COSYNE 2012
The 9th annual Computational and Systems Neuroscience meeting

Main meeting program
February 23-26
Salt Lake City

www.cosyne.org
Program Summary

Thursday, 23 February
4:00 pm  Registration opens
5:30 pm  Welcome reception
6:20 pm  Opening remarks
6:30 pm  Session 1: Spikes - correlations and oscillations
         Invited speakers: F. Rieke, E. Brown
8:30 pm  Poster Session I

Friday, 24 February
7:30 am  Breakfast
8:30 am  Session 2: Motor systems
         4 accepted talks
10:00 am Session 3: MINISYMPOSIUM: Olfaction
         Invited speakers: N. Sobel, Z. Mainen; 2 accepted talks
12:00 pm Lunch break
2:00 pm  Session 4: Neural representations – models and theory
         Invited speaker: T. Griffiths; 3 accepted talks
4:00 pm  Session 5: Navigation and Movement
         Invited speaker: D. Ballard; 2 accepted talks
5:15 pm  Dinner break
6:30 pm  Special workshop: “NSF: Theory and Applications”, Ken Whang, NSF
7:30 pm  Poster Session II

Saturday, 25 February
7:30 am  Breakfast
2:00 pm  Session 6: Linking neural activity and behavior–optogenetics
         4 accepted talks
10:00 am Session 7: MINISYMPOSIUM: Cognitive representation
         Invited speakers: J. Assad, S. Fusi; 2 accepted talks
12:00 pm Lunch break
2:00 pm  Session 8: Dendrites and synapses
         Invited speaker: N. Brunel; 3 accepted talks
4:00 pm  Session 9: Representing beliefs
         Invited speaker: R. Saxe; 1 accepted talk
5:00 pm  Dinner break
7:30 pm  Poster Session III
Sunday, 26 February

7:30 am  Breakfast
8:30 am  **Session 10: Visual circuitry**
          Invited speaker: T. Hensch; 3 accepted talks
10:30 am **Session 11: Auditory processing**
          Invited speaker: S. Wooley; 3 accepted talks
12:00 pm Lunch break
2:00    **Session 12: Visual representation**
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About Cosyne

The annual Cosyne meeting provides an inclusive forum for the exchange of experimental and theoretical/computational approaches to problems in systems neuroscience. It has attracted a growing number of participants, rising to over 550 in 2011. The Cosyne 2011 meeting featured 43 invited and contributed talks, 297 poster presentations, and 14 workshops incorporating a total of 116 presentations. This year, the conference has received a record number of abstracts.

To encourage interdisciplinary interactions, the main meeting is arranged in a single track. A set of invited talks are selected by the Executive Committee and Organizing Committee, and additional talks and posters are selected by the Program Committee, based on submitted abstracts.

Cosyne topics include (but are not limited to): neural coding, natural scene statistics, dendritic computation, neural basis of persistent activity, nonlinear receptive field mapping, representations of time and sequence, reward systems, decision-making, synaptic plasticity, map formation and plasticity, population coding, attention, and computation with spiking networks. Participants include pure experimentalists, pure theorists, and everything in between.

Cosyne 2012 Leadership

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- **Workshop Chairs**: Jessica Cardin (Yale), Brent Doiron (University of Pittsburgh)
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- Denise Soudan, Conference and Events Office, University of Rochester
About Cosyne

Travel Grants

The Cosyne community is committed to bringing talented scientists together at our annual meeting, regardless of their ability to afford travel. Thus, a number of travel grants are awarded to students, postdocs, and PIs for travel to the Cosyne meeting. Each award covers at least $500 towards travel and meeting attendance costs. Three award granting programs were available in 2012.

The generosity of our sponsors helps make these travel grant programs possible.

Cosyne Presenters Travel Grant Program

These grants support early career scientists with highly scored abstracts to enable them to present their work at the meeting.

This program is supported by the following corporations and foundations:

- The Gatsby Charitable Foundation
- Qualcomm Incorporated
- Brain Corporation
- Cell Press/Neuron
- Evolved Machines

The 2012 recipients and their individual sponsors are:
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Cosyne New Attendees Travel Grant Program

These grants help bring scientists that have not previously attended Cosyne to the meeting for exchange of ideas with the community.

This program is supported by a grant from the National Science Foundation.

The 2012 recipients are:


Cosyne Mentorship Travel Grant Program

These grants provide support for early-career scientists of underrepresented minority groups to attend the meeting. A Cosyne PI must act as a mentor for these trainees and the program also is meant to recognize these PIs (“NSF Cosyne Mentors”).

This program is supported by a grant from the National Science Foundation.

The 2012 NSF Cosyne Mentors are listed below, each followed by their mentee:

Carina Curto and Ashley Sullivan; Jonathan Pillow and Evan Archer; Ronen Segev and Irina Segal; Eric Shea-Brown and Natasha Cayco Gajic; Christopher Rozell and Allison Del Giornio; Jonathan Wallis and Jen Sloan; Michael Wenger and Julie Hammons.
Program

Note: Printed copies of this document do not contain the abstracts; they can be downloaded at: http://cosyne.org/c/index.php?title=Cosyne2012_Program.
Institutions listed in the program are the primary affiliation of the first author. For the complete list, please consult the abstracts.

Thursday, 23 February
4:00 pm Registration opens
5:30 pm Welcome reception
6:20 pm Opening remarks
Welcome from the General Co-Chairs (Jim DiCarlo and Rachel Wilson)
Overview of the program selection from the Program Co-Chairs (Jonathan Pillow and Nicole Rust)

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(Chair: Tatyana Sharpee)
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6:30 pm  Special workshop: “NSF: Theory and Applications”, Kenneth Whang, Program Director, Division of Information and Intelligent Systems, National Science Foundation.
Location: Deer Valley Room, Marriott
This will be part tutorial, but mostly informal discussion. Ken will be pleased to take questions in advance about any aspects of NSF, or your experiences with NSF, by e-mail to kwhang@nsf.gov or anonymously to tomas.hromadka@gmail.com. Please use *Subject: NSF Cosyne*

7:30 pm  Poster Session II
Saturday, 25 February

7:30 am  Continental breakfast

Session 6: Linking neural activity and behavior–optogenetics
(Chair: Naoshige Uchida)

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T-1. Noise correlations and neural coding

Fred Rieke\textsuperscript{1,2} \hspace{1cm} RIEKE@WASHINGTON.EDU
\textsuperscript{1}University of Washington
\textsuperscript{2}HHMI

Computation in the nervous system often relies on integrating multiple inputs with different functional properties. Correlated noise in these input signals can, in principle, strongly affect the reliability of computations based on them. Such theoretical predictions have rarely been tested experimentally because of a scarcity of preparations that permit measurement of both covariation of a neuron’s input signals and the effect of manipulating such covariation on a cell’s output. We have developed an approach to measure covariation of the excitatory and inhibitory inputs received by individual and nearby retinal ganglion cells and determine how such covariation affects spike output. I will describe what this approach reveals about the impact of correlated noise on the coding of motion direction by a defined class of retinal ganglion cells.

T-2. The Neurophysiology of the Unconscious Brain Under General Anesthesia

Emery Brown\textsuperscript{1,2} \hspace{1cm} ENB@NEUROSTAT.MIT.EDU
\textsuperscript{1}Massachusetts Institute of Technology
\textsuperscript{2}Harvard University

General anesthesia is a drug-induced, reversible condition comprised of five behavioral states: unconsciousness, amnesia (loss of memory), analgesia (loss of pain sensation), akinesia (immobility), and hemodynamic stability with control of the stress response. The mechanisms by which anesthetic drugs induce the state of general anesthesia are considered one of the biggest mysteries of modern medicine. We have been using three experimental paradigms to study general anesthesia-induced loss of consciousness in humans: combined fMRI/EEG recordings, high-density EEG recordings and intracranial recordings. By using a wide array of signal processing techniques, these studies are allowing us to establish precise neurophysiological, neuroanatomical and behavioral correlates of unconsciousness under general anesthesia. Combined with our mathematical modeling work on how anesthetics act on neural circuits to produce the state of general anesthesia we are able to offer specific hypotheses as to how changes in level of activity in specific circuits lead to the unconscious state. We will discuss the relation between our findings and two other important altered states of arousal: sleep and coma. Our findings suggest that the state of general anesthesia is not as mysterious as currently believed.
T-3. Electrophysiological Foundations of Human Speech Production

Kristofer Bouchard¹
Nima Mesgarani¹
Miranda Babiak¹
Keith Johnson²
Eddie Chang¹

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No behavior is as unique to humans as the ability to produce spoken language, and few behaviors that every human performs are as complicated to control as speech. Understanding the spatio-temporal organization of cortical signals that control the articulators of the vocal plant during the production of basic speech elements (consonants and vowels) is fundamental to our understanding of how the brain produces the complex sequence of movements that compose spoken language. We recorded neuro-electrical activity from the surface of speech somato-motor cortex using high-density electrocorticography (ECoG) in neurosurgical patients during the production of a large and expansive set of American English consonant-vowel (CV) syllables. These recordings revealed that different syllables are produced by the graded activation of multiple cortical sites in overlapping spatio-temporal patterns. Across subjects, we found that the functional temporal structure of speech somato-motor cortex is sequenced to first shape the upper vocal tract, through movement of the lips and tongue, filtering the sound produced at the larynx and released from the vocal tract by the jaw. Furthermore, the functional modulations of neuro-electrical activity underlying speech production are somatotopically organized, with both anatomically well isolated as well as overlapping representations of the speech articulators. Analysis of the spatial patterns of activity (neural state-space) at both consonant and vowel time points reveals a hierarchically clustered structure that is primarily organized by the pattern of articulatory engagements. Finally, the neural state-space exhibits divergent and convergent dynamics that smoothly reflect the time dependent relationship between neural and articulatory states for both consonants and vowels. Together, our results lay the foundations of an electro-physiological understanding of speech production in humans. More generally, our results provide insight into how the human neocortex dynamically controls complex, multi-articulator behaviors, which is crucial to our understanding of basic nervous system function.

T-4. On the Origins of Motor Noise

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Voluntary movements cannot be repeated to arbitrary precision. We undertook a study to characterize movement variability and its relation to motor planning activity in the cortex, and found that cortical response variability manifests in behavior only on slow time scales. Over 26 experimental sessions, Macaque monkeys made a large number of center-out reaches (with delay) to three targets as multielectrode arrays chronically implanted in dorsal premotor cortex (PMd) and primary motor cortex (M1) recorded the activity of 37–115 neural units. We found that population activity in PMd and M1 predicts a significant amount of variability in the speed of upcoming reach movements (cp. Churchland & al 2006) as well their initial direction. Analysis of the time course of reach variability shows, however, that 20–40% of the variability in the speed and direction of reach movements is due to a slowly moving (~minutes) drift in the mean behavior; behavioral variability can thus be described as the superposition of this drift and trial-to-trial fluctuations. Analysis of 2011 Major League Baseball data shows that human subjects (pitchers) exhibit an analogous behavioral drift (in release point). We make the surprising observation that neural activity in PMd/M1 populations are, at best, weakly related to the trial-to-trial fluctuations in behavioral variation. Instead, in analogy with behavior, neural responses also exhibit a slow drift in mean...
response; this drift is persistent, not specifically tied to motor planning and related to/predictive of the drift in behavior. These results suggest that the central contribution to short time scale motor variability is minimal. Longer time scale drift is central in origin, and—as suggested by the (comparable) autocorrelation structures of both behavior and neural activity—may be the result of noise in a continuous online learning process (Cheng & Sabes 2007).

**T-5. Neural dynamics of reaching following incomplete or incorrect planning**

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Reaction times (RT) are faster when subjects prepare an action before moving. During preparation, primary motor cortex (M1) and dorsal premotor cortex (PMd) neurons display activity specific to the upcoming reach. This has led to the model that during preparation, motor cortical activity achieves a state (“optimal subspace”) which is beneficial for generating the planned movement. We asked what happens if neural activity is outside the optimal subspace when movement initiation is instructed. One model suggests that passing through the optimal subspace is necessary for movement; the RT deficit for improperly planned trials results from “re-planning” before moving. Alternatively, the optimal subspace might convey an RT benefit, yet not be obligatory. In this model, movement can be initiated from outside the optimal subspace, albeit with a temporal penalty. We trained monkey N to perform two tasks while we recorded simultaneous M1 and PMd activity using two 96 electrode arrays. The first task contained interleaved blocks of delayed and non-delayed reaches (incomplete plan). The second was an instructed delay task in which the cued target changed locations in 20% of trials (incorrect plan). We computed low-dimensional neural trajectories by performing PCA on PSTH’s for each neuron and condition. When a target switch was followed by a second delay, providing time to re-plan, neural activity changed from one plan to the other, indicating that re-planning is possible. However, when not given time to re-plan, improperly planned neural trajectories did not pass through the optimal subspace identified using “correctly planned” conditions. Instead, these neural trajectories took a parallel but separate path which converged with the correctly planned neural trajectories over the course of movement. This indicates that passing through the optimal subspace is not obligatory for movement, providing evidence against a strict “multi-step” model of movement generation.

**T-6. Energy-conservation and generalized power-law for curved hand movements**

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In physics, equations of motion can be derived from optimizing the total integrated cost. Noether’s theorem states that if such Lagrangian formulation is invariant under time-translation, then energy of the system must be conserved. Recently, it has been shown that human movements can be accurately modeled by the optimality principle in a similar manner. A crucial observation we made was that these optimal control models share the same time-translation invariance property, from which we successfully derived a novel conservation principle for human movements: Defining A as the minimum total cost, the conserved quantity (energy) is the partial differentiation of A with respect to time, \( E = -\delta A / \delta T \). One important contribution of our energy-conservation-principle (ECP) is that it extends the optimal control models to predict movement durations. For example, ECP predicts \( T \propto D^{-1/3} \) for reaching movements (T=duration, D=reaching distance), and \( T \propto R^{-1/3} \theta \) for circle-
drawing movements (R=radius, \( \Theta \)= angular distance), which we confirmed in experiments. In general, time-profile of movements scales with 1/3 power of movement size. Another prediction regards how angular speed \( w \) fluctuates with curvature \( k \) in curved hand movements. Traditionally, the relationship has been incorrectly known to follow the 2/3 power-law, \( w(t) \propto k(t)^{2/3} \). Instead, ECP predicts a family of power-laws with exponents ranging between 1/3 and 1, depending on how frequently the curvature fluctuates (e.g. spiral movements follows 1/3 power-law - closely related to the scaling-law above), which we confirmed in experiments (fig1). For movements with multiple frequency components, \( w(t) \) depends not only on the local \( k(t) \) but also on nearby curvatures (\( \pm dt \)). This result also allows us to estimate the amount of pre-planning required for generating curved movements.

In summary, ECP not only yields a fresh perspective for understanding human movements, but it also makes new predictions we have experimentally confirmed.

T-7. Predicting odorant perception and neural activity from odorant structure

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Although it is agreed that physicochemical features of molecules determine their perceived odor, the rules governing this relationship, and its neural underpinnings, remain unknown. A significant obstacle to such understanding is the high dimensionality of features describing both percepts and molecules. We applied a statistical method to reduce dimensionality in odor percepts, in odorant physicochemical descriptors, and in odorant-induced neural activity for a large set of molecules. We found that the primary axis of perception was odor pleasantness, and critically, that the primary axis of physicochemical properties reflected the primary axis of olfactory perception. Moreover, the primary axis of perception and the primary axis of structure were both related to the primary axis of neural activity. These relationships allowed us to predict the pleasantness of novel molecules either by their physicochemical properties alone, or by their induced neural activity. Olfactory perception is strongly shaped by experience and learning. However, our findings suggest that olfactory pleasantness is also partially innate, corresponding to a natural axis of maximal discriminability among biologically relevant molecules.

T-8. Odor-guided decisions in the rat: The origins and uses of uncertainty

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As scientists, we construct knowledge about the world by conducting experiments, formulating hypotheses and sharing information with one another, such as in this talk. Because our observations, models and communication are all imperfect, quantification of the reliability of information plays a fundamental role in this process. All animals, as they seek to understand and negotiate complex environments, face similar problems. Yet we still know little about the precise roles that uncertainty plays in neural information processing and behavior.

My laboratory has been studying the behavior of rats in a decision task where the value of a left or right choice depends on the identity of an odor cue. To investigate the origins of the uncertainty crucial for performance in this task, we have manipulated the cues and other task parameters to find the psychophysical limits of the subjects. We have also probed how decision uncertainty may itself be quantified and used by the brain. Through this approach, together with simultaneous recordings from several brain areas and simple formal models, we have begun to elucidate some of these issues.

At this meeting, I will discuss experiments revealing that uncertainty in olfactory decision-making arises from multiple sources. I will argue that one form of uncertainty reflects rapid, sensory noise fluctuations while a second form reflects slower fluctuations in decision criteria driven by trial-to-trial reinforcement learning. Only the fast fluctuations are subject to integration during stimulus presentation. Thus, the two kinds of uncertainty have
different effects on the speed-accuracy relationships of decisions. This helps to explain why accuracy benefits more from increased sampling time in some decision problems than in others. I will also discuss experiments showing that confidence in odor-guided decisions is explicitly re-represented in the orbitofrontal cortex and that this brain area is not necessary for these decisions but is critical for post-decision wagers.

T-9. Temporal segregation of olfactory bulb output

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Neuronal oscillations are observed ubiquitously in the nervous system and are thought to underlie many aspects of neuronal functions. In the main olfactory bulb of mammals, the activities of excitatory output neurons, mitral and tufted cells, are tightly linked to the breathing rhythm, which occurs in a theta frequency range. However, a systematic study of breathing-related temporal coding in identified mitral and tufted cells has been lacking. Using whole cell patch recordings in vivo in mice anaesthetized with ketamine and xylazine as well as in awake head-fixed mice, subthreshold membrane potentials and action potentials of mitral and tufted cells with respect to sniffs were investigated. We find that morphologically identified mitral and tufted cells prefer distinct phases of sniff cycles, separated by 180 degrees. To probe the source of this phase separation, a combination of GABA antagonist and agonist (0.4 mM and 2 mM) was superfused to block phasic GABA activation while maintaining network stability. While the tufted cell phase was unperturbed in this condition, the mitral cell phase collapsed on to the tufted cell phase, indicating that the GABAergic selectively delays mitral cell activation. Furthermore, we find that when excitatory odours are presented, while tufted cells increase firing rates without significant change in preferred phase, mitral cell phase gradually advances towards the tufted cell phase. To understand mechanisms further, we constructed 107 firing rate models of the OB network with connectivity parameters drawn from uniform distributions. Analysis of models consistent with the experimental observations show that stronger olfactory sensory connections to tufted cells compared to mitral cells, as well as prominent feed-forward inhibition on mitral cells, underlie the phase-shift. In conclusion, mitral and tufted cells differentially couple to sniffs, which results in distinct odour coding. Olfactory bulb thus segregates information into at least two streams of processing.

T-10. Do rats make optimal olfactory decisions under perceptual uncertainty when rewards are unstable?

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Making optimal decisions requires the integration of different sources of information. For instance, past experience with rewards enables animals to make predictions about their quality, size and predictability. When the main source of uncertainty is due to a perceptual decision process, estimating decision uncertainty provides a mechanism for predicting reward outcomes. Can rats combine experienced reward value and decision uncertainty to make optimal choices? And how does the brain dynamically compute and integrate these different estimates to make predictions? We designed a reward-biased psychometric decision task to dissociate reward estimates based on decision uncertainty and reward history and recorded neurons in the orbitofrontal cortex (OFC), an area implicated in computing reward predictions. Rats were trained on a binary odor mixture categorization task. We varied decision uncertainty by interleaving trials of different odor-mixture ratios and biased reward expectations
by changing reward size or probability for correct choices across blocks. The effect of reward bias on the psychometric function was strongest for uncertain odor mixtures and minimal for pure odors, suggesting that rats relied increasingly on prior knowledge with increasing decision uncertainty. Our simple Bayesian model for combining decision uncertainty and experienced reward value well predicted both behavioral choices and reaction times. Next we examined how decision uncertainty and experienced value are combined in OFC neurons. We found a heterogeneous representation with some neurons signaling either decision uncertainty or experienced value separately, while the majority of neurons showed mixed representations. These results suggest that rat OFC has the capacity to integrate different types of reward expectations and contribute to optimal choices to maximize reward acquisition.

T-11. Monte Carlo as mechanism: Sampling and human cognition

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Human behavior is consistent with the predictions made by Bayesian models of cognition across a wide range of problems. This raises an interesting question: How are people solving these problems, given the computational challenges posed by Bayesian inference? When we look at the distribution of people’s responses on specific tasks, we often see that this distribution is similar to the posterior distribution produced by applying Bayes’ rule. This phenomenon - which we call “probability matching to the posterior” - suggests a possible answer to our question: That people are approximating Bayesian inference by producing a small number of samples from the posterior distribution. Recent work in computer science and statistics has resulted in a number of sophisticated Monte Carlo methods for approximating Bayesian inference, such as importance sampling and particle filters, which we have explored as candidate explanations for human behavior. Considering the unique constraints of human cognition has also led us to develop novel algorithms that have surprising properties, such as a sequential Monte Carlo scheme based on the “win-stay, lose-shift” principle. I will present the results of experiments with both adults and children that explore the potential of the Monte Carlo principle as an account of human cognition and consider the implications of these results for computational neuroscience.

T-12. Noise correlations in population codes with finite information

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Although theoretical studies have shown that correlations can either increase or decrease information, conventional wisdom has it that the kind of correlations typically observed in the brain (large among neurons with similar tuning and small among neurons with different tuning) reduce information. Recently, however, Ecker and colleagues suggested that the conventional wisdom is wrong [1]. They showed that whenever tuning curves have a range of amplitudes, and those amplitudes are not related to the correlational structure, the information in a network is proportional to the number of neurons. Surprisingly, this is true for just about any correlational structure one can write down, including biologically realistic ones. While this is a profound result, it seems to conflict with the observation that information can’t scale with the number of neurons, since the number of neurons is fixed while information is set by noise in the outside world. The resolution, it turns out, is that the amplitudes of the tuning curves and the correlational structure are necessarily related. This is because the correlations that reduce
information are the ones that mimic a shift in the stimulus. This shift adds a very specific component to the covariance matrix, so to show that changes in correlations affect information, it is necessary to show that this particular component of the covariance matrix changes, not just its overall size. Importantly, the specific component of the covariance matrix that limits information might be very small compared to the other correlations, to the point of being difficult to measure experimentally with small numbers of trials. However, one can evaluate their impact on information by applying the optimal decoder to a cross validation data set, but this requires a large population of simultaneously recorded neurons.

T-13. Emergence of selectivity in recurrent random networks with balanced excitation and inhibition

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Visual, auditory and somatosensory cortical representations in several species consist of spatial feature maps. In contrast, experiments in piriform cortex (Stettler and Axel, 2009) and in visual cortex of rodents (Ohki and Reid, 2007) indicate that in these systems, stimulus preferences are distributed randomly without apparent spatial organization, although many individual neurons show sharp stimulus selectivity. Previous analysis suggests that cortical connectivity depends primarily on spatial proximity (Shapley et al 2000) indicating that in rodent olfactory and visual cortex connectivity might be poorly tuned to feature similarity. This raises the question: Can sharp stimulus selectivity be maintained in a cortical circuit with random untuned connections? To answer this question, we consider a recurrent network of excitatory and inhibitory spiking neurons with untuned sparse random connectivity. The network is driven by untuned random projections from an input layer of stimulus selective neurons. In such architecture, the stimulus modulation of total synaptic input to a neuron is weak compared to the untuned component. Surprisingly, we find despite its random architecture the network can exhibit high stimulus selectivity. This is due to the network’s balanced state (van Vreeswijk and Sompolinsky, 1996), in which strong synapses amplify the variation in synaptic input, and recurrent inhibition cancels the mean. We test this mechanism in a model of orientation selectivity in layer 2/3 of rodent V1. The network exhibits robust orientation selectivity, similar to experimentally observed values. We also study a model of olfactory cortical circuit driven by odor activation of the bulb. The population sparseness and lifetime selectivity are evaluated as a function of network parameters. We predict that when the strength of the stimulus activation is low (e.g., low contrast or low odor concentration) the stimulus selectivity decreases due to the increasing dominance of stochasticity at low rates.

T-14. A general, accurate, closed-form rate model derived as an approximation to spiking network dynamics

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Firing-rate models provide an attractive approach for studying large neural networks because they can be simulated rapidly and are amenable to mathematical analysis. Traditional firing-rate models assume the dynamics are governed by a single time constant, which is mathematically convenient but not justified in general, and they can only describe completely asynchronous activity. This is a serious limitation because transient synchronization of subgroups of neurons has often been suggested as an important mechanism for generating rapid behavioral responses. To address this issue without losing the advantages associated with a firing-rate description, we have
developed a model derived from an eigenfunction expansion of a Fokker-Planck equation, a common approach to describe the distribution of membrane potentials for a population of spiking neurons receiving noisy input. We depart from previous approaches by stressing simplicity along with sufficient accuracy. We find that a closed-form expression for the firing rate can be derived by assuming that a single eigenmode dominates the dynamics. Although the assumption of a single dominant mode is not true in general, it turns out to provide a good approximation across a wide range of parameter space. This approach is equally valid for any Integrate-and-Fire-type model (including the Exponential, Quadratic, and Leaky models). The simplicity of this rate model makes it highly amenable as a tool for understanding spiking networks. Using this approach, we study large randomly-connected networks of excitatory and inhibitory neurons. We find that the firing rate network gives a surprisingly accurate approximation to the time-varying activity of a spiking network across a wide range of parameters and well into the synchronous activity regime. The rate network has a phase diagram that is virtually identical to that of the spiking network, predicting not just rate instabilities but also the bifurcation line between synchronous and asynchronous states.

T-15. A New Look at Human Motor Control

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Much research has tackled motor control with the tools of classical mathematical optimization theory widely used in robotic models. Although dynamical systems can be modeled with classical Newtonian equations, for mammalian systems with very high numbers of degrees of freedom, these equations prove prohibitively expensive to solve except in the case of small subsystems. Nonetheless, humans themselves are an existence proof that some kind of practical solution must exist, since they have exquisite motor coordination. At the same time, since their physical properties are so unique, one must be prepared that the human solutions might look very different than those dictated by the robotics-inspired classical approach. A major point of departure is in the musculoskeletal design. Anthropomorphic bipedal designs can successfully walk downhill in a completely passive mode, implying that much of the machinery needed for human movements has been incorporated in the mechanical design itself. Further, passive muscle synergies augment basic mechanical degrees of freedom. By using activation to direct set contractions, the muscles can guide the complete motor system through a series of posture changes that are designed to both respect the basic joint limitations of the mechanical system and at the same time be efficient. The idea of movement control as a series of postural changes has long been espoused, but has so far resisted a tight mathematical formulation. Our research shows how to reduce elaborate posture changes into a compact code that has several advantages. First of all, it provides an overview of how the elaborate computations in abstract motor control could be parcellated into the brain’s primary subsystems. Secondly, its parametric description could be used in the extension of learned movements to similar movements with different goals. Thirdly, the sensitivity of the parameters can allow the differentiation of very subtle variations in movement.

T-16. Tuning to 3-D head-direction in the bat presubiculum

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Head-direction cells are active whenever the animal’s head points in a specific direction in space, and were suggested to be a key component of the mammalian navigation system. Surprisingly, head-direction cells in the
rat were reported to be indifferent to movements of the head in the up-down (pitch) axis, suggesting that these cells in rodents are inherently 2-D spatially-tuned. We asked whether such tuning is a universal property of the mammalian brain, by recording from flying mammals—Egyptian fruit bats—that may be better adapted to 3-D behavior. Here, we developed a special 3-D tracking apparatus that allowed monitoring the three head-rotation angles: yaw, pitch and roll. Cells modulated by head-direction were recorded in the bat presubiculum, while the bats were actively crawling in an open-field arena, or were passively moved in an upside-down orientation. We found that these cells were tuned to one or more of the three rotation angles (yaw, pitch, or roll). Furthermore, in contrast to rats, most neurons retained their head-direction tuning while the bat was held upside-down. Taken together, these results demonstrate for the first time a 3-D head-direction mechanism in mammals, which may be part of a broader neuronal network supporting navigation in 3-D space.

T-17. Awake hippocampal sharp-wave ripples support spatial working memory
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The hippocampus is critical for the storage and retrieval of spatial memories. In particular, hippocampal damage or dysfunction leads to deficits in two distinct types of memory: working memory, where representations of specific past experiences must be retrieved to guide subsequent choices, and reference memory, where choices are made based on longer term, accumulated memories rather than based on specific experiences. There also are two dominant neural activity patterns in the hippocampus of awake animals, namely place field activity seen during exploratory behavior and replay of past experience during sharp-wave ripples (SWRs) seen primarily during immobility and low speed movement. The relationship between these activity patterns and the spatial memory functions of the hippocampus is not understood. We specifically disrupted hippocampal neural activity during awake SWRs as animals learned a hippocampally-dependent spatial memory task to determine how these events contribute to spatial working and reference memory. We found that transient suppression of hippocampal activity during awake SWRs caused a marked learning deficit specific to spatial working memory with no discernable effect on spatial reference memory. SWR interruption did not affect place field activity during behavior, indicating that place field activity is not sufficient to support working memory processes. Further, reactivation during SWRs in rest periods after behavior, which has been linked to memory consolidation, also remained intact following awake SWR interruption. Our results suggest that the awake replay of past experience during SWRs is an essential component of working memory processes that allow an animal to retrieve specific memories and use them to guide behavior.
T-18. Bending waves during C. elegans locomotion are driven and organized by proprioceptive coupling

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Locomotion requires mechanisms that coordinate motor activity throughout an animal’s body. Here, we show that forward locomotion in C. elegans is both driven and coordinated by a novel form of proprioceptive coupling within the motor circuit. To characterize this mechanism, we engineered microfluidic devices that enabled us to control the bending of specific body regions while quantifying movement and neuromuscular activity throughout the animal. We show that positive stretch-sensitive feedback compels each body region to bend in the same direction and shortly after bending in the neighboring anterior region. To determine how proprioceptive coupling is integrated into the neuromuscular network, we performed optogenetics and calcium imaging to directly manipulate and monitor motor circuit activity of worms in our microfluidic devices. We show that the cholinergic motor neurons both generate and propagate the proprioceptive signal from anterior to posterior body regions. We also show that body wall muscles in C. elegans can sustain contraction without synaptic input. Thus, in the C. elegans motor circuit, motor neuron output is used to trigger changes in bending state, not to maintain bending. We use our quantitative physiological measurements to build a mathematical model of locomotion. This model shows how proprioceptive coupling drives and organizes the undulatory gait, and also provides a biophysical explanation for gait adaptation when the external load on a moving worm is gradually increased.
**T-19. Activation of Specific Interneurons Improves V1 Feature Selectivity and Visual Perception**

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Inhibitory interneurons are essential components of the neural circuits underlying a variety of brain functions. In the neocortex, a large diversity of GABAergic interneurons have been identified based on their morphology, molecular markers, biophysical properties, and innervation pattern. However, how the spiking activity of each subtype of interneurons contributes to sensory processing remains largely unknown. Here we show that optogenetic activation of parvalbumin-positive (PV+) interneurons in mouse primary visual cortex (V1) sharpens neuronal feature selectivity and improves perceptual discrimination. Using multichannel recording with silicon probes and channelrhodopsin 2 (ChR2)-mediated optical activation, we found that elevated spiking of PV+ interneurons markedly sharpened orientation tuning and enhanced direction selectivity of nearby V1 neurons. These effects were caused by the activation of inhibitory neurons rather than decreased spiking of excitatory neurons, since archaerhodopsin-3 (Arch)-mediated optical silencing of calcium/calmodulin-dependent protein kinase IIα-positive (CaMKIIα+) excitatory neurons caused no significant change in the cortical stimulus selectivity. Moreover, the sharpening of orientation tuning specifically required inhibition from PV+ interneurons: although activating somatostatin (SOM+) interneurons increased direction selectivity, it caused no sharpening of orientation tuning, and activating vasointestinal peptide (VIP+) interneurons had no effect on either response property. Notably, optical activation of PV+ interneurons in awake mice caused a significant improvement in their orientation discrimination, mirroring the sharpened V1 orientation tuning. Together, these results provide the first demonstration that visual coding and perception can be improved by elevated spiking of a specific subtype of cortical inhibitory interneurons.

**T-20. Entraining gamma oscillations in somatosensory cortex enhances performance in tactile detection**

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The utility of gamma oscillations in primary sensory cortices is a contentious issue, largely due to the fact that experiments have thus far provided only correlative, rather than causal, evidence for their beneficial nature. A previous study from our lab demonstrated that it is possible to bring gamma-band synchrony under experimental control in the somatosensory cortex. Here we demonstrate that entraining gamma oscillations in somatosensory cortex enhances tactile discrimination performance in awake animals. Using optogenetics, we were able to manipulate gamma oscillations and test their impact on tactile detection in awake monkeys. Our results provide evidence for a causal role of gamma oscillations in tactile perception and highlight the potential for optogenetics to manipulate brain rhythms and improve cognitive function.
control by varying the temporal offset between an environmental stimulus and an imposed gamma rhythm in cortex (i.e., varying the phase of a laser stimulus at the cortical surface). Here, we apply this manipulation in mice trained on a tactile detection task, with the goal of testing whether or not entraining gamma in a primary sensory area has any effects on perception. PV-Cre mice were injected with AAV-DIO-ChR2-mCherry in SI, had a head post affixed to the skull, and had electrodes chronically implanted near the injection site to monitor the efficacy of optogenetic gamma induction. Following a recovery period, mice were trained to lick a reward spout in response to 40 Hz vibrissal deflections. Once mice became proficient at the task (and viral expression levels reached a plateau) we added a 40 Hz optogenetic stimulus on approximately half the trials. Performance varied as a function of laser phase, as indicated by hit rate, reaction time, and d’ (a measure of overall accuracy). On trials with imposed gamma at the phase shown to enhance spike synchrony most robustly, mice performed significantly better than on trials without any optogenetic stimulus (baseline). On trials with imposed gamma at the phase shown to have the greatest detriment to synchrony, mice performed significantly worse than baseline. Enhanced performance was also observed in a task which included a vibrissa stimulus that mimicked the statistics of natural vibrissa movements. These results provide causal evidence that gamma-range oscillations can benefit perception in a mammalian model system.

**T-21. Phosphene induction in monkeys using optogenetics**

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Optogenetics has had a remarkable impact on our understanding of the causal influences of neural activation on the behavior of rodents and lower animals. A key area of development is to adapt this technology to non-human primates for which more sophisticated models of behavior exist. Here we demonstrate the use of optogenetics to drive a behavioral response in two rhesus monkeys (Macaca mulatta). We expressed channelrhodopsin-2 (ChR2) in a small region of the primary visual cortex (V1), and asked whether ChR2-mediated activation produced phosphenes at the location of the corresponding receptive fields (RFs). Our behavioral paradigm consisted of two trial types, “Fix” and “Tar”. On “Fix” trials, monkeys received liquid rewards for maintaining fixation on a central spot. On “Tar” trials, monkeys received rewards for making a saccade to a visual target that was presented after fixation spot offset. Unbeknownst to the monkeys, half of the trials in each category were coupled with optical stimulation (“Op+Fix” and “Op+Tar”). The key finding was that on Op+Fix trials, in which no visual target was presented, monkeys made saccades toward the RF of neurons at the injection site (top panels). Simultaneous recording showed that optical stimulation modulated spiking activity near the injection site (bottom panels). To ensure that the behavioral effect was not due to a nonspecific association between stimulation and saccadic response, we performed a control experiment in which the visual target was presented in the hemifield opposite the RF location of the ChR2-mediated activity. In Op+Fix trials of the control task, monkeys continued to orient toward the location of the RF suggesting that the saccadic responses were induced by phosphene perception. To the best of our knowledge, this is the first application of optogenetics for evoking an overt behavioral response from a non-human primate.

**T-22. Categories, decisions and parietal cortex**

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The inferior parietal lobe is involved in the perception of visual space and the control of eye movements. Neurons
in the primate lateral intraparietal area (LIP) have also been implicated in perceptual decision-making. In those experiments, monkeys typically signal their percept by making saccadic eye movements in specific directions. We asked whether parietal neurons are involved in decisions that do not have a spatially specific motor read-out. In our first experiment, we trained monkeys to group directions of motion into two 180°-wide “categories”. After training, we found that LIP neurons reflected the learned category boundary, in that individual neurons tended to respond similarly within direction categories but differently between categories. We examined the generality of these effects by training animals in a paired-associate task in which the animals learned to group pairs of arbitrarily chosen static shapes. We found again that LIP neurons reflected the learned pair-associations, in that individual neurons tended to respond more similarly for associated pairs of shapes than for unassociated pairs of shapes. In both the direction-categorization task and the shape-paired-associate task we used a delayed match-to-category (-pair) paradigm that dissociated the category (pair) identity from the hand movement the animal used to signal its report. We also controlled carefully for behavioral artifacts that could have produced the observed neuronal selectivity. Our results suggest that parietal neurons provide decisional signals that do not fit in a spatial- or motor-based framework. These findings challenge the generality of models positing that categorical decisions are represented in an action- or intention-based framework. Action-based frameworks have been proposed for other brain representations, such as for the representation of value. However, we also find action-independent neuronal representations of value in orbitofrontal cortex. We hypothesize that non-action-based representations are prevalent in the brain and can be revealed by appropriate experimental design.

**T-23. The role of disordered representations in neural dynamics**

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The response properties of neurons recorded in the prefrontal cortex are very diverse in space (i.e. for different neurons) and time (i.e. selectivity changes in different epochs). Often, neurons respond to conjunctions of events and other task related aspects (mixed selectivity). This variability makes the neuronal responses seemingly disordered and hard to interpret. It is natural to ask whether this variability is just disruptive noise, or whether it plays a functional role. We addressed this question by analyzing and manipulating the neural activity recorded in prefrontal cortex during an object sequence memory task(Warden & Miller, 2010). We found that: 1) all relevant aspects of the task can be decoded with great accuracy on a trial by trial basis from the neuronal population activity, despite the fact that the information is intermixed and distributed across multiple neurons; 2) even when the selectivity to a specific aspect of the task is individually removed from all recorded neurons, it is still possible to decode that specific aspect by harnessing the mixed selectivity components of neural activity; and 3) the disordered neural representations that have been recorded are significantly more efficient at driving the dynamics of a simulated neural circuit than representations based on neurons that are purely selective to one aspect of the task. We show that the main limitation of pure selectivity neurons is caused by the low dimensionality of their population activity. Typically, for these neurons, the number of effective dimensions representing the different aspects of the task is much smaller than the number of task conditions. In contrast, the effective dimensionality of the recorded representations is significantly higher, making the representations more suited to drive the activity of individual neurons. In conclusion, our study demonstrates that the diversity of the response properties of recorded neurons does not limit the amount of information stored in the neural representations. Moreover it actually provides a great computational advantage. This work has been done with M. Rigotti, O. Barak, M.R. Warden, N. Daw, X-J. Wang and E.K. Miller.
T-24. Separable Influences of Reward on Prefrontal Control of Attention and Target Selection

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Understanding the neural mechanisms of value-dependent choice and attention have been two of the most important research objectives in systems neuroscience. However, difficulties in dissociating attentional and reward-dependent mechanisms have greatly limited progress in understanding these two processes and how they relate to one another. These difficulties have arisen for two reasons: First, attentional deployment is often manipulated by changing reward contingencies. Second, attentional deployment and value-dependent target selection typically yield a single action (e.g. a saccadic eye movement), so it is difficult to dissociate the two processes. By combining modeling and experimental approaches, we examined the influence of value on target selection and attention using saccade metrics in a free-choice task. Specifically, monkeys selected between two visual targets, each of which was a drifting grating. It has been shown that saccades directed to such targets are displaced in the direction of visual motion. This “motion induced bias” (MIB) provides an untrained, implicit measure of attentional deployment as it depends on the features of the target and reveals the extent of processing of those features. Therefore, on each trial we could independently assess the monkeys’ target selection and attentional deployment. We also examined how target value interacts with microstimulation of the frontal eye field (FEF) to shape target selection and spatial attention. We first show that attention is influenced by reward history even when it is not required to obtain reward, and that reward integration for attention differs from that of target selection. Second, we show that FEF microstimulation and reward history exert additive effects on attention, while they interact to guide selection. Third, we show that our experimental observations can be explained by a model in which the efficacy of microstimulation-driven signals and endogenous reward signals interacts competitively.

T-25. Human single-unit responses in the nucleus accumbens during a financial decision-making task

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Central to flexible human behavior is our ability to bind stimulus value to action and to evaluate expectation to outcome. Despite this, very little is understood on the mechanisms underlying these computations in humans. Here, we report single-unit responses recorded from the human nucleus accumbens (accumbens) in patients undergoing deep brain stimulation while engaged in a financial decision-making task. The task is modeled as a simplified version of the classic card game “war”. The subject is dealt a card and asked to make a high or low wager ($5 or $20). Immediately following their choice they are shown their opponent’s card—the player with the highest card.
wins. We recorded 25 individual neurons from 8 patients. We restricted our analysis to 19 well isolated units based on stability of the recording, quality of isolation, and minimum number of trials. We found that during the 500 msec interval following the go-cue, accumbens activity predicted whether the subject would ultimately place a high or low bet (ROC, a.u.c.=0.62 ; randomization test, p<0.001). This activity occurred on average 2±.81 sec before the bet was manifested. No other pre-choice interval predicted bet direction. Furthermore, we found that accumbens activity encoded a reward prediction error signal; accumbens activity selectively increased for unexpected wins and decreased for unexpected losses during a 500 msec interval in the feedback period (two-tailed t-test, p<.01). There was no change in activity for expected wins and losses. In conclusion, these findings suggest that the accumbens encodes two reinforcement learning signals during financial-decision making: (i) binding predicted stimulus value to action, and (ii) evaluating discrepancies between expectation and outcome. This represents the first report of single-neuronal responses from the human accumbens during financial decision-making.

T-26. Dynamics of a calcium-based plasticity rule: from single synapses to networks
Nicolas Brunel
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Calcium is known to play a fundamental role in synaptic plasticity. However, it is still unclear to what extent the dynamics of calcium concentration in post-synaptic spines alone can account for the phenomenology of plasticity. In this talk, I will first present a simplified calcium-based synaptic plasticity model, and show that it can reproduce quantitatively a large amount of experimental data in several preparations (hippocampal cultures, hippocampal slices and cortical slices). Differences between plasticity outcomes in such preparations are predicted to arise due to differences in parameters controlling calcium dynamics (such as the extracellular calcium concentration). I will then present some consequences of this plasticity rule at the network level.

T-27. Long-term modification of cortical synapses improves sensory perception
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Synapses and receptive fields of the cerebral cortex are plastic. However, changes to specific inputs must be coordinated within neural networks to ensure that excitability and feature selectivity are appropriately configured for perception of the sensory environment. Here we report that long-lasting positive and negative changes to auditory cortical excitatory synapses were induced by pairing acoustic stimuli with activation of the nucleus basalis
cholinergic neuromodulatory system. We examined synaptic tuning curves for sound level intensity and found that initially, as previously reported, most neurons showed a monotonically-increasing amount of tone-evoked excitation as sound level grew louder. However, pairing a quiet, low-intensity tone with nucleus basalis stimulation ('nucleus basalis pairing') increased these initially weak responses while the strongest responses to louder tones were depressed. These synaptic modifications were precisely orchestrated across entire receptive fields, conserving mean excitation while reducing overall variance, and each parameter of cortical synaptic receptive fields (frequency and intensity) could be modified independently of the other. Computational analysis indicated that decreased variability should increase detection and recognition of near-threshold or previously imperceptible stimuli, and this was confirmed psychophysically with nucleus basalis pairing in behaving animals. Pairing in anesthetized animals could lead to behavioral improvements after animals woke up. The effects of pairing lasted only a few hours unless pairing was performed daily for several (6+ days), after which the effects of pairing endured. Furthermore, pharmacological manipulations indicated that changes to auditory cortex were both necessary and sufficient for behavioral enhancement. Thus direct modification of specific cortical inputs leads to wide-scale synaptic changes, which collectively support improved sensory perception and enhanced behavioral performance.

T-28. Plasticity and stability in motor cortex during learning

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Animals move their sensors to collect information about the world, and movements in turn are guided by sensory input. Interactions between movement and sensation are critical for robust motor control and also shape complex learned behaviors, where sequences of movements are required to achieve a given goal. The motor cortex is thought to play important roles in learning new motor skills, but the underlying mechanisms at the level of neural circuits are unknown. Superficial layer neurons in the primary motor cortex likely participate in sensorimotor integration and learning; they receive input from sensory cortex, and excite deep layer neurons, which control movement. Here we used chronic population imaging with genetically encoded calcium indicators (GCaMP3) to track the same set of superficial neurons in the motor cortex over weeks, while mice learned to detect objects with their whiskers and report detection with licking. Neuronal activity correlated with whisker position and whisking amplitude, with the forces exerted on the whiskers during touch, as well as with licking during reward collection. The representations of individual neurons changed with learning, but in a restricted manner so that licking neurons never changed into whisking neurons and vice versa. This indicates that neurons tend to encode default behavioral features, which might be immutable to learning. In expert mice, the representation of behavioral parameters was stable at the population level, despite continuing changes at the level of individual neurons. Finally, in a sub-population of neurons the representation of licking triggered by whisker touch emerged with learning, suggesting that the superficial layers of motor cortex participate in linking task-related sensory inputs and actions.
T-29. Nonlinear dendritic processing during active sensing produces an object localization signal

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Despite decades of research it remains unknown if the powerful processing capabilities of active dendrites are actually involved in any behaviorally relevant neuronal computations. Here we report that a novel global dendritic nonlinearity is linked to object localization and an associated motor refinement during an active sensing task. Layer 5 pyramidal neurons are the primary output of the barrel cortex and they receive functionally distinct inputs onto separate dendritic regions. Previous studies show that coincident input from these segregated pathways initiates regenerative dendritic electrical events that shift the action potential output mode to burst firing, representing a powerful dendritic nonlinearity that could mediate computations based on input correlation. However, the presence and the functional roles of large Ca2+ transients in the distal dendritic tuft in awake behaving animals are yet unknown. Here we designed a whisker-based tactile detection task where mice were trained to detect the presence of a tactile object (a vertical pole) by active whisking, and performed in vivo two-photon Ca2+ imaging from distal apical dendrites of layer 5 neurons in the barrel cortex using genetically encoded Ca2+ indicator (GCaMP3) (see figure below, left). Large amplitude, global Ca2+ signals were observed throughout the entire apical tuft dendrites that are tightly linked to active touch in a whisker position-dependent manner during active sensing (see figure below, right). Dendritic recordings in anesthetized mice and in vitro suggest these novel global signals are produced by dendritic plateau potentials that are coincident with widespread layer 1 (L1) synaptic input. Quantitative behavioral assessment also shows that learned refinements in the whisking pattern were co-evolved with dendritic signals. These data represent the first direct observation of dendritic Ca2+ signals at subcellular resolution in awake mammalian brain, revealing nonlinear dendritic integration underlying sensory processing during active sensation.

T-30. Thinking about thinking about thought

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Perhaps one of the most surprising discoveries of cognitive neuroscience is the existence of brain regions involved in thinking about thoughts. I will describe neuroimaging evidence to provide clues about the functional responses of these regions, including their response profiles and selectivity, the developmental mechanism that produced them, and the representational features that are encoded there. These data open a window on deep and fundamental questions about how the mind goes ‘beyond the data’, inventing abstract concepts and invisible causes to make sense of the world, especially the social world around us. Nevertheless, the most interesting questions about these brain regions remain unanswered.
T-31. The beads task, information sampling and impulsivity

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Decisions are most effective after collecting sufficient evidence to accurately predict rewarding outcomes. We investigated whether healthy participants optimally seek evidence and we characterized the brain areas associated with their evidence seeking using fMRI. Participants viewed sequences of colored beads drawn from a hidden urn and attempted to infer the majority bead color in the urn. After participants were shown each bead, they could choose to infer the majority bead color in the urn, or draw another bead from the urn. We compared the number of beads they drew against a Bayesian model and found that participants sampled less evidence than optimal. Also, when faced with urns that had bead splits closer to chance (60/40 vs. 80/20) or potential monetary losses, participants increased their evidence seeking, but by an amount less than that predicted by the ideal observer model. When participants decided to infer the majority bead color, rather than draw additional beads, we found activity in insula, striatum, anterior cingulate and parietal cortex. The parietal responses were greater for participants who sought more evidence on average and for participants who more increased their evidence seeking when draws came from urns with ratios closer to chance ratios. Parietal cortex and insula were associated with potential monetary loss. Insula responses showed modulation with estimates of the expected gains of urn choices. Our findings show that participants sought less evidence than predicted by an ideal observer model and their evidence-seeking behavior may relate to information communicated by insula and parietal cortex. In addition to the fMRI experiment, we also compared evidence seeking across several patient groups characterized as impulsive. The beads task proved to be highly sensitive to impulsivity. We found that drug abusers, pathological gamblers, and PD patients with dopamine induced impulse control disorders all drew significantly less than control groups.

T-32. Shaping neural circuits by early experience

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Early life experience potently shapes brain function and adult behavior. The biological bases underlying these windows of plasticity are increasingly being resolved in the developing mouse neocortex. This talk will cover core concepts of “critical periods” across sensory systems (visual, auditory, cross-modal). Pioneering the use of a molecular/genetic approach, we revealed that specific GABA circuits orchestrate the functional and structural rewiring of neural networks during sensory cortical development. Consequently, shifting excitatory-inhibitory (E-I) circuit balance or lifting a variety of molecular ‘brakes’ enables plasticity even beyond the early critical period. Understanding these events offers novel biomarkers of maturational milestones and deeper insight into neurodevelopmental disorders and therapeutic strategies in humans.
T-33. Patterns of activity initiated by individual photoreceptors in primate retina

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Purpose: The elementary input to a sensory system is the activation of a single sensory receptor. However, few direct measurements reveal how this signal diverges to produce patterns of activity in downstream neural circuits, nor how signals initiated in different receptors interact. We sought to understand how visual signals initiated in individual cone photoreceptors propagate and interact in the circuitry of the primate retina.

Approach: Extracellular recordings were performed simultaneously from hundreds of retinal ganglion cells (RGCs) of identified types in isolated primate retina. High resolution white noise stimuli and reverse correlation were used to map RGC receptive fields, revealing the functional inputs of complete populations of cone photoreceptors to complete populations of RGCs of several types simultaneously. Punctate visual stimuli were then used to stimulate single cones in isolation, or two cones simultaneously. Results: Visual stimulation of a single cone produced robust firing in RGCs of two or more major types simultaneously. Surprisingly, midget (parvocellular-projecting) RGCs responded at least as strongly to single cone stimulation as did parasol (magnocellular-projecting) RGCs, suggesting that previous reports of greater contrast sensitivity in parasols may merely reflect the larger number of cones in their receptive fields. The relative strength of RGC responses to stimulation of two cones individually was not fully consistent with the predictions of a linear model of light response implicit in the receptive field. This nonlinearity was confirmed by failures of additivity in response to stimulation of pairs of cones, for both midget and parasol cells.

T-34. Multiple spectral inputs improve motion discrimination in the Drosophila visual system

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From humans to insects, colour and motion information are thought be channelled through separate neural path-
ways for efficient visual processing, but it remains unclear if and how these pathways interact in improving perception of moving coloured stimuli. Such computations are hard to investigate in any species, because the spectral sensitivities of the colour and motion channels typically overlap extensively. This interference makes it difficult to activate one pathway without activating the other, as needed for assessing the independence of their individual parts. To overcome this problem, we used two genetic approaches, complemented by intracellular electrophysiology, 2-photon optical imaging of genetically encoded reporters and behaviour.

Firstly, we generated “UV-flies”, where the blue-green opsin of R1-R6 photoreceptors was genetically replaced with an ultra-violet opsin, abolishing the spectral sensitivity overlap between the R1-R6 and R8 channels. Thus, their R8s could be independently excited by long-wavelength light (>460 nm), while R1-R6s should only respond to UV, allowing us to directly examine whether the early motion and colour channels crosstalk at different processing stages in the fly visual system.

Secondly, by using photoreceptor-specific genetic rescue of a blind transduction mutant we generated flies in which only one spectral class of photoreceptor was light-sensitive. By repeating this for R1-R6 and each of the four spectral classes of R7 and R8, we were able to uniquely test the contribution of each spectral class in turn. Using these approaches we were able to directly and unequivocally demonstrate that colour photoreceptors (R7/R8) feed directly into the motion pathway at an early stage, and that this significantly improves their optomotor behaviour performance in a flight simulator system. Our results disprove the 40-year old dogma that motion vision in flies is mediated exclusively by the single spectral class, R1-R6 photoreceptors, changing our understanding of how motion vision operates in insects.

Visual attention increases synaptic efficacy in thalamocortical circuits

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Visual attention modulates neuronal activity across visual cortical areas, however the mechanisms by which attention alters neuronal activity remain elusive. In order to ascertain potential mechanisms of attentional modulation, we examined whether attention enhances the efficacy of synaptic communication at the earliest stage of cortical processing—the thalamocortical synapse. Specifically, we asked whether attention changes the probability of a postsynaptic spiking response in primary visual cortex (V1) given a presynaptic input from the lateral geniculate nucleus of the thalamus (LGN). In two alert monkeys, we first identified pre- and postsynaptic neurons by electrically stimulating the LGN and recording extracellular postsynaptic responses in layer 4C of V1. We then measured neuronal responses to drifting, sinusoidal gratings to determine the visual physiology of identified postsynaptic neurons, allowing us to identify neurons as recipients of magnocellular or parvocellular stream inputs. We measured the efficacy of electrically evoked LGN activity in driving postsynaptic cortical responses while animals performed an attention task to assess attentional modulation of thalamocortical communication. Animals were instructed to attend to one of two drifting gratings—one within and one outside the receptive field of the recorded neuron—and to report the occurrence of a contrast change in the attended grating. Importantly, electrical stimulation was delivered prior to the contrast change (during the peak attentional window); shocks occurred in both trial conditions (attend toward and attend away); and stimulation levels were set such that less than half of the shocks evoked postsynaptic spikes. Results of recordings from 61 postsynaptic neurons in V1 demonstrate a significant enhancement of thalamocortical synaptic efficacy with attention. Both magnocellular- and parvocellular-recipient neurons in layer 4C demonstrate this attention-mediated increase in synaptic efficacy. Interestingly, the synaptic efficacy effect is independent of the influence of attention on the overall firing rate of postsynaptic neurons in V1.
T-36. Mechanisms and consequences of transforming dense codes to sparse codes in the auditory system

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Processing communication signals is a crucial, natural function of the brain’s sensory systems. Sensory systems generate neural representations of external stimuli that lead to perception and guide behavior. A shared feature among sensory systems is the hierarchical flow of information from periphery to higher cortex through multiple processing stations. An important part of understanding how sensory processing leads to perception is explaining the mechanisms whereby neural representations of complex sensory signals such as communication sounds transform along sensory coding pathways. The auditory system is unique with regard to the large number of distinct processing stations involved in the coding of sensory stimuli. It is therefore advantageous for studying hierarchical signal transformations from brainstem to cortex. We study the hierarchical auditory coding of complex vocal communication sounds in the songbird. I will present our work on the song coding properties of single neurons in the midbrain, primary forebrain and higher forebrain. We have examined coding of individual songs presented in auditory scenes and alone. We observe subtle but consistent differences in the dense and nonselective coding of song between the midbrain and primary forebrain. In contrast, we observe a transition from a dense coding scheme to a sparse and highly selective coding scheme between the primary and higher forebrain, as little as one synapse away. We present a model for the transformation of song coding from dense to sparse and selective, and the consequences of dense versus sparse codes for the neural extraction of a target signal from a complex auditory scene.

T-37. Changes in cortico-striatal connectivity strength during flexible sound-action associations in rats

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Our ability to adapt to different environments often depends on modifying the actions associated with a given stimulus. To study the neuronal mechanisms underlying flexible associations between sounds and actions, we developed a two-alternative choice paradigm for rats in which the meaning of some sounds (the location of reward associated with these sounds) changed several times within a behavioral session. Trained rats reached asymptotic performance in less than 40 trials after each change.

What brain circuits mediate rapid changes in the behavioral responses associated with a given sensory stimulus? We found that the activity of neurons from both the auditory cortex and the auditory striatum of behaving rats was modulated not only by sound identity but also by the animal’s action, with striatal neurons displaying a stronger dependence on action than cortical neurons. We therefore hypothesized that changes in sound-action association may be mediated by changes in functional connectivity between the auditory cortex and the striatum.

To test this hypothesis, we developed a method for estimating the strength of connections between these brain areas in the behaving animal. After expressing channelrhodopsin-2 (ChR2) in auditory cortical neurons, we photostimulated the axons of these neurons that project to the striatum. The release of neurotransmitter from these axons generates postsynaptic potentials that can be measured extracellularly, and whose magnitude reflects the strength of the cortico-striatal connections. Using this method, we found changes in connectivity between the auditory cortex and its striatal target that were correlated with changes in sound-action associations. These results support the hypothesis that the auditory cortico-striatal pathway mediates flexible associations between sounds and actions.
T-38. Emergence of pitch from natural sound statistics in a hierarchical, dual-pathway sparse coding model

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The neural basis of pitch perception, our subjective sense of the tone of a sound, has been a great ongoing debate in neuroscience. Variants of the two classic theories—spectral Place theory and temporal Timing theory—continue to drive new experiments and debates (Shamma, 2004). Here we approach the question of pitch by applying a theoretical model based on the statistics of natural sounds. Motivated by gist research (Oliva and Torralba, 2006), we extended the nonlinear hierarchical generative model developed by Karklin & Lewicki (2003) with a parallel gist pathway. The basic model encodes higher-order structure in natural sounds capturing variations in the underlying probability distribution. The secondary pathway provides a fast biasing of the model’s inference process based on the coarse spectrotemporal structures of sound stimuli on broader timescales. Adapting our extended model to speech demonstrates that the learned code describes a more detailed and broader range of statistical regularities that reflect abstract properties of sound such as harmonics and pitch than other standard models. The spectrotemporal modulation characteristics of the learned code better match the modulation spectrum of speech signals than alternate models, and its higher-level coefficients capture information which not only effectively cluster related speech signals but also describe smooth transitions over time, encoding the temporal structure of speech signals. Finally, we find that the model produces pitch-related units which combine temporal and spectral qualities.

T-39. Sound encoding in the neocortex by combinations of discrete activity patterns in local neuronal ensembles

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It is believed that patterns of activity are the neuronal correlate of the perception of an external stimulus, e.g. a sound. Here, we used in vivo two-photon calcium imaging to better understand how sounds are encoded at the level of local layer 2/3 ensembles in the mouse auditory cortex. We found that activity patterns are highly constrained into a few discrete response modes, i.e. that a wide range of different sounds evoke the same population response pattern. Using online synthesis of sound stimuli to map the transition across response modes with fine resolution, we observed highly non-linear dynamics suggesting attractor-like competition between response modes. The combination of sounds that were associated in a specific response mode varied across local populations and was not predictable based on the population’s pure-tone frequency tuning. We used linear classifiers to test whether different pairs of sound could be discriminated on a single trial basis based on population activity. Global response patterns constructed by the combination of multiple local patterns largely out-performed local populations for the number of discriminated sound pairs, indicating that much more information is contained at the global scale. Interestingly, strong dimensionality-reduction by decomposition of single trial patterns into response modes did not lead to significant information loss. Furthermore, we found that global activity patterns in the mouse auditory cortex quantitatively predict discrimination and spontaneous categorization of sounds in behaving mice. We suggest a model of auditory cortex function in which local non-linear dynamics shape a broad basis set of spontaneous, distinct associations of stimuli that form a representation of sounds available for behavioral decisions.
T-40. A unified neuronal population code fully explains human object recognition

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Our goal is to understand the neuronal mechanisms that underlie human visual object recognition (OR). While previous work has argued for qualitative links between neuronal responses in the ventral visual stream and human shape judgements, no study has asked which, if any, neuronal responses are quantitatively sufficient to explain broad domain human OR performance. The shift from qualitative to quantitative hypotheses requires a framework to link neuronal responses to behavior (“unified code”). Here we ask: is there a common neuronal basis (e.g., in IT cortex) and a simple (e.g., linear) transformation that will predict all of human OR performance? We first defined OR operationally by obtaining human psychophysical measurements using images that explore shape similarity and identity preserving image variation, resulting in OR benchmarks that span a range of difficulty. Using the same visual images, we measured neuronal responses in V4 and IT in two monkeys. We implemented 14 unified codes based on those neuronal data and computed cross-validated neuronal discriminability indices (d’s) to compare to the human d’s. The dynamic range across those d’s sets a high bar for when a putative code is sufficient to explain behavior: it is not sufficient for a code to perform well (high d’) or to match one d’. Instead, a sufficient unified code must also emergently predict the entire pattern of behavior over all tasks. Remarkably, we found a few unified IT-based codes that meet this high bar. Interestingly, many other IT codes and all V4 codes are insufficient. While humans outperform computer vision systems on many of our OR tasks, their abilities reliably depend on the images tested. These dependencies in human performance are fully explained by a simple, unified reading of monkey ventral stream neurons, a feat unmatched by any computer vision system we tested.

T-41. Linking physiology and perception in V2

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Area V2 is the largest extrastriate visual area, but its functions remain enigmatic. We used experimental stimuli generated from a hierarchical model of natural image structure (Portilla and Simoncelli, 2000) to differentiate the responses of neurons in V2 from those in V1, and to explore their role in perception. The model has two stages: the first captures local orientation and spatial frequency content with rectified responses of oriented filters, and the second computes correlations between these responses at different orientations, frequencies, and positions, capturing naturalistic features found in visual textures. Starting from original texture images (leaves, fabric, bricks, etc) we computed model responses at both stages, and generated pairs of novel images that produce the same average responses at just the first stage, or both stages. Only the latter contain complex naturalistic features. We measured responses of V1 and V2 neurons in anesthetized macaque to these pairs of synthetic images. In V1, the images within each pair yielded similar single-unit responses, suggesting that they are approximately matched with respect to neural sensitivities in V1. In contrast, firing rates in V2 were reliably higher for the second (naturalistic) image in each pair (64% of single units in V2, compared to 10% in V1). fMRI responses to these image pairs also reliably differentiate V2 from V1 in humans. To relate these differential responses to perception, we asked human observers to discriminate between images drawn from the two ensembles. Strikingly, the texture
categories for which perceptual discrimination is best are those that exhibit the largest differential responses, both in macaque V2 neurons and human fMRI. We conclude that neuronal responses in V2, but not V1, are sensitive to the joint statistics of local structure found in natural images, and may reflect an emerging specialization for these features in the extrastriate visual pathway.

T-42. Visual Coding in the primary visual cortex is enhanced during active navigation

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The sequence of visual stimuli that an animal encounters in nature is largely determined by the animal's navigation through the environment. Yet, responses of visual cortex are typically studied in stationary animals, using pre-defined visual stimuli independent of behavior. Does the visual cortex respond similarly to these stimuli as to stimuli generated by the animal's navigation? We recorded from primary visual cortex (V1) of mice that navigated a virtual environment. Head-fixed mice walked on an air-suspended ball, whose movements were captured to update the visual scene. The environment was a 2.5 m long virtual track with grating and plaid textures on the floors, ceilings and walls. We recorded from 203 V1 neurons in 5 mice using multisite probes (NeuroNexus). Mice traversed the track 20 times, running 88% of the time (average speed 15 cm/s). We compared V1 responses during active navigation of the virtual reality environment with responses to a playback of the same stimuli, unrelated to the mouse's current movements (open-loop). We asked to what degree the following three factors could predict (cross-validated) responses: visual scene (determined by position in the room), visual velocity, and running velocity. During active navigation the latter two are equal. Prediction of responses by both visual scene and velocity was enhanced during active navigation compared to the open-loop condition. During active navigation, responses could be better predicted based on velocity than on visual scene. In the open-loop condition, responses were predicted best by running velocity and least by visual velocity. Responses did not appear to be coding for a simple mismatch between running and visual velocities, but rather depended on both running speed and visual speed. These observations suggest that primary visual cortex contains mechanisms that are specialized to process the information that arises from active navigation.

T-43. Linear and non-linear receptive fields for optimal disparity estimation in natural stereo-images

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Many animals make use of the disparities between the images in the two eyes to judge distance, depth, and shape. Despite vast neurophysiological, psychophysical, and computational literatures on disparity processing there is no formal theory for how disparities should be estimated (i.e. how to solve the correspondence problem). The absence of such a theory makes it difficult to interpret response properties of binocular neurons and behavioral performance in disparity estimation and discrimination tasks. Here, we present a formal theory of optimal disparity estimation in natural scenes. Using a set of natural scenes, a model of the human vision system's optics and photoreceptors, and Bayesian statistical methods, we determine the binocular receptive fields (filters)
that maximize accuracy in disparity estimation. These linear filters bear strong similarities to the widely reported receptive fields of binocular simple cells in primate and cat. The theory also specifies how the filter responses should be combined to obtain nonlinear filters that encode the posterior probabilities of particular disparities. The combination rules are biologically plausible, and the tuning characteristics of the resulting nonlinear filters are similar to those of binocular complex cells in primate visual cortex. Optimal estimation performance (based on appropriate weighted summation of the nonlinear filter responses) parallels human psychophysical performance. Additionally, the optimal estimation performance shows modest but systematic improvements over current computational accounts of disparity estimation. Thus, on the basis of an analysis of the information available at the level of the photoreceptors, we improve upon existing computational methods, and provide a normative account of a range of established neurophysiological and psychophysical findings.

I-1. Kinematic limitations to texture discrimination by whiskers

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Rodents discriminate texture with a sensitivity which rivals that of human touch by moving their whiskers across surfaces, despite the sparsity of contact points. The mechanisms underlying this perceptual feat are not well understood, and its reliability has not been thoroughly investigated. Therefore, we studied the physical limits set by the mechanical properties of the whisker to discriminate textures. To this end we use high-speed videography to track the vibrations of different whiskers while sandpaper of different grades is moved across them under naturalistic conditions. Whisker motion is analysed with respect to high-speed events which have been suggested previously to be prominent features of texture-induced vibrations. A physically realistic model of the whisker, combining both its mechanical properties and features from the stimulus, is subsequently used to model the response at the base of the whisker. Based on an ideal observer model, we can predict the rodent psychophysical response curve for the texture discrimination tasks. This curve reflects the sensory properties of whiskers and their ability to distinguish textures. In the absence of further sensory processing, this curve sets an upper limit to rodents’ behavioural performance. We can use our approach to directly compare our whisker biomechanical data to published behavioural experiments (Morita et al. 2011). Our results are based on measurements from 6 different whiskers from mice (C57BL/6) and show that the raw whisker response cannot account for the observed performance, suggesting active motor-control by the mouse to improve sensory acuity. Control experiments on rat whiskers are currently under way to avoid trans-species comparison. This is to our knowledge the first study thoroughly investigating the quality of whiskers as texture sensors and provides a baseline against which the behavioural acuity of rodents can be compared in order to e.g. assess the effectiveness of neural computations in the barrel cortex.

I-2. Fast encoding model estimation via expected log-likelihoods

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Receptive fields are critical to our understanding of neuronal tuning properties and are traditionally measured using the spike-triggered average (STA). Recent work has shown that the STA is a special case of a family of estimators derived from the "expected log-likelihood" of a Poisson model (Park and Pillow, 2011; Paninski, 2003). We generalize these results to the broad class of neuronal response models known as generalized linear models (GLM), and develop fast iterative methods for including spike-history and interneuronal interaction effects. The basic idea is that the GLM log-likelihood may be written as a large sum over all observed stimuli. This sum
can often be well approximated by an expectation. This expectation, in turn, can often be computed analytically, drastically reducing the computational complexity of GLM estimation. For example, in the Poisson setting, the expected log-likelihood can be expressed as a simple quadratic function in some cases, leading to a surprisingly simple linear optimal estimator. We discuss a number of applications of this basic idea. First, we show that MAP estimation of the GLM parameters can be sped up by orders of magnitude under some simple conditions on the priors and likelihoods involved. Second, we perform a risk analysis, using both analytic and numerical methods, and show that the “expected log-likelihood” estimators come with a minimal cost in accuracy (and in some cases even improved accuracy) compared to standard MAP estimates. Third, we find that these methods can significantly decrease the computation time of marginal likelihood calculations for model selection and of Markov chain Monte Carlo methods for sampling from the posterior parameter distribution. We use the multi-unit, primate retinal responses to stimuli with naturalistic correlation to validate our findings.

I-3. Unconstrained Gaussian mixture models: the best models for natural image statistics?

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Modeling the statistics of natural image patches has been of great interest in recent years. Such models may shed light on many of the problems encountered in vision, neuroscience and image processing. While many of these models differ in their motivation, learning, and statistical structure they have much in common. In a recent work we have observed that a simple Gaussian Mixture Model (GMM) learned from natural image patches is able to outperform several current models of natural images both in log likelihood and image restoration performance. This is indeed a surprising result! These results motivate several questions: How does the GMM model compare to cutting edge models of natural image patches? What makes the GMM model such a good performer? What kind of constraints or properties in the other models hinders their performance? We train an unconstrained GMM with zero means and full covariance matrices on a set of natural image patches. We learn both 8x8 and 16x16 models, with a varying number of mixture components, ranging from 1 to several hundreds. Likelihood increases with the number of components, but seems to converge at a couple of hundreds. We show that the resulting model (with ~200 components) is able to outperform current models in terms of likelihood. The resulting model has zero means and full rank covariances which capture interesting properties of natural images such as textures, oriented textures, texture boundaries and edges. We suggest that this model can be related to structured sparse coding and to mixtures of elliptical contour distributions.

I-4. Biophysically accurate inhibitory interneuron properties in a sparse coding network

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While theoretical models based on the efficient coding of natural scene statistics can account for some aspects of biological sensory systems (e.g., receptive field structure, non-classical response properties), these models are rarely expressed in terms of biophysically realistic mechanisms. In particular, these types of models often implement excitation and inhibition in the same model neuron, and the unique properties of inhibitory interneu-
I-5. Sparse coding model of binocular receptive field development reproduces changes in abnormal rearing

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Some of the best evidence for the importance of sensory input in the development of receptive fields in the visual system comes from the effect of abnormal rearing conditions. For example, stripe-reared (Stryker et al., 1978), strabismic (Hubel & Wiesel, 1965) or partially monocularly reared animals (Mitchell et al., 2006, 2009) all develop markedly different receptive fields to those of conventionally reared subjects. By contrast, most modelling of the unsupervised development of receptive fields has characterised normal development. Here, we examine the capacity of one of the more powerful approaches to unsupervised development, sparse coding (Olshausen & Field, 1996), to account for the effects of abnormal visual input under 6 different rearing conditions. A number of abnormal rearing conditions involve differing manipulations to each eye, however, most existing sparse coding models of receptive field development have considered only monocular receptive fields for simplicity. We extend this work to consider binocular receptive fields. In addition to allowing comparison with abnormal rearing conditions, this exposes some important changes in representation due to binocular receptive fields. In particular, asymmetries in inter-ocular correlation between orientations leads to orientation-specific receptive field properties. We find that sparse coding models retrodict the qualitative changes in receptive fields found in abnormally reared animals for all six modified rearing conditions considered. This reinforces the validity of sparsity as a principle of early sensory coding and provides evidence that V1 receptive fields are, at least in part, optimised during development. Additionally, