, we selected the best-fitting template, and decide to include it in the match or not according to a criterion that compared the fitting improvement with a cost function. This latter aimed at forcing the spike amplitudes to be close to 1, and imposing a sparseness constraint corresponding to the fact that the overlapping of many spikes is highly unlikely. This process was then iterated to match additional templates to the raw data, similar to the "iterative thresholding" algorithm [3].

Since a first pass clustering did not capture all the cell's templates, we then repeated these two steps. After the fitting part, we did another clustering by taking the minima and the maxima for each putative spike after having subtracted the surrounding contribution of the other templates. This improved clustering made extraction of the templates easier, leading to better fits to the raw data. This alternation of clustering and matching was then run iteratively until no additional templates were found.

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30. Decoding Fine Spatial Details from Retinal Responses

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Visual stimuli on the retina are in constant motion due to involuntary body and eye movements, yet the limit of human visual acuity is substantially finer than the amplitude of these movements.

In fact, for certain stimuli, human acuity is even smaller than the width of the photoreceptors detecting the signal. In this study, we examine how the retina relays fine spatial information in the presence of fixational movements and how the visual system might decode the retinal output.

We recorded the activity of mouse retinal ganglion cells (RGCs) using an extracellular multi-electrode array. Visual stimuli were presented to the retina that mimicked the viewing of static images in the presence of full-field fixational movements. Images consisted of a pair of bars, offset in space by a fraction of a receptive field width. We then constructed a set of decoders to estimate that offset from single-trial responses of the RGC population.

We find that a decoder can quickly and accurately estimate the relative position of the bars without tracking their absolute position on the retina. In fact, such a decoder performs nearly as well as a more complicated version that does track the absolute position using the known statistics of the stimulus drift. The simpler decoder has a straightforward neural implementation and is robust to changes in drift statistics or cell response properties. Furthermore, we find that the population response is most informative when the drift velocity is high.

31. Nonlinear dendritic interactions induce propagation of synchrony in complex neural networks

Raoul Memmesheimer
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We study implications of nonlinear dendritic interactions as recently uncovered in neurobiological experiments, on the dynamics of networks of spiking model neurons. We show numerically and analytically that such networks allow for the propagation of synchrony even if they have random topology. This generates intermittent, strong increases of activity with high frequency oscillations. The models predict the event shape and the oscillation frequency. As an example, for the hippocampal region CA1, they predict events with an oscillation frequency of approximately 200Hz in agreement with experimental observations.

32. Modeling the interaction of biological elements involved in Hebbian and homeostatic plasticity

Authors: Taro Toyoizumi and Kenneth Miller
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We model biological elements with different time constants that are involved in ocular dominance plasticity. We construct and simulate a simple model that includes three separable plasticity processes: (a) Rapid weakening of the deprived eye under MD -- not affected by blockade of TNF-alpha or TrkB. (b) Strengthening of the open eye after about 3 days of MD -- specifically prevented by blockade of TNF-alpha, which blocks a global form of homeostatic synaptic scaling, but not of TrkB. (c) Recovery from MD under binocular vision, specifically blocked by blockade of TrkB.

We modeled the total synaptic strength as the product of (1) A synapse-specific strength (e.g. the percent of potential AMPA receptor sites occupied), modulated by NMDA-dependent LTD as well as by NMDA- and BDNF-dependent LTP. (2) A postsynaptic-cell-specific scaffolding factor (e.g. the number of potential AMPA receptor sites per spine), modulated by TNF-alpha-mediated homeostatic plasticity.

The model captures the transient behaviors of ocular dominance plasticity, which many traditional models do not. First, the learning rule must depend on past as well as present synaptic strengths in order to reproduce the MD result in the monocular cortex. Second, the fast Hebbian component requires a built-in stabilization mechanism, e.g. maximal and minimal weight limits. Slow homeostatic plasticity cannot stabilize an unstable Hebbian component. Third, in order to robustly avoid an overshoot of synaptic strength under MD, homeostasis and LTP/LTD should control independent factors. In the present model, homeostasis and LTP/LTD control two independent factors that multiply to determine synaptic strength, allowing the homeostatic response to build up slowly without being overwritten by fast LTD.

