Contextual influences on visual processing

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The visual image formed on the retina represents an amalgam of visual scene properties, including the reflectances of surfaces, their relative positions, and the type of illumination. The challenge facing the visual system is to extract the "meaning" of the image by decomposing it into its environmental causes. For each local region of the image, that extraction of meaning is only possible if information from other regions is taken into account. Of particular importance is a set of image cues revealing surface occlusion and/or lighting conditions. These information rich cues direct the perceptual interpretation of other more ambiguous image regions. This context-dependent transformation from image to perception has profound – but frequently under-appreciated – implications for neurophysiological studies of visual processing: To demonstrate that neuronal responses are correlated with perception of visual scene properties, rather than visual image features, neuronal sensitivity must be assessed in varied contexts that differentially influence perceptual interpretation. We review a number of recent studies that have used this context-based approach to explore the neuronal bases of visual scene perception.

Neural noise and spatio-temporal patterns of movement-related activity in the supplementary motor area

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We analyzed the variability and coding capacity of simultaneously recorded pairs of neurons in the primate supplementary motor area (SMA). The coding performance was analyzed to determine whether the temporal precision of spike arrival times and the interactions within and between neurons improve the prediction of the upcoming movement direction. There were three main findings in the analyses. First, analysis of neuronal variability showed that the variance of spike counts was smaller than its mean in many SMA neurons, suggesting that a Poisson process is not a good model for the neural responses we recorded. Second, we found that the correlation in spike count variability between pairs of neurons was concentrated at low frequencies (<10 Hz). Third, we tested multiple decoding models that differed in the temporal resolution and the correlations in the spike trains which were utilized for decoding. The results showed that in about 68% of neuron pairs, the arrival times of spikes at a resolution between 66 and 40 ms carried more information than spike counts in a 200 ms bin. In addition, in 24% of neuron pairs, inclusion of within- or between-neuron correlations in spike trains significantly improved decoding accuracy. These results suggest that in some SMA neurons there is more information in the spatio-temporal pattern of activity than there is in the rate code of independent neurons.

The relationship between temporal integration and onset and offset latency for a velocity white-noise stimulus in direction selective neurons in V1 and MT/V5

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Using extracellular, single-unit recording, we have studied the temporal dynamics of direction selective (DS) cells in primary visual cortex (V1) and in area MT/V5 in anesthetized macaque monkeys. Visual stimuli consisted of sinusoidal gratings that were optimized in size and orientation for each neuron and were moved randomly along the neuron's axis of preferred motion according to a white-noise velocity signal. We compared integration time, onset and offset latency, and response strength as a function of the variance of the velocity signal and the spatial frequency and contrast of the sinusoidal grating. Generally, integration time and response latency were longest in DS cells in both V1 and MT/V5 for slowly moving, high spatial frequency, and low contrast stimuli. We compared the neuronal responses to predictions from a motion energy model and to predictions from a phenomenological model built from adaptive linear filters and an integrate-and-fire compartment with excitatory and inhibitory conductances. The latter model accounts for many of the temporal response properties that we have observed.

Spike transfer and sensitivity control in thalamic and cortical 'hybrid networks'

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The response of thalamic and cortical neurons to individual synaptic inputs is potentially influenced by local synaptic interactions and by the state of the network in a continuum from sleep to waking. We examine these properties using new hybrid technology (Le Masson et al., 2002) in which a biological neuron is connected to silicon and computer-based simulated neurons through artificial synaptic connections. Individual membrane currents of the simulated and biological neurons and the properties of their synaptic connections can be selectively and quantitatively controlled throughout their dynamic range.

The thalamus is the major gateway for the flow of sensory information to the cerebral cortex. In early stages of sleep, when sensory perception drops, this structure is the source of robust network synchronized oscillations in the 6 to 14 Hz frequency range (spindle waves). We examine the role of these thalamic oscillations in the gating of synaptic inputs. We show that feedback inhibition from cells of the thalamic reticular nucleus controls spike transfer in thalamocortical cells in a state-dependant manner.

Neurons in the cerebral cortex are under a constant state of bombardment by synaptic potentials. We have used a computational model (Destexhe et al., 2001, Neurosci. **107**:13) that mimics the synaptic bombardment of thousand of cells. This 'noise' injected in pyramidal cells reproduces the spontaneous activity recorded in the biological network in vivo or in vitro. Using the hybrid system, we can the test the impact of background synaptic activity on the probability of spike response to individual synaptic inputs.

A mechanism for hippocampal place cell firing during the hyperpolarizing phases of the theta rhythm

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During phase precession, hippocampal place cells fire over a range of phases of the population theta rhythm. The majority of spikes occur, however, around the peaks of the theta rhythm when the somatic membrane of the cell is presumably most depolarized. During REM sleep, on the other hand, place cells associated with familiar environments fire preferentially at the troughs of the theta rhythm when the somatic membrane of the cell is most hyperpolarized (Poe et al, Brain Research, 2000). A locus of similar place cell firing in the theta trough has been identified in a recent analysis of phase precession data from awake animals (Yamaguchi et al, J Neurophysiol, 2002). We propose that such preferential firing in the theta trough could result from a gating of synaptic inputs by the 180 degree phase differential in the theta rhythm at the distal dendritic and cellular layers. In particular, distal dendritic synaptic inputs (from layer III of the entorhinal cortex) arriving at the peak of the dendritic theta rhythm, equivalently the trough of the somatic theta rhythm, would be successfully propagated to generate an action potential while those arriving at the trough of dendritic theta, equivalently the peak of somatic theta, would generate only subthreshold responses. We use a realistic, multicompartment CA1 pyramidal cell model (Migliore, J Comput Neurosci, 2002) to investigate this proposed mechanism.

A burst-timing based learning rule at the retinogeniculate synapse

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Synaptic refinement in the mammalian lateral geniculate nucleus (LGN) requires neural activity. Learning rules that specify how combinations of pre- and postsynaptic activity lead to changes in synaptic efficacy are thought to underlie this activity-dependent development, though it is unclear how natural activity patterns drive such refinement. We address this question using an integrated experimental and theoretical approach. First, we determined what aspects of the spontaneous activity in the retina present during this development carry information that could instruct refinement, leading to the prediction of a learning rule based on the timing between presynaptic and postsynaptic bursts. Then, using perforated patch recording in slice preparations of early postnatal rat LGN, we recorded from LGN neurons and measured the size of postsynaptic currents evoked by optic tract stimulation, both before and after a burst-time-based stimulation paradigm. We found that the magnitude and direction of synaptic plasticity depends on the latency between pre- and postsynaptic bursts, suggesting how a "burst-time dependent" learning rule could use natural activity patterns to drive synaptic refinement. We then use simple simulations of the retinogeniculate system to demonstrate how the observed rules of synaptic plasticity observed in vitro at the single synapse can explain the system-level activity-dependent development observed in vivo.

Temporal resolution of ensemble visual motion signals in primate retina

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Recent studies have examined the temporal precision of spiking in visual system neurons, but less is known about the time scale that is relevant for behaviorally important visual computations. We examined how spatio-temporal patterns of activity in ensembles of primate retinal ganglion cells convey visual motion information to the brain. The direction of motion of a bar was estimated by comparing the timing of responses in ensembles of parasol (magnocellular-projecting) retinal ganglion cells simultaneously recorded, using a cross-correlation approach similar to standard models of motion sensing. To identify the temporal resolution of motion signals, spike trains were low-pass filtered before estimating the direction of motion. The filter time constant that resulted in most accurate motion sensing was 10-50 ms for a range of stimulus speeds and contrasts, and was on average comparable to the inter-spike interval. Motion-sensitive neurons in the brain could filter their inputs on this time scale, discarding the precise times of indvidual spikes in afferent signals in order to sense motion most reliably.

Bayesian inference and belief propagation in cortical networks

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To infer the properties of the environment or the most appropriate action from multiple noisy sensory sources, the brain must represent and manipulate the joint uncertainties over many variables. It has been proposed that population codes represent uncertainties by encoding distributions of probability of sensory variables. However, it is still unclear how these representations could be used to perform inference on multiple uncertain sources, and how statistical dependencies between these sources could be represented and learned.

In particular, Bayesian inference on large numbers of jointly dependant variables is generally intractable. Bayesian networks are a convenient graphical representation of statistical structures through which one can render inference and learning tractable. They represent groups of dependant variables as nodes, and conditional independencies as links (or lack thereof) between these nodes.

In this presentation, we will show how propagation of activity in interconnected cortical networks with population codes can be interpreted as a propagation of belief in an equivalent bayesian network. From this observation we will propose a new theory for the correspondence between cortical connectivity and modularity, neural response curves in multi-modal brain areas, statistical dependencies in the natural environment and cognitive modularity. As an example we will consider a minimal version of belief propagation were only means and covariance of input variables are propagated and show that it predicts some neural response properties in multi-sensory and sensorimotor areas.

Directionally selective calcium signals in dendrites of starburst amacrine cells

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The detection of image motion is fundamental to vision. In many species, unique classes of retinal ganglion cells selectively respond to visual stimuli that move in specific directions. It is not known which retinal cell first performs the neural computations that give rise to directional selectivity in the ganglion cell. A prominent candidate has been an interneuron called the “starburst amacrine cell”. Using two-photon optical recordings of intracellular calcium concentration, here we find that individual dendritic branches of starburst cells act as independent computation modules. Dendritic calcium signals, but not somatic membrane voltage, are directionally selective for stimuli that move centrifugally from the cell soma. This demonstrates that direction selectivity is computed locally in dendritic branches at a stage before ganglion cells.

Analysis and modeling of sensory systems with Rate Distortion Theory

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We present an analytical approach through which the relevant stimulus space and the corresponding neural symbols of a neuron or neural ensemble can be discovered simultaneously and quantitatively, making few assumptions about the nature of the code or relevant features. The basis for this approach is to conceptualize a neural coding scheme as a collection of stimulus-response classes akin to a dictionary or 'codebook', with each class corresponding to a spike pattern 'codeword' and its corresponding stimulus feature in the codebook. The neural codebook is derived by quantizing the neural responses into a small reproduction set, and optimizing the quantization to minimize an information-based distortion function. This approach uses tools from Rate Distortion Theory for the analysis of neural coding schemes. Its success prompted us to consider the general framework of signal quantization with minimal distortion as a model for the functioning of early sensory processing. Evidence from behavioural and neuroanatomical data suggested that symmetries in the sensory environment need to be taken into account as well. We suggest two approaches - implicit and explicit - which can incorporate the symmetries in the quantization model.

Songs, Sequences and Time: Neural mechanisms of sequence generation in the brain

Michale Fee

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Sensitivity to temporal order is a nearly universal aspect of brain function - at the sensory, motor, and cognitive levels. The ability of the brain to step rapidly through a learned sequence of states underlies not only the performance of complex motor tasks such as speech, but perhaps our ability to think and plan as well. While little is known about the neural and circuit mechanisms underlying the generation and learning of sequences, songbirds provide a marvelous animal model in which to study these phenomena.

We have used a new miniature motorized microdrive to record from large numbers of neurons in two premotor song-control brain areas in the songbird: nucleus RA, which projects to motor neurons of the vocal organ, and nucleus HVC, which projects to RA. During singing, each RA neuron generates a distinctive and reproducible sequence of spike bursts. Until recently, a widely held view was that the burst patterns in RA are largely generated by circuitry intrinsic to RA, an idea we have directly tested by measuring inputs to RA from nucleus HVC. We found that burst sequences in RA are directly driven from HVC, and that each antidromically identified RA-projecting HVC neuron generates a single brief burst of spikes at one moment in the song. We suggest that HVC neurons produce a detailed code for the temporal ordering of vocal gentures on a 10 ms timescale, and form an explicit representation of time in the brain. Such a sparse code for temporal order has broad implications for sequence learning.

Reinforcement learning of songbird premotor representations in a spiking neural network model

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The birdsong motor circuit is a hierarchical structure: nucleus HVC projects to premotor nucleus RA, which in turn drives motor neurons. Recent experiments show that RA-projecting HVC neurons have temporally sparse neural sequences that drive activity in RA. In this context, the role of RA appears to be the conversion of abstract neural sequences in HVC into motor activity.

In this study, we illustrate how an appropriate map of HVC to motor activity could be learned via plastic connections between HVC and RA. Such learning is commonly thought to be driven by reinforcement (Doya & Sejnowski 1995, Troyer & Doupe 2000), with a reward signal generated by comparing the bird's vocal output with an internally stored copy (template) of its tutor song.

We construct a reinforcement model with spiking neurons that learns HVC-to-RA connections in a feedforward network of HVC, RA, and a motor layer. We assume that HVC provides a sparse sequence, and learning is governed by a synaptic plasticity rule that exploits correlations between fluctuations in the motor output due to noisy neural inputs, and a positive scalar global reward that depends on the match between network output and the stored template. We explore motor fluctuations arising from the inherent stochasticity of HVC-to-RA synapses, or from (possibly LMAN-generated) noise injected into RA. The learning rule performs stochastic gradient ascent on the reward, and is robust over a wide range of parameters. Patterns of RA activity in the trained model are compared with data from zebra finches.

Response of the instantaneous firing rate to high frequency inputs

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In sensory systems, neuronal populations have to track rapidly fluctuating inputs. We explain here how ionic current dynamics leading to spike emission is a limiting factor of this ability. Previous analytical studies have investigated the response of the instantaneous firing rate of the leaky integrate-and-fire (LIF) model to noisy oscillatory inputs at high frequency f. The firing rate temporal modulation $A(f)$ decreases as $1/\sqrt{f}$ with a phase lag $L(f)$ of 45 degrees in presence of white noise while it stays finite with no phase lag with temporally correlated noise. In contrast, numerical simulations of several conductance-based models reveal a different behavior: $A(f)$ decays as $1/f$ and $L(f)$ tends to 90 degrees. To explain this qualitatively different behavior, we introduced and analytically investigated a family of 1-variable models which incorporate active properties. The 'quadratic' integrate-and-fire neuron, which describes the subthreshold dynamics of a large class of neurons near the firing onset, is a particular model in this family. However, it cannot account for the $1/f$ behavior: $A(f)$ decays as $1/f^2$ and $L(f)$ tends to 180 degrees. Another model in the family is the 'exponential' integrate-and-fire (EIF) neuron, in which a simplified sodium current with an instantaneous exponential voltage-dependent activation is responsible for spike generation. For white as well as for temporally correlated noise, we show analytically that, in the EIF model, $A(f)$ decreases in $1/f$ and $L(f)$ tends to 90 degrees. The stationary and dynamical properties of the EIF model matches well the properties of the simulated conductance-based models for input frequencies up to about 1000 Hz. At large noise, the firing rate response is a low pass filter, with a cutoff frequency that can be determined analytically. The cutoff frequency is given by the largest of two quantities: (i) the inverse of the membrane time constant (ii) a cutoff frequency proportional to the background firing rate and to the sharpness of the activation curve of the 'active current', and inversely proportional to the slope of the f-I curve.

Neural and synaptic mechanisms of the gamma rhythmic activity in local cortical circuitry

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The activity of the brain engaging in cognitive process often exhibits rhythmic oscillations. In particular, synchronization of neuronal activity in the gamma band (20-70Hz) is considered to play significant functional roles in sensory perception, motor control and higher cognitive processes. Chattering neuron is a possible neocortical pacemaker for the gamma oscillation (Gray & McCormick, 1996). Based on our recent model of chattering neurons (Aoyagi et al., 2002), we investigate computationally how the gamma-frequency bursting is synchronized in small- and large-scale networks of chattering neurons. In a weak-coupling range, the synchronized bursting of chattering cells entrains activity of the regular spiking pyramidal cells in the gamma band. However, synchronization occurs only slowly with a transient time of about 500 ms. On the other hand, in a strong-coupling range, the chattering cells can quickly synchronize, but they do not entrain regular spiking cells. We find that both transient and steady state properties of synchronization are greatly improved by incorporation of short-term synaptic depression. In addition, we investigate the synchronization phenomena in networks of fast-spiking (FS) interneurons simultaneously interconnected by electric and GABAergic synapses. Our model of FS interneurons is based on the Kv3.1/3.2 type delayed potassium channels characteristic of these neurons. We find that, in a physiologically reasonable range of the intensity ratio between electric and GABAergic synapses, the network of FS interneurons shows bistability between synchronous and asynchronous firing states. How chattering neurons and fast-spiking interneurons together govern the coherence of local cortical activity is now under investigation.

Spike-timing-dependent plasticity enhances reliability of predictive spike coincidences

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Pairs of premotor (PM) and primary motor (MI) neurons show significant increases of coincident spikes at those times when monkey is expecting a behavioral event (Riehle et al., 1997). Typically, the longer the preparatory period for a motor response, the higher the temporal precision of coincidences. These results provide evidence that synchrony has predictive power. To ellucidate the underlying neuronal mechanism, we model the predictive synchronous firing in a paradigm similar to classical conditioning. In this model, the firing sequence that is losely time-locked to a cue signal with 20- to 30-ms precision represents temporal information, which should be accessible to those PM/MI neurons. We examine whether the loosely timed spikes can be associated with the target events by spike-timing-dependent plasticity (STDP) to evoke the statistically significant number of spike coincidences at the expected times of the events. We find the cooperation of activity regulation function of STDP with coincidence detection essential to the emergence of predictive power. Our model accounts for the modulations of the temporal precision based on the synaptic self-organizing mechanism. Therefore, we propose that this phenomenon is independent of higher cognitive processes. We also show that the spike coincidences are easily reorganized when the to-be-predicted times of events are changed.

The nature of memory

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In the behaviorist framework within which most neuroscientific discussions of memory occur, memory is conceived of as the rewiring (changes in synaptic conductance) produced by experience, which rewiring adapts the animal's behavior to its circumstances. In this conception, the problem of coding does not arise. From an information processing perspective, on the other hand, memory is the mechanism that carries information forward in time. Formulated this way, the coding question is central to our understanding of the mechanism of memory. Yet, the coding question is seldom raised in discussion of the neurobiological mechanisms of memory and the most popular suggestions regarding this mechanism (e.g., LTP) do not offer any very plausible solutions to it. Moreover, current autoassociative memory proposals based on something like this mechanism have shockingly poor quantitative properties. It is argued that we should shift our focus to the coding problem.

Dendritic bistability increases the robustness of persistent neural activity in a model oculomotor neural integrator

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The oculomotor neural integrator converts velocity-coded eye movement commands into eye position signals. In the absence of velocity commands, integrator neurons maintain a steady rate of firing for tens of seconds. To achieve these long persistence times, most models use neurons with a continuous firing rate vs. injected current relationship and precisely tuned positive feedback. Bistability in neuronal responses has been proposed as a mechanism to maintain persistent activity. However, neuronal bistability tends to produce large discontinuities in firing rate with small changes in eye position. Thus, the firing rates of bistable neurons do not exhibit an analog coding of eye position. We show how dendritic bistability can enhance the robustness of eye fixations to mistuning while preserving the experimentally observed threshold linear relationship between firing rate and eye position. We analytically model a network in which the firing rate of each neuron is a linear sum of the contributions from multiple bistable dendritic compartments, plus tonic background and external velocity-command inputs. The network's tolerance to mistuning is related to the range of bistability of the dendritic compartments and to the slopes and thresholds of the neurons' firing rate vs. eye position relationships. Severe mistuning leads to approximately exponential decay towards a nonzero null eye position, in agreement with experimental observation. The response of the model to continuously varying inputs makes testable predictions for the performance of the vestibuloocular reflex. Analytic model results are reproduced in a biophysical model.

The role of NIf in the generation of sleep-related burst sequences in HVC

Richard Hahnloser, Alexay Kozhevnikov, and Michale Fee

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We have recently shown that premotor burst activity in nucleus RA of the zebra finch is directly driven by RA-projecting HVC neurons (HVC(RA)), each of which bursts at a single precise time in the song motif, and as a population burst throughout the song. This explicit representation of time has also been observed to underlie the generation of RA burst sequences during sleep. To understand the origin of the time representation in HVC, we are investigating the role of premotor inputs to HVC. Injections of lidocaine or muscimol into premotor nucleus Uvaeformis (Uva) in the sleeping bird resulted in a 2-3 fold increase in the rate of sleep-bursts in HVC. In contrast, injections into premotor Nucleus Interface (NIf) completely and reversibly abolished sleep-burst activity in HVC. Antidromically identified HVC-projecting NIf (NIf(HVC)) neurons generate dense patterns of bursts; during sleep a fraction of these bursts are highly correlated with subsequent bursts in HVC(RA) neurons. This result suggests that during singing, NIf(HVC) neurons will likewise generate dense patterns of bursts, some fraction of which will be tightly locked to the song vocalization. This prediction is being tested by recording identified NIf neurons in the singing bird. Furthermore, robust activation of the HVC neuron populations by electrical stimulation in RA or X has only a transient effect on song output (sim20ms). Thus we suggest that the HVC time code originates from dynamics in NIf, is transmitted to HVC in a temporally dense code, and that the sparseness of the HVC time representation results from network or biophysical properties within HVC.

The classification problem in the olfactory system of insects

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UCSD

The olfactory system of the locust has a puzzling variation of coding schemes throughout its various information relay stations. The identity-coded information of the Antenna is compressed into spatio-temporal patterns in the antennal lobe that are relayed towards the mushroom body where they are transformed into a series of quasi-static snapshots of sparse activity. The understanding of these coding schemes is recently starting to emerge. The spatio-temporal coding in the Antennal Lobe seems to be important for at least two important functions: a) learning and memory and b) robust discrimintation of similar odors. In this talk we concentrate on the later stages of processing in particular on the advantages of sparse coding and on an adequate network design for classification purposes. To this end we will for now only consider single snapshots of Kenyon cell activity. The classification task is then accomplished in two steps. The first step is a nonlinear expansion from the Antennal Lobe to the Kenyon cells in the Mushroom Body. This nonlinear projection into a higher dimensional space allows information conservation via sparse coding even if carried out with a non-specific connectivity matrix. In the second phase the sparse code on the Kenyon cell screen is linearly classified in the next processing layer. The neurons that perform this linear classification are hyperplanes whose connections are tuned by local Hebbian learning and competition due to mutual inhibition. We show that the number of Kenyon cells and the degree of sparseness in coding are crucial elements for efficient classification.

Fast convergence of spike sequences to periodic patterns in recurrent networks

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Dynamical attractors are thought to underlie many functions of biological neural networks. Previously, rate based models are used to prove the convergence properties of recurrent neural networks. Here we extend the attractor idea to biologically more realistic models of neural networks with neurons interacting with individual spikes rather than averaged spike rates. Specifically, we show that stable periodic spike sequences with precise timings are the attractors of the spiking dynamics in recurrent neural networks with global inhibition. Almost all spike sequences converge within a finite number of transient spikes to these attractors. The convergence is fast, especially when the global inhibition is strong. Our results support the possibility that precise spatio-temporal sequences of spikes are useful for information encoding and processing in biological neural networks.

Novel effects of adaptation in area MT

Adam Kohn and J. Anthony Movshon

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We have evaluated the effect of prolonged (40 s) adaptation on the direction tuning of macaque area MT/V5 neurons using drifting sine wave gratings. Preferred adaptation consistently caused a narrowing of direction tuning, because the response in the adapted direction was reduced less strongly than that in other nearby directions. A similar phenomenon was observed following adaptation at near-preferred ('flank') directions, with the consequence that the direction tuning of MT cells was attracted toward the adapted direction. Flank adaptation of complex cells in primary visual cortex (V1) did not cause an attractive shift in direction tuning. Finally, null adaptation often caused an increase in direction tuning bandwidth in MT neurons, but did not alter their preferred direction or responsivity. We suggest that these novel effects of adaptation on direction tuning in area MT are consistent with perceptual aftereffects and provide functional benefits not afforded by the repulsive shifts in tuning typically observed in V1.

Motor- and auditory-related activity of identified HVC neurons in the singing zebra finch

Alexay Kozhevnikov, Richard Hahnloser and Michale Fee

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Nucleus HVC of the songbird plays a role in both song generation and song learning. HVC projects to neurons in the premotor nucleus RA, which generate complex patterns of bursts during singing. HVC also projects to Area X, a nucleus that is involved in song learning. HVC neurons have robust auditory responses to song playback in anesthetized birds. We have made single-unit recordings of antidromically identified RA-projecting (HVC[RA]) neurons, X-projecting (HVC[X]) neurons, and HVC interneurons in the singing zebra finch. HVC interneurons spike at a high rate (sim100Hz) throughout the song. In contrast, projection neurons display stereotyped high-frequency bursts of spikes that are tightly locked to the vocal output. HVC[X] neurons generate 0-5 discrete bursts per song motif, while HVC[RA] neurons burst extremely sparsely – at most once per motif. As a population, HVC[RA] neurons appear to burst throughout the song, suggesting that they form an explicit representation of time in the song motif. We suggest that ensembles of active RA neurons are directly driven, at each time in the motif, by a subpopulation of HVC[RA] neurons that is active only at that time. It has been shown that distorted auditory feedback during singing results in a decrystallization of the zebra finch song. Our preliminary studies of the auditory responses of HVC neurons during singing show that their firing patterns are not affected by distorted auditory feedback during directed song.

Engineering principles for detection and control in the vibrissa sensorimotor system

David Kleinfeld

UCSD

The sensory system of animals is of limited value without the participation of the elaborate motor apparatus that moves the sensors into useful positions. The material in this talk focuses on behavioral and computational aspects of the vibrissa somatosensory system in rat. I will review the experimental evidence for phase-sensitive detection as a model for discriminating contact with an object and as a means to control the position of the vibrissae.

Time encoding with the integrate and fire neuron

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A key question in theoretical neuroscience is how to represent an arbitrary stimulus as a sequence of action potentials. The temporal requirements imposed on this representation might dependent on the information presented to the sensory neurons. The temporal precision of auditory processing, for example, involves measurements of interaural time delays with sub millisecond accuracy (Hudspeth and Konishi, PNAS, **97**:11690-11691). This imposes very stringent temporal requirements on the transduction process. We formulate the question of stimulus representation as one of time encoding, i.e., as one of encoding amplitude information into a time sequence. A Time Encoding Machine is the realization of such a mechanism.

We show that a Time Encoding Machine consisting of an integrate and fire neuron with feedback is invertible. Under simple conditions, bandlimited stimuli encoded with the Time Encoding Machine can be recovered loss-free from the neural spike train at its output. This result is somewhat unexpected because the Time Encoding Machine is non-linear. Less surprising is that simple non-linear algorithms provide for perfect recovery. The recovery algorithms are realized as a Time Decoding Machine.

The Time Decoding Machine helps elucidate some of the key open questions of temporal coding. We show that:

- Stimuli encoded by a single integrate and fire neuron can be recovered loss-free from the neural spike train. The recovery of the stimulus from a single running experiment is a defining biological requirement.
- The error introduced by dropping individual action potentials or by measurement jitter of the time of occurrence of action potentials can be explicitly evaluated. The resulting error is a measure that quantifies the importance of temporal coding.
- Stimulus time-delays in the sub millisecond range can be readily estimated.

Finally, we present the relationship between time encoding and the representation of bandlimited signals in classical information theory. In the latter, uniform sampling (Shannon's sampling theorem) together with quantization of the discrete signal amplitude is the representation of choice. We will also show the relationship between time encoding, frequency modulation and asynchronous Sigma-Delta modulation.

Decoding memory of sequential experience in the hippocampus during slow wave sleep

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Rats repeatedly ran through a sequence of spatial receptive fields of hippocampal CA1 place cells in a fixed temporal order. A novel combinatorial decoding method reveals that these neurons repeatedly fired in precisely this order in long sequences involving 4 or more cells during slow wave sleep (SWS) immediately following, but not preceding, the experience. The SWS sequences occurred intermittently in brief (∼100-millisecond) bursts, each compressing the behavioral sequence in time by approximately 20-fold. This rapid encoding of sequential experience is consistent with evidence that the hippocampus is crucial for spatial learning in rodents and the formation of long term memories of events in time in humans.

Local structural balance and functional interaction of excitatory and inhibitory synapses in hippocampal dendrites

Guosong Liu

MIT

Theoretical and experimental studies on the computation of neural networks suggest that neural computation results from a dynamic interplay of excitatory and inhibitory (E/I) synaptic inputs. While most studies have focused on E/I interactions at the cell body, a significant portion of inhibitory synapses are instead distributed along the dendritic tree, resulting in E/I interactions within individual dendrite branches. If so, E/I synapses may be organized structurally and functionally according to principles that facilitate meaningful interaction. Here we show that E/I synapses are indeed regulated across dendritic trees to maintain a constant ratio of inputs, and that this structural property is accompanied by an E/I functional balance maintained by a "push-pull" feedback regulatory mechanism capable of adjusting E/I efficacies in a coordinated fashion. We also find that during activity, inhibitory synapses can determine the impact of adjacent excitatory synapses only if they are co-localized on the same dendritic branch and are activated coincidentally. These fundamental relationships between E/I synapses provide organizational principles relevant to deciphering the structural and functional basis for neural computation within dendritic branches.

Synaptic balancing guided by spike-timing-dependent plasticity in olfactory cortex model

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Synaptic balancing, based on the spike-timing-dependent synaptic plasticity (STDP), has been recently shown to be able to drive a neuron from integrator to coincident-time detector mode of operation, maximizing the neuron's information transmission. The circuits of pyramidal cells of piriform cortex are an example of a neural system that may need such balancing, as these neurons are known to be sensitive to the relative timing of the afferent and association input signals. Not only piriform cortex is likely to be in need of such STDP-based balancing, it also is, in a sense, an ideal "hardware" for its implementation. Highly structured spatio-temporal dynamics of the postsynaptic potentials at the dendrites of pyramidal cells could be easily used in spike-time-dependent learning. We develop a model of piriform cortex, which employs recently proposed principle of synaptic balancing, based on the STDP learning rule with a larger window of synaptic weakening. We argue that this phenomenon could take place in this part of olfactory cortex and play a crucial role in learning spatio-temporal sequences of the postsynaptic potentials at the dendrites of the pyramidal cells.

Spectro-temporal receptive fields in auditory cortex

Christian Machens, Mike Wehr, Carlos Brody, and Tony Zador

Cold Spring Harbor

How do cortical neurons represent the acoustic environment? To address this question, we use in vivo whole cell methods in rat auditory cortex and record subthreshold membrane potentials of single neurons in response to complex acoustic stimuli, including animal vocalizations and music.

In a first step, we estimated the linear component–the spectro-temporal receptive field (STRF)–of the transformation from the sound (as represented by its time-varying spectrogram) to the neuron's membrane potential. We find that the STRF has a rich dynamical structure, including excitatory regions positioned in general accord with the prediction of the simple tuning curve. While the STRF successfully predicts the responses to some of the natural stimuli, it surprisingly fails completely to predict the responses to others. Hence, much of the neuron's response, although deterministically related to the stimulus, cannot be predicted by the linear component.

In a second step, we now investigate to what extent the STRF can be amended by including the time-varying dynamics of different adaptation mechanisms.

Optimal olfactory discrimination in one theta cycle

Zach Mainen

Cold Spring Harbor

To investigate the significance of temporal coding in the mammalian olfactory system, we monitored the behavior of rats performing a two-alternative odor mixture discrimination task. This paradigm allowed us to obtain reliable psychometric discrimination functions in order to assay the relationship between accuracy and response time. As expected from a coding strategy involving temporal integration of an evolving sensory representation, mean odor sampling time increased significantly from the easiest pure odor discriminations to the most difficult near-threshold mixture discriminations. However, the amount of this increase was only ~50 msec (from 300 to 350 msec). Moreover, regardless of discrimination difficulty, performance levels saturated with only 200 msec combined odor sampling and decision time. Simultaneous measurement of sniffing during the behavior revealed that this time correspondeds to a single respiration cycle at theta frequency (7 Hz). These data place limits on the role of slow temporal patterning in olfactory coding and suggest that the formation of olfactory sensory images is constrained by a basic temporal cycle (theta) for sensorimotor integration.

Experience dependent nature of hippocampal temporal code

Mayank Mehta, Albert Lee, and Matt Wilson

MIT

Precise spike timing is critical for Hebbian synaptic plasticity. However, neither a mechanism for generating such precise spike timing in vivo, i.e. a temporal code, nor the effect of experience on such a temporal code have been established.

In order to learn the temporal order of events through plasticity, two neurons representing sequential events A and B should be repeatedly activated in the same order over short time scales, about 10 ms, of Hebbian synaptic plasticity. During behavior neurons A and B would be typically active over time scale of about 1000 ms. However, neurons are believed to fire in a rate-modulated Poisson fashion. Hence, the behavioral order of events A and B, occuring over 1000 ms, would be rarely reflected over the short time scales of synaptic plasticity, resulting in poor learning.

A novel mechanism that can solve this scaling problem was proposed rescently (Mehta et al 2000), inolving an interaction between periodic inhibition and slowly varying excitation. Consistent with the predictions of this model, we find that the hippocampal temporal code is asymmetric and it becomes more robust with experience (Mehta et al. 2002). In particular, the correlation between the phase of the theta rhythm (at which a neuron fires a spike) and the position of the rat improves two fold with experience. As a result, the hippocampal spatio-temporal receptive fields change their structure from random to inseparable within a few trials.

This mechanism generalizes easily to other modalities such as the structure of spatio-temporal receptive fields of direction selective neurons in V1.

Optimal mutual information quantization is NP-complete

Brendan Mumey and Tomas Gedeon

Montana State University

We consider the computational complexity of quantizing a joint (X, Y) probability distribution in order to maximize the mutual information of the quantization. We show that, in general, this problem is NP-complete via reductions from various forms of the PARTITION problem. In recent years, the problem of optimal quantization of the mutual information between two random variables has received increased attention. We note the application to discovery of neural coding scheme in early sensory system of the cricket as well as the central role of quantization of mutual information in the closely related "Information bottleneck" optimization scheme. The latter method has been applied to a variety of coding applications. In the application to neural coding, one models the input to the system as a random variable X and the output as a random variable Y. To simplify the situation, as well as to acknowledge inherent discreteness of collected data, X and Y are assumed to be discrete random variables. Mutual information is always nonnegative and tells us, roughly, how well we can predict X by observing Y, and vice versa. Since noise is omnipresent in neural processing, sensory systems must be robust. As such, they must represent similar stimuli in a similar way and then react to similar internal representations of the outside stimuli in a consistent way. This leads to a conclusion that individual input and output patterns are not important for understanding neural function, but rather classes of input stimuli and classes of output patterns and their correspondence is the key. Therefore we are led to a problem of optimal assignment of input and output patterns to classes, where the optimality is judged on how much original mutual information is still present between the collections of classes. More specifically, we will consider two different quantization methods one-sided quantization and two-sided (joint) quantization. In a one-sided quantization, we quantize (cluster) only one variable, let us say Y, to a space of finitely many abstract classes, Y_N, where N represents the number of classes. In two-side quantization, both variables are simultaneously quantized. In both cases, we have shown that finding the quantization that maximizes mutual information is NP-complete. While it has been speculated that theses two problems (and some associated quantization problems) were NP-complete, to the authors' knowledge our work is the first formal demonstration that this is so.

Novel approach to estimation of entropies of discrete variables with applications to neural coding

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We will review a recently introduced estimator of entropies for undersampled discrete nonmetric variables, which is based on the Occam factors inspired averaging over a set of popular Dirichlet priors. We will analyze performance of the estimator numerically for simple toy problems and analytically for various asymptotic regimes. One conclusion is that, at least for some classes of probability distributions involved, the estimator is nearly unbiased and performs well even with no a priori assumptions about the cardinalities of variables being studied. We will present some preliminary results from applications of the method to the estimation of information in spike trains from the H1 neuron in a fly visual system.

Hippocampal bidirectional plasticity arising from transitions in a synaptic ensemble

Daniel H. O'Connor, Gayle M. Wittenberg, and Samuel S.-H. Wang

Princeton University

In bidirectional synaptic plasticity, change in synaptic strength has been observed to occur in graded amounts of potentiation or depression. However, measurements are almost always made from ensembles of synapses; this is true even in recordings from connected pairs of neurons. Such measurements therefore represent the sum of many single-synapse potentiation or depression events occurring at once. This point of view suggests that it may be possible to dissect bidirectional plasticity into separate processes of potentiation and depression/depotentiation. We tested this at the Schaffer collateral-CA1 synapse by driving synaptic ensembles into conditions from which only potentiation or depression/depotentiation are possible. When LTP is saturated with theta-burst stimulation or its induction blocked with the kinase inhibitor K252a, only long-term depression (LTD) or depotentiation can be induced. Conversely, when LTD is saturated or its induction blocked with the phosphatase inhibitor okadaic acid, only LTP can be induced. From a fully potentiated state, or in the presence of K252a, stimulus frequencies of 1 Hz or higher lead to LTD/depotentiation. From a fully depressed state, or after treatment with okadaic acid, stimulus frequencies of 5 Hz or higher lead to LTP. To account for our data we present a model of bidirectional synaptic plasticity in which synapses begin from a mixture of low-strength, high-strength, and recently-potentiated states.

Tight correlation between the time course of sensory and motor estimates

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The sensory task of the smooth pursuit system is to extract an estimate of target velocity from image motion on the retina, and its motor task is to accelerate the eyes to match target velocity. We have quantified the directional accuracy of early pursuit eye movements and related this to the cortical sensory signals in visual area MT likely to mediate the behavior. We computed the signal-to-noise ratio as a function of time in primate eye velocity responses to visual targets whose trajectories differ by small angles. We found that about 80is achieved within its first 100ms. In seperate experiments in anesthetized macaques, we measured the responses of single units in MT to moving stimuli differing by small angles. Computing the time course of direction information available in MT responses, we found that neurons also provide about 80their maximal information within the first 100ms of their responses. Therefore, target direction information can be extracted from single units as quickly as behavioral performance requires it. Individual MT neurons were much less directionally accurate than the eye movement itself, necessitating a mechanism for pooling information from many neurons to achieve the observed behavioral accuracy.

Spatial summation in L5 pyramidal cells

Hysell Oviedo and Alex Reyes

NYU

Dendrites have various voltage and time dependent conductances whose distribution and properties vary with distance from the soma. To examine how these conductances affect summation of inputs in the subthreshold range and while the neuron is firing, we performed simultaneous, whole-cell recordings from the soma and two locations on the apical dendrite of pyramidal neurons in slices of rat (¿P21) sensorimotor cortex. Transient current was injected through each electrode to evoke EPSP-like potentials. The currents injected at the dendrite were adjusted so that the resultant EPSPs measured with the somatic electrode were identical. A computer simulation calculated a composite current for a hypothetical population of presynaptic cells, which was then injected into the cell. A specified number (n) of inputs was injected at the two dendritic locations individually and then simultaneously (2n); the resulting responses were compared to the predicted linear sum. In the subthreshold range summation changed from linear to supralinear as n was increased. In the suprathreshold range summation of firing rates changed from supralinear to sublinear. Sublinear summation at high rates was due to changes in dendritic conductances rather than to saturation effects since current injection at the soma evoked higher firing rates. Similar observations were obtained when the inputs were injected under dynamic clamp (to mimic the conductance changes caused by synaptic input) although summation in the subthreshold and suprathreshold ranges tended to be less supralinear. Efficacy of inputs was always least when the inputs were injected at the site farthest to the soma, and the greatest when the inputs were either injected at the site closest to the soma or split between the two dendritic locations.

Correlates of perceptual learning in extrastriate visual cortex

Gregor Rainer

Max Planck Institute

Experience with objects can allow us to recognize them more accurately and efficiently. To study the neural basis of these perceptual improvements, we have developed parametric sets of stimuli consisting of natural scenes at different levels of coherence corresponding to perturbations of Fourier phase spectra. Practice with a particular set of natural scenes allowed monkeys to identify them at lower coherence levels compared to novel natural scenes. We recorded local field potentials (LFPs) and single unit activity (SUA) from extrastriate visual area V4. Several distinct modes of processing were evident in the LFP recordings. While LFPs showed little learning related changes during the transient visual response (∼50 to 90ms after onset), large robust changes were observed later in the response. The systematic changes in mean LFPs reflecting inputs to V4 were correlated with changes in SUA representing V4 output. In particular, while neurons communicated similar amounts of information about novel and familiar objects early during the response, information was amplified for familiar objects at intermediate coherence levels during later portions of the response. Many V4 neurons showed higher activity during difficult discriminations particularly for familiar objects, consistent with participation in recurrent processing. Our results reveal that while V4 neural activity is determined by sensory stimulus properties early in the response, the later response reflects recurrent processing probably involving feedback from higher areas.

Bayesian computation in recurrent cortical circuits

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A large number of human psychophysical results have been successfully explained in recent years using Bayesian models. However, the neural implementation of such models remains largely unclear. In this talk, we discuss how a network architecture commonly used to model the cerebral cortex can implement Bayesian inference for an arbitrary Markov model. We illustrate the suggested approach using a visual motion detection task. Our simulation results show that the model network exhibits direction selectivity and correctly computes the posterior probabilities for motion direction. When used to solve the well-known random dots motion discrimination task, the model generates responses that mimic the activities of evidence-accumulating neurons in cortical areas LIP and FEF. In addition, the model predicts reaction time distributions that are similar to those obtained in human psychophysical experiments that manipulate the prior probabilities of targets and task urgency.

Instructive signals in the cerebellum during motor learning

Jennifer Raymond

Stanford

Learning requires that changes occur at appropriate sites in the relevant neural circuits. What are the neural events that trigger such changes? Which neurons carry the instructive signals that control the induction of plasticity in vivo? We are using a simple motor learning task as an experimental system for exploring these questions in the cerebellar circuitry. The answers are critical for understanding how the synaptic plasticity mechanisms that have been described in vitro operate in the functional context of the intact brain.

Temporal precision in coincidence detecting auditory neurons

John Rinzel, G. Svirskis, V. Kotak, and D. Sanes

NYU

Localization of low frequency sounds involves precise computation of interaural time differences (sub-ms range). The first neurons that receive binaural input and participate in this computation are, for mammals, in the medial superior olive (MSO) and they have distinct biophysical properties. They spike in response to transient but not to slowly varying stimuli and phase-lock well to periodic input. A low-threshold potassium current I_{K-lt} contributes to the MSO neuron's temporal processing qualities partly because the membrane's "time constant" is shortened by this extra conductance but the dynamic aspects of I_{K-lt} activation also play a role. Transient signals must outrace the activation of I_{K-lt} if they are to cause the cell to spike. We characterize the role of I_{K-lt} through in vitro experiments (gerbil MSO) and with computational models, of the Hodgkin-Huxley and enhanced integrate-and-fire types. We focus particularly on what makes these coincidence-detecting cells fire, i.e. on how they integrate subthreshold signals in the presence of a noisy synaptic background, typical of the peripheral auditory system. Our results show that partial block of I_{K-lt} reduces: (1) the signal-to-noise ratio, (2) the probability to fire in response to closely-timed inputs, (3) the quality (vector strength) of phase-locking, and (4) the temporal sharpness of transient currents that cause spiking (as seen with reverse correlation analysis).

Information properties of transient responses to motion in visual cortex area MT

Simon Schultz

NYU

Neurons in area MT of the monkey visual cortex often exhibit distinct transient responses to step changes in visual motion, in addition to a sustained response. We were interested in understanding whether spikes in this initial transient had qualitatively or quantitatively different information properties to those from the sustained response. We recorded extracellularly from single units in the anaesthetised, paralysed macaque monkey during presentation of brief (320 ms) visual motion stimuli consisting of drifting gratings and plaids. The reliability of spike counts in the transient was slightly greater than in the sustained response, as measured by a signficantly lower Fano factor. It appears that this effect can be accounted for by relative refractory effects at elevated firing rates. The information efficiency of the transient spikes (the spike count mutual information about motion direction normalised by the response entropy used to convey it) was however no higher than for sustained spiking activity. The transient response did however show differences from the sustained in the temporal information content of the spike trains, with significant synergy and redundancy between spikes observed only in the transient. This synergy/redundancy was due to stimulus-independent spike time correlations, was distributed about zero but with a wide spread between cells, and may be due to characteristic but brief temporal structure in onset transients for individual cells.

Combinatorial representation of color in visual cortex

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The responses of many neurons in primary visual cortex of monkeys are selective for the color of homogeneous color patches in their receptive fields presented on a neutral gray background. When stimuli were presented on colored backgrounds, chromatic tuning was different in most neurons, and the changes in the tuning curves depended on the chromatic contrast between stimulus and background. Although the response tuning curves and their modulation by the background color do not appear to be separable, the likelihood of the ratio of spike counts can be fit by a product of two terms one of which depends only on the color in the receptive field and the second only on the color in the nonclassical receptive field. This type of separability may be a general mechanism that the cortex uses to combine information from different contexts.

Learning dynamics of reaching movements

Reza Shadmehr

Johns Hopkins University

When one moves their hand from one point to another, the brain guides the arm by relying on neural structures that estimate physical dynamics of the task and transform the desired motion into motor commands. If our hand is holding an object, the subtle changes in the dynamics of the arm are taken into account by these neural structures and this is reflected in the altered motor commands. These observations have suggested that in generating motor commands, the brain relies on internal models that predict physical dynamics of the external world. Here, I will review the neural and computational data on how the brain learns internal models of reaching movements. Data suggests that internal models are sensorimotor transformations that map a sensory state of the arm into an estimate of forces. If we assume this neural computation is performed via a population code, one can infer properties of the tuning curves of the computational elements from the patterns of generalization and trial-to-trial changes in performance. A new theory is presented that allows for quantification of generalization from trial-to-trial changes in performance. The patterns of generalization appear consistent with computational elements that are bimodal in velocity space and the discharge is modulated linearly as a function of the static position of the hand. These gain-field properties are consistent with tuning curves of some cells in the primary motor cortex and the cerebellum.

A digital methodology integrating experimental and theoretical neuroscience

Ross Snider

Montana State University

A digital methodology integrating experimental and theoretical neuroscience is being developed by the creation of a reconfigurable on-line modeling platform (ROMP). The platform will perform real-time analysis of multi-channel data streams for data-driven neural simulations and modeling. The computational architecture is a distributed real-time system of modular design consisting of computational nodes that contain a floating-point digital signal processor (DSP) and a field programmable gate array (FPGA). Configuring the system as a multi-dimensional mesh will allow it to scale in order to process an arbitrary number of real-time data streams. The platform will be used to aid the discovery process where neural encoding schemes through which sensory information is represented and transmitted within a nervous system will be uncovered. The system will enable real-time decoding of neural information streams and it will allow neuronal models to be inserted in simple nervous systems. Allowing experimental perturbation of neural signals while in transit between peripheral and central processing stages will provide an unprecedented degree of interactive control in the analysis of neural function, and could lead to major insights into the biological basis of neural computation.

Spike time attractors in cortical neurons

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The responses of cortical neurons in vitro to fluctuating current injections show stereotyped patterns of spike-time relationships, and similar spike-time histograms occur across neurons with different firing rates, as recently observed by Reinagel & Reid in the cat lateral geniculate nucleus. The observed spike trains do not form renewal processes. Instead, these observations can be interpreted as evidence for socalled spike time attractors. I will introduce methods to detect and analyze spike time attractors. I will show how postsynaptic neurons can detect their non-renewal structure via short-term depression and facilitation. Furthermore, I will discuss how spike time attractors can form the basis for methods to assess synchrony between two spike trains and efficient methods to calculate mutual information between input stimuli and output spike trains.

Pooling of rod inputs and limits to sensitivity in primate retinal ganglion cells

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Dark-adapted humans can detect flashes producing only 5-20 photoisomerizations across a pool of hundreds or thousands of rod photoreceptors. How can the visual system detect whether and when a sparse signal occurs in an array of many noisy detectors? We examined this question by comparing the detection and temporal sensitivity of retinal ganglion cells (RGCs) to that of their pooled rod inputs.

Primate rod and RGC detection and temporal sensitivity were characterized using a two-alternative forced choice linear discrimination of responses to dim flashes delivered at different times. Responses from isolated rods were obtained using suction electrode recordings. Multielectrode extracellular recordings from RGCs were obtained from isolated retinas maintained *in vitro*. Detection and temporal sensitivities of RGCs were compared to those of their linearly pooled rod inputs. For this comparison, simulated rod signals were created whose signal and noise characteristics were matched to real rod signals. These simulated rod signals were then weighted by a RGC receptive field and summed. A linear discriminant was applied to the time course of the summed rod signal to determine whether and when a flash occurred.

Most ON cells showed detection sensitivity 1-3 times lower than the physical limit imposed by spontaneous isomerizations of rhodopsin, indicating that rod signals may be processed nearly optimally in the primate retina. ON cell detection sensitivity was 2-4 times higher than predicted from linear pooling of rod inputs, indicating that the observed sensitivity requires nonlinear processing of rod signals. ON cell temporal sensitivity ranged from 20-50 ms, finer than the rod integration time of 200 ms. OFF cell detection and temporal sensitivity were lower. These results show that primate RGCs efficiently detect and discriminate the timing of sparse signals in thousands of noisy rod inputs.

Interpreting the notion of simultaneous confinement in space and spatial frequency in terms of confinement, not variance, yields a rich class of intrinsically two-dimensional patterns

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Well-established theoretical reasons lead to consideration of functions that are limited in space and spatial frequency as the starting point for modeling receptive fields of visual neurons. Limited spatial spread economizes on connection length and allows for spatial localization. Limited spread in spatial frequency allows for analysis at a particular spatial scale. In the traditional view, spread is measured by variance. As Daugman (1985) showed via analogy with the uncertainty principle, the Gabor functions have the smallest joint spread in space and spatial frequency. While it is interesting to note that Gabor functions resemble receptive fields in V1, this view provides little insight into receptive fields in other visual areas, and also does not provide an indication of why typical V1 receptive fields have only a few lobes.

Here we present an alternative construction of the notion of "limited in space and spatial frequency," based on the concept of confinement. From this notion, a much richer set of functions, the 2-dimensional Hermite functions, emerge. These functions form a natural hierarchy. The first levels of this hierarchy contain functions that resemble Gabor functions with a small number of lobes, and thus resemble V1 receptive fields. Further down in the hierarchy are intrinsically two-dimensional functions, some of which resemble the non-Cartesian gratings, to which some V4 neurons respond preferentially (Gallant, 1996). In addition to their many interesting mathematical properties, the two-dimensional Hermite functions allow for efficient ("sparse") local synthesis of images.

While we make no claim that this view suffices to account for visual receptive field structure, we suggest that it provides a framework for a principled study of receptive fields, and that it is useful to think of receptive fields (along the V1-to-V2-to-V4 pathway) as not only expanding, but also increasing in their combined space-bandwidth aperture.

Energetic costs and speed limits in neocortical axons

Samuel S.-H. Wang, Kimberly H. Harrison, Jennifer R. Shultz, Mark J. Burish, and Matthew W. Wagers

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In large brains, action potentials must travel for long distances, potentially increasing the time taken for information processing. This scaling problem is particularly apparent in mammalian brains, which vary in diameter by nearly 100-fold. Here we present evidence for adaptations for speed and energetic efficiency in long-distance axons of the neocortex. Axonal propagation speed can be increased by making axons wider and by adding myelin sheaths. We find that across species, the mean axon diameter and the degree of myelination increase steeply with brain size, indicating that conduction is faster in larger brains. The largest axons are proportional in width to brain diameter, suggesting that minimum cross-brain conduction time is conserved among mammals. Myelination also reduces the energetic cost of generating action potentials. As a result, the estimated per-volume cost of spike activity scales as the -0.300.09 power of body size, consistent with previously observed scaling of metabolic rates. Increases in axon size also account for the disproportionate growth in white matter volume, which for large brains can occupy nearly half the neocortex. Brain tissue is energetically expensive, and thus improvements in processing speed may be limited by the metabolic costs of an expanding white matter architecture.

Efficient induction of long-term potentiation and depression under behaviorally relevant activity conditions

Gayle M. Wittenberg and Samuel S.-H. Wang

Princeton University

The relative timing of pre- and post-synaptic action potentials has been shown to influence both the sign and magnitude of synaptic plasticity. Such spike timing-dependent plasticity has been observed in a number of synapses. However, neural activity also has structure on longer time scales. One example is the hippocampal theta rhythm, which in rats occurs during active spatial exploration and has a characteristic frequency of 5-10 oscillations per second. Here we report how the induction of hippocampal CA3-CA1 synaptic plasticity depends on neural events with realistic overall temporal structure. We found that the induction of spike timing-dependent long-term potentiation (LTP) required two events that are likely to occur during theta rhythm: burst firing in the postsynaptic CA1 neuron and sustained pairing at 5 Hz. Low-frequency pairing (0.5 Hz) of single presynaptic action potentials followed by single postsynaptic action potentials was insufficient to generate LTP. This surprising finding was observed if the patch pipette contained a physiological, potassium-based recording solution, but not if the pipette contained a cesium-based recording solution (Nishiyama et al. 2000 Nature 408:584-588). Reversing the firing order within each pairing resulted in long-term depression (LTD). These results suggest that key features of behaviorally relevant neural activity, in this case burst firing associated with the theta rhythm, can be essential for gating synaptic plasticity.

On-line information extraction in a noisy environment

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The notion of on-line coding refers to that the decoding process for stimulus is in concurence with the encoding one. This construsts to the off-line paradigm in which decoding occurs after encoding. In the on-line coding paradigm, stimulus is estimated sequentially, with each step's result being used as prior knowledge for the consequetive decoding. Mathematically, this is best expressed as Bayesian inference. In this study, we will show how on-line coding could be implemented in a neural circuitry, and it outperforms off-line coding in a non-stationary encoding process.