33. Near zero noise correlations and active sampling underlie fast population codes in olfactory cortex

Keiji Miura
Harvard University

Neural representations can in general be elaborated over ensembles of neurons and over time. In the simplest case, integration of spikes across neurons or through time can improve signal to noise. However, positive correlations in neuronal noise curtail the benefits of integration, a factor thought to play a major role in the neural coding of visual stimuli (Zohary et al., 1994).

Here, we investigated the impact of noise in the coding of odors in the rat olfactory cortex. Rats were trained to perform an odor-mixture categorization task (using 4 mixtures of 3 odor pairs) and simultaneous recordings were made from multiple single units (3-21) in anterior piriform cortex (aPC). Odor-evoked responses in aPC were sparse, tightly locked to sniffing, and robust, with firing rates sometimes > 200 Hz. We first considered noise correlations across aPC neurons. Surprisingly, whereas noise correlations in visual cortex are substantial (0.1-0.2), in aPC they were near zero (0.0046 ± 0.099; mean ± S.D; spike counts in the 1st sniff). Accordingly, trial-shuffling had little effect on the ability of an observer to decode odor identity from aPC ensembles, with 20-100 neurons being sufficient to account for behavior performance.
We next considered the integration of odor information in time. On average many fewer spikes occurred on the 2nd sniff compared to the 1st. Moreover, inter-sniff spike counts showed a strong positive noise correlation (0.093 ± 0.14). Thus, decoding performance showed only minor improvement after the first sniff, consistent with the observation that behavior accuracy asymptotes after just one sniff. Inter-neuronal noise correlations are generally thought to arise from common inputs to neighboring neurons with similar tuning specificity, a prominent feature of the neocortex. In contrast, and consistent with the sparse and distributed connectivity of piriform cortex, inter-neuronal noise correlations in aPC were independent of the similarity of odor tuning and the distance between recorded neurons. If low inter-neuronal noise correlations in aPC are solely due to anatomical features of the olfactory system then one might expect them to be constant. However, to the contrary, noise correlations were dynamic, being higher during non-task periods and lower during sniffing before and during odor presentation. Thus, both active sampling and connectivity appear to shape information flow within neuronal ensembles in aPC.

Together, these observations indicate that dynamical processes during active sampling and widely distributed neuronal ensembles, more than temporal integration, are important components of neural representations of odor in the aPC.

34. Network dynamics for motor control: creating distributed > representations of time

Eran Mukamel
Harvard University

Coordinated control of movement requires properly timed motor control signals. In many cases, such timing must be ensured by an internal clock within the central nervous system (Eagleman et al., 2005; Ivry and Spencer, 2004; Mauk and Buonomano, 2004). Despite a wealth of models for specific mechanisms and general principles for temporal processing in neural circuits (Bullock et al., 1994; Buonomano, 2007; Desmond and Moore, 1988; Hong et al., 2008; Yamazaki and Tanaka, 2005), we still lack a framework that can explain the temporal precision of animal behavior in a way that reflects known patterns of circuit connectivity. We study theoretically how brain circuit structure, as defined by the wiring diagram of synapses among network cells, gives rise to temporal dynamics that could support representation and processing of temporal information. By analyzing the problem of motor learning in a statistical estimation framework, we derive a quantitative figure of merit for the neural representation of time.

Our measure is the number of effective degrees of freedom in the class of movement control signals which constitute the system's repertoire of outputs. We apply our framework to analyze network dynamics in the cerebellar cortex, which has been proposed to serve a broad range of temporal processing functions and which works closely with motor neocortex.

Our simulations show that the striking geometric organization of cerebellar cortex, particularly the anisotropic and near crystalline arrangement of the granule cell parallel fiber system, may improve the representation of time as compared with alternative network geometries. Our framework complements recent information theoretic analyses of temporal processing and memory storage in linear networks, and may provide a statistical interpretation of the bounds on computational processing provided by other techniques.

35. Dendritic cable properties determine rapid signaling in fast-spiking GABAergic interneurons

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Fast-spiking, parvalbumin-expressing basket cells (BCs) play a key role in feedforward and feedback inhibition in cortical neuronal networks. However, the dendritic mechanisms underlying the rapid activation of these inhibitory cells remain unclear. To obtain a quantitative picture of the generation, propagation, and integration of excitatory synaptic potentials in BCs, we developed detailed passive cable models of these interneurons. Voltage responses to short and long current pulses were recorded in a dual somatic or somatodendritic configuration in the presence of the I_h channel blocker ZD 7288. Cells were filled with biocytin during recording for subsequent morphological analysis. Constrained by the detailed and complete morphological reconstruction of soma, dendrites, and axon, cable parameters of BCs were obtained by direct fitting of the experimentally recorded voltage transients. We found that models with non-uniform specific membrane resistance (R_m) described the experimental data significantly better than uniform models, with R_m being lowest in the proximal somatodendritic region (R_m = 7.6 ± 1.7 kΩ cm^2), intermediate in distal dendrites (R_m = 74.3 ± 56.1 kΩ cm^2), and highest in the axon (R_m = 281.6 ± 108.2 kΩ cm^2). On average, the specific membrane capacitance (C_m) and the intracellular resistivity (R_i) were C_m = 0.93 ± 0.04 μF cm^{-2} and R_i = 172.1 ± 18.5 Ω cm (3 dual somatic and 3 somatodendritic recordings; 32 – 34°C). Thus, C_m and R_i were comparable to those of pyramidal neurons, but the average somatodendritic R_m was lower and the somatodendritic gradient of R_m was reverse to that in pyramidal neurons. Simulation of synaptic events revealed that these cable properties contribute to the optimization of rapid signaling in BCs. In particular, the low value and the non-uniformity of R_m in BCs accelerate the dendrosomatic propagation of excitatory postsynaptic potentials (EPSPs) and the decay time course of somatic EPSPs. At the same time, the efficacy of slow inputs is maintained. Additionally, the extensive axon and the multipolar dendritic tree represent a current sink, leading to further speeding of somatic EPSPs. In conclusion, structural and non-uniform cable properties of BC dendrites promote fast signaling, facilitating rapid phasic and efficient tonic activation of these interneurons in hippocampal microcircuits.

36. Structural plasticity and pathway formation in cortical networks

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BCCN

The cortical micro-circuitry is considerably shaped by activity-dependent metabolic processes in neurons that govern neuronal wiring in the course of development. Herein, the protein kinase C (PKC) takes a key-position cross-linking many biochemical pathways involved in structural regulation and targeting many cytoskeletal proteins directly.

In a simplified scheme, activation of PKC via metabotropic glutamate receptor downstream signaling mobilizes cytoskeletal proteins, thereby promoting structural plasticity, since antagonistic pathways in turn promote cytoskeletal assembly and stabilization (Quinlan '96). Previous studies showed that inhibition of PKC activity in cerebellar slice cultures promotes dendritic outgrowth and arborization in Purkinje cells (Metzger '00) and that climbing fiber pruning is impaired in PKC deficient mice (Kano '95). Further in vitro data demonstrate the importance of PKC activity for the experience-dependent modulation of synaptic weights on the basis of AMPA receptor trafficking (Zheng '08).

Not surprisingly, behavioral studies show that spatial learning crucially depends on PKC activity (Alvarez-Jaimes '04, Bonini '08). It remains, however, largely unknown how differentially regulated PKC activity i.e. structural and synaptic plasticity during development results in particular network structures and dynamics. We investigate these dependencies in cortical cell cultures developing on micro-electrode arrays. These generic random networks display a self-regulated maturation process with similar phases as the developing cortex, during which we interfered with neuronal differentiation by chronically inhibiting PKC activity. Applying new morphometrics, we found significantly increased arborization and extent of dendrites as well as increased synapse density, indicating increased connectivity in these networks. Reduced neuronal clustering further suggests impaired cell migration. The resulting increased topological homogeneity was accompanied by reduced complexity in the emerging network oscillations. Pronounced and, moreover, developmentally conserved wave-like neuronal recruitment patterns in network-wide bursting events further indicate a homogeneous connectivity lacking distinct neuronal pathways.

We conclude that PKC activity is essential for the continuous reorganization of network structure and dynamics in developing cortical cell cultures. This supports the idea that the embedding of functional pathways in the cortex depends on the coordinated regulation of structural plasticity by PKC.
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37. The role the retina plays in shaping predictive information in ganglion cell populations: correlations, synergy and optimization

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Prediction is important for almost all modes of behavior and our research focuses on how a population of neurons implements predictive computations. We have examined how groups of retinal ganglion cells (the output neurons of the retina) encode predictive information in their collective firing patterns. The population response is represented as a binary word, indicating a spike or no-spike from each neuron in a small time window of size Δt. We can then ask how precisely a word at time t specifies a future word at time $t+\Delta t$. This predictive information is due, in part, to the intrinsic firing properties of the ganglion cells, as well as to correlations in the stimulus. We attempt to disentangle these effects by breaking various correlations between cells and within cells in time. We also examine responses to temporally uncorrelated while noise stimuli. We compare responses to natural movies and synthetic motion to the white noise stimulus, by computing the total population predictive information to that obtained by summing individual neurons, the difference being the 'synergy' in the population. Finally, we ask whether or not the retina is optimized for prediction, in the sense that it retains specific information about the past that is most informative about the future, by computing directly the stimulus information for a simple 1D bar movie.

38. A Bayesian Method to predict the optimal diffusion coefficient in random fixational eye movements

David Pfau
Columbia University

Under natural viewing conditions, our eyes alternate between saccadic movement and fixation. However, even during fixation there are constant small movements, which can be decomposed into miniature saccades and diffusion-like random eye movements. Some diffusion helps prevent adaptation to a particular stimulus, but diffusion also blurs the image of the world across the retina. Despite this, humans can resolve fine spatial detail very well, and this diffusion may even enhance the ability to distinguish high-frequency components of an image [1]. This suggests that the brain compensates for fixational eye diffusion and may even extract useful information from it.

To investigate the effect of eye diffusion on image reconstruction, we extended a generalized linear model (GLM) of retinal encoding/decoding to incorporate random-walk drift of the image falling on the retina. GLMs have been successfully applied to modeling a range of neural systems, including retinal ganglion cells [2]. Previously developed GLMs of the retina, directly estimated from spiking data, generate simulated network spike trains with the correct spatiotemporal filtering and correlation structure. Finally, given this network spiking encoding model and a statistical model of the spatiotemporal visual inputs, there is a natural Bayesian method for decoding the response [3].

For our model incorporating fixational eye diffusion, the decoding model would assign a probability to all possible random walks the image could take. However, the number of possible paths grows exponentially with time, making this method computationally intractable. Instead, we approximate the posterior distribution of images given the observed spikes as a mixture of Gaussians, and track the diffusive movements of the mixture components by a particle filtering approximation. This method is both computationally tractable and effective at reconstructing the encoded image.

Preliminary results show that the image reconstruction is poor at both very low and very high diffusion rates, while reconstruction works reasonably well at intermediate diffusion rates. Thus, a well-defined optimal diffusion rate exists, and in general depends on statistical properties of both the stimulus and the retinal spatiotemporal receptive fields, such as the strength of the sustained response component and whether the transient component lasts longer than the persistence time of the eye movements. We are currently pursuing quantitative comparisons to the real diffusion coefficient during head-fixed viewing.

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39. Periodicity in the V1 extra-classical receptive field

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Studies of the V1 extra-classical receptive field have revealed neurons that exhibit nonmonotonic changes in response to increasing stimulus size. In length- and width-tuning experiments, some neurons show two peaks of firing rate as a function of stimulus size (De-Valois et al. 1985, Sengpiel et al. 1997, Wang et al. 2009), and more generally, length-tuned cells show nonmonotonicity in their inhibitory synaptic conductance (Anderson et al. 2001). While it has been proposed that the latter arises from multiple, distinct sources of inhibitory input, an alternative explanation is that the cortical network drives a periodic pattern of inhibitory-cell firing rate over retinotopic space. Given oscillations with a fixed period and phase pegged to the edge of the stimulus representation, the firing rate at the center of the stimulated region will rise and fall with increasing stimulus size (Adini et al. 1997).

To better understand what sort of cortical network could produce such an effect, we constructed a linear firing-rate model of V1 comprised of a one-dimensional recurrent network of excitatory and inhibitory neuronal populations. We assume, as in cortical networks, that inhibitory connections are localized while excitatory are longer range. Using a combination of both analytic and numeric modeling techniques, we find that in order for inhibitory firing rates in a generic network without periodic connectivity to oscillate as a function of space, several specific requirements must be met. The most significant of these is that the network must be an "inhibition-stabilized network" (ISN), meaning that excitatory to excitatory connectivity is strong enough to make the network unstable by itself, but the network is stabilized by feedback inhibition. Substantial evidence exists that cortical circuits operate within this regime (Ozeki et al. 2009, Tsodyks et al. 1997).

Our analysis leads to a number of testable predictions: excitation and inhibition should resonate at different spatial frequencies, and the relative phases of excitation and inhibition in response to a drifting grating should depend on the spatial frequency of the stimulus. As stimulus spatial frequency is varied, the response phase of inhibitory neurons vs. excitatory should jump abruptly by 180 degrees at a critical spatial frequency. Additionally, through the implementation of a biologically-based input-output nonlinearity, this model is able to explain an important contrast-dependent qualitative change in the V1 response. The presence of the second peak in length-tuning curves only at higher contrast (Anderson et al. 2001, Sengpiel et al. 1997) occurs due to an input-driven transition into the inhibition-stabilized regime. This mechanism may be important for other contrast-dependent changes in the V1 response.

40. Modeling Firing Rate Dynamics

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Columbia University

Our goal is to describe the output of individual neurons as a time-varying firing rate given an arbitrary input. Traditional models of firing rate dynamics are overly simple in assuming that neural activity is asynchronous, which is often not true even in populations of unconnected neurons. Conversely, many mathematical methods exist for deriving approximations to the firing rate of spiking models, but such methods tend to lead to cumbersome equations. We show here that the firing rate of uncoupled Integrate-and-Fire model neurons can be well approximated by a simple two-variable rate model that accounts for the degree of synchrony in the underlying spike trains. This model can be used both as a tool for understanding transitions between synchrony and asynchrony in generally as a firing rate model that more closely matches true spiking dynamics.

41. Trial-to-trial variability of phase precession in the hippocampus

Robert Schmidt
BCCN Berlin

During the crossing of the place field of a pyramidal cell in the rat hippocampus, the firing phase of the cell decreases with respect to the local theta rhythm. This phase precession is usually studied on the basis of data in which many place field traversals are pooled together. Here, we study properties of phase precession in single trials and compare them to the properties of pooled-trial phase precession. We find that single-trial and pooled-trial phase precession are different with respect to three fundamental properties: phase-position correlation, phase-time correlation, and phase range. While pooled-trial phase precession may span 360 degrees, the most frequent single-trial phase range is only around 180 degrees. Further, an important source of variability of phase precession pooled over trials is the large trial-to-trial variability. Only a part of this trial-to-trial variability may be explained by running speed and firing rate differences across trials, but the larger part of the variability remains to be explained. Finally, comparison with surrogate trials indicates that single trials are not randomly drawn samples from the pooled data and that pooling over trials changes basic measures of phase precession.

42. A Model for Retinal Pattern Adaptation

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Retinal ganglion cells are known to adapt to patterns present in the visual field. The spatio-temporal receptive fields of these cells change dynamically over timescales of a few seconds depending on the spatial, temporal or spatio-temporal correlation in the visual image [1]. Here we present a retinal circuit consisting of LN-model bipolar and amacrine cells that provide the input to such ganglion cells. The pattern-dependent effectiveness of the amacrine cell inhibition combined with the activity-dependent depression of the bipolar-ganglion synapses can explain the experimental results obtained previously [1].

[1] Dynamic predictive coding by the retina. T. Hosoya, S. A. Baccus, and M. Meister, Nature 436:71-77, July 2005.

43. Hydrodynamic Objects: Localization, Feature Extraction, and Recognition

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All fish and some aquatic amphibians possess a unique sensory facility, the lateral line. The lateral-line system is a mechanosensory facility of aquatic animals that enables them not only to localize prey, predator, obstacles, and conspecifics, but also to recognize hydrodynamic objects. We present on the one hand a mathematical discussion of the characteristics fish print into the flow field and on the other hand we introduce an explicit model explaining how the lateral line can use the imprinted information to distinguish differently shaped submerged moving objects. Our model is based on a hydrodynamic multipole expansion and uses the unambiguous set of multipole components to identify the corresponding object. Furthermore, we show that within the natural range of one fish length the velocity field contains far more information than that due to a dipole. Finally, the model we present is easy to implement both neuronally and technically, and agrees well with available neuronal, physiological, and behavioral data on the lateral-line system.

44. Encoding fine spatial detail with irregular receptive fields

Frederick Soo
Princeton University

Classical ganglion cell receptive fields have a smooth, approximately Gaussian spatial profile with high overlap among nearby cells of different morphological type. In the salamander, each point in visual space is covered by ~60 receptive field centers, as measured by white noise (Segev et al., J. Neurophysiol 2006). At higher resolution, however, individual receptive fields can be irregular (Brown et al., Neuron 2000). We explored how the fine structure of receptive fields affects the encoding of spatial information. Specifically, we probed the retina with spots of light much smaller than the receptive field center (20 μm in diameter, 100ms, ~10^3 photons/L-cone/sec).

Intracellular responses of ganglion cells were recorded during the repeated presentation of twenty small spots at distinct spatial locations within the receptive field. Taken alone, ganglion cells, on average, conveyed about 0.9 bits about the identity of the spot (out of 4.3 bits possible). When the responses of multiple ganglion cells were pooled, the information increased as if the cells were almost independent, reaching ~80% of the maximum possible for groups of seven cells. The information conveyed by the group was predicted by a simple model in which pairwise redundancy between ganglion cells (~5-10%) is uniformly distributed among the cells in the group and the signaling is otherwise independent (Puchalla et al., Neuron 2005). The measured performance was significantly better than expected from a smooth Gaussian model derived from the measured linear receptive field. The receptive fields at high spatial resolution were inhomogenous, not Gaussian, and only weakly correlated between ganglion cells. Despite their close spacing, individual spots of light generated measurably different responses among the different ganglion cells sampling the region, allowing them to be distinguished from one another. These results show that a population of retinal ganglion cells can convey more information at spatial scales much smaller than the receptive field center than is predicted by smooth, Gaussian receptive fields.

45. On synaptic weight distributions in spike timing-dependent plasticity

M. Tierz
Brandeis University

We study in detail the synaptic weight distributions that form in the presence of spike timing-dependent plasticity, in the case of weight-dependent plasticity rules. We use a well-known stochastic approach, based on Fokker-Planck equations, to study non-equilibrium phenomena. In particular, we study how the synaptic weight distribution tends to its equilibrium and stable form.

46. Working Memory-Based Reward Prediction Errors in Human Ventral Striatum

Michael Todd
Princeton University

47. Modeling the interaction of biological elements involved in Hebbian and homeostatic plasticity

Taro Toyoizumi and Kenneth Miller
Columbia University

We model biological elements with different time constants that are involved in ocular dominance plasticity. We construct and simulate a simple model that includes three separable plasticity processes: (a) Rapid weakening of the deprived eye under MD -- not affected by blockade of TNF-alpha or TrkB. (b) Strengthening of the open eye after about 3 days of MD -- specifically prevented by blockade of TNF-alpha, which blocks a global form of homeostatic synaptic scaling, but not of TrkB. (c) Recovery from MD under binocular vision, specifically blocked by blockade of TrkB.

We modeled the total synaptic strength as the product of (1) A synapse-specific strength (e.g. the percent of potential AMPA receptor sites occupied), modulated by NMDA-dependent LTD as well as by NMDA- and BDNF-dependent LTP. (2) A postsynaptic-cell-specific scaffolding factor (e.g. the number of potential AMPA receptor sites per spine), modulated by TNF-alpha-mediated homeostatic plasticity.

The model captures the transient behaviors of ocular dominance plasticity, which many traditional models do not. First, the learning rule must depend on past as well as present synaptic strengths in order to reproduce the MD result in the monocular cortex. Second, the fast Hebbian component requires a built-in stabilization mechanism, e.g. maximal and minimal weight limits. Slow homeostatic plasticity cannot stabilize an unstable Hebbian component. Third, in order to robustly avoid an overshoot of synaptic strength under MD, homeostasis and LTP/LTD should control independent factors. In the present model, homeostasis and LTP/LTD control two independent factors that multiply to determine synaptic strength, allowing the homeostatic response to build up slowly without being overwritten by fast LTD.

48. Mechanism of gait adaptation in *C. elegans*

Quan Wen
Harvard University

C. elegans moves by generating sinusoidal body waves. When navigating in different environments, such as fluids with different viscosities, the roundworm adapts its gait by changing the frequency and wavelength of undulation. How does the motor circuit in *C. elegans* generate and propagate body undulation? What is the functional role of mechano-sensory feedback? To address both questions, we analyzed *C. elegans* locomotion with behavioral assays that probe the motor circuit by defining the mechanical load at different points along the worm's body. We also developed a phenomenological model to explain existing observations. Preliminary results suggest that *C. elegans* likely use a hybrid strategy for forward movement: the motor circuit near the head may contains a pattern generator to initiate and control undulation; yet to propagate undulatory wave and to adapt body gait require local couplings between body segments via mechano-sensory feedback.

49. Slowness in Hierarchical Networks for Visual Processing

Niko Wilbert
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Primates are very good at recognizing objects and at the same time assessing their viewing angle and relative position. In such tasks they outperform existing computer vision systems. We present a model for the unsupervised learning of object identities and codes for position and viewing angle (including depth rotation). The model is based on a hierarchy of Slow Feature Analysis (SFA) modules, which were shown to be a good model for complex cells in the early visual system. Our model is trained and tested with visual input data generated from virtual 3D-objects. To show that the model extracts useful information we use linear regressions (for position and viewing angle) or simple classifiers (for object identity). This supervised step extracts the feature codes with high invariance under the transformations.

50. Spatial Spread of the Local Field Potential and its Laminar Variation in Visual Cortex

Dajun Xing
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Currently there is still a debate about what is the cortical spatial scale of the Local Field Potential (LFP). Different studies provided various estimates of the LFP's spatial spread, ranging from 100 to 3000 μm. Furthermore, it is unknown yet how much the laminar variation for the spatial scale of the LFP in cortex. In this study, we provide a general method to estimate the cortical spread of the Local Field Potential (LFP) in any cortical area that has a topographic map. We applied this new method to estimate the cortical spread of the LFP throughout all layers of Macaque primary visual cortex, V1. For the first time, we demonstrate the cortical spread of the LFP in different cortical layers in V1. We mapped multi-unit activity and LFP visual responses with sparse-noise at several cortical sites simultaneously. The cortical magnification factor near the recording sites was precisely estimated by track reconstruction. The experimental measurements together with a model of signal summation let us obtain the cortical spread of the LFP. V1's LFP was the sum of signals from a very local region, the radius of which was on average 250 μm. The LFP's cortical spread varied across cortical layers, reaching a minimum in layer 4B of 120 μm. The spatial scale of the visual responses, the cortical spread, and their laminar variation led to new insights about the sources and utility of the LFP.

51. Dscam diversity and neuronal self-recognition

Qing Yuan
Columbia University

The Drosophila Dscam gene encodes a diverse repertoire of cell surface recognition molecules through alternative splicing. Combinatorial stochastic expression of multiple Dscam isoforms in each neuron constitute a unique cell surface identity which allows it to distinguish between itself and the numerous neurons co-occupies its dendritic field. They carry out highly specific homophilic interaction and trigger dendritic repulsion. Kinetic modeling of Dscam synthesis and metabolism for different gene regulatory models reveal critical kinetic parameter ranges for establishing unique cell surface identity and normal self-avoidance behavior in a homogenous neuronal population. Live imaging studies of the Drosophila Dscam using photo-convertible fluorescent protein (mEosFP) in the dendritic arborization (da) neurons allows us to quantify these parameters and determine which gene regulatory model best fits the experimental observations.

52. OFF direction-selective cells in the mouse retina

Yifeng Zhang, In-Jung Kim, Joshua Sanes, and Markus Meister
Harvard University

Our vision is extremely sensitive to object motion. Detection of motion starts in the retina, and the motion information is further extracted, processed, and refined along the visual pathway. The mouse retina has three types of retinal ganglion cell that report object motion in a specific direction. Based on morphology and response properties, one distinguishes: the ON-OFF direction selective-ganglion cells (DSGCs), the ON DSGCs, and the recently discovered OFF DSGCs, also known as J-RGCs [1]. For both the ON-OFF and the ON DSGCs, direction selectivity depends on synaptic input from starburst amacrine cells, which

is itself already directionally selective. J-RGCs, on the other hand, receive little or no input from starburst cells, and therefore must generate direction selectivity by different means. To explore these mechanisms, we exploited a transgenic mouse line in which J-RGCs are fluorescently marked, and targeted these neurons for electrical recording.
J-RGCs have a highly asymmetric organization: Their dendritic arbors are fan-shaped and point from dorsal to ventral across the retina. This same axis corresponds to the preferred direction for spot movement. We recorded the synaptic input currents of J-RGCs and studied their roles in the emergence of direction selectivity. Using reverse correlation to flicker stimuli, combined with whole-cell voltage clamp at a range of holding potentials, we measured the receptive fields for both the excitatory and inhibitory inputs. The receptive field for inhibition has an ON center and is limited to a region close to the soma. By contrast the receptive field for excitation has an OFF center that extends over the entire dendritic tree. Moreover, the excitatory input to the J-RGCs is “directionally asymmetric”: a stimulus applied at the distal dendrites paradoxically excites the cell with shorter delay than one at the proximal dendrites. We propose that this timing difference between spatially offset excitatory inputs combined with a spiking threshold could produce the observed direction selectivity in J-RGCs.

Acknowledgments
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53. Conditions on connectivity to achieve surround suppression in primary visual cortex

Jun Zhao, Daniel B. Rubin and Kenneth. D. Miller
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Recent results (Ozeki et al. 2009,Song and Li 2008) show that inhibitory as well as excitatory cells in cat V1 are suppressed by surround stimuli. Ozeki et al found that this required that the local circuit function as an inhibition-stabilized network (ISN) when responding to a visual stimulus, meaning that excitatory recurrence is so strong as to destabilize visual responses by itself, but the responses are stabilized by feedback inhibition.

In Ozeki et al (2009), we only modeled a single local circuit, and assumed that the surround evoked lateral excitatory input to this local circuit. Now, we model a spatial array of excitatory and inhibitory neuronal populations, so that we are modeling both the neurons that respond to the center and the surround stimuli and the interactions between them. We study a linear model of cells preferring a single orientation, and assume that all 4 types of connectivity (E->E, E->I, I->E, I->I) fall off as a Gaussian with distance between the neurons. Each type of connectivity has its own amplitude and falloff distance. In this model, some spatial patterns of response may behave as ISNs while others behave as non-ISNs, so we define a stable network to be an ISN if at least one pattern is an ISN, that is, if the excitatory sub network alone has at least one unstable mode. We assume, as is seen biologically, that the inhibitory projections are shorter-range than the excitatory projections.

We study the response in the steady state of the neurons at the center of the stimulus, for varying stimulus size. We ask under what conditions on the connectivities (i.e. on the 4 amplitudes and falloff distances) do both excitatory and inhibitory neurons at the stimulus center show surround suppression? We can show analytically that for inhibitory response to be decreasing with stimulus size for large stimuli, two conditions must hold: (1) the network must be an ISN; (2) the E->I connections must be longer-range than the E->E connections (biologically, this means that the probability of E->I vs. E->E connections must increase with increasing connection distance). A general numerical solution by exhaustive parameter space search confirms that these conditions must hold to see non-trivial surround suppression

(suppression ratio >= 5%, defined as percent decrease from peak response to maximally suppressed response). Furthermore, to achieve strong suppression (suppression ratio >= 50%), the network response must be dominated by a characteristic spatial frequency at which the linear network approaches instability, suggesting that nonlinear models may be needed to more fully characterize this regime.

54. Chaos and Lyapunov spectra of Integrate- and fire neuronal networks

Douglas Zhou
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It has been shown that a standard single integrate-and-Fire (I&F) neuron under a general time-dependent stimulus cannot possess chaotic dynamics despite the firing-reset discontinuity. Here we address the issue of whether conductance-based pulsed-coupled network interactions can induce chaos in an I&F neuronal ensemble. Using numerical methods, we demonstrate that all-to-all, homogeneously pulse-coupled I&F neuronal networks can indeed give rise to chaotic dynamics under an external periodic current drive. We also provide a precise characterization of the Lyapunov spectra for these high dimensional non-smooth dynamical systems.

55. Grouping variables in an underdetermined system for invariant object recognition

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An important problem in neuroscience is object recognition invariant to transformations, such as translation, rotation and scale. During recognition one recovers the object and the transformation that best explain an input image. To gain insights on the recognition dynamics and the organization of stored objects, we propose a model system as an abstraction of invariant recognition. Without constraints, the system is underdetermined when the number of possible transformations plus objects exceeds the available information in the system, which is the size of the image. We propose a coarse-to-fine strategy where variables are first grouped (share the same dynamics) such that a unique solution can be obtained. Then variables within the winning groups resume their own dynamics, using the group solution as initial value. We show that this coarse-to-fine dynamics can recover true sparse causes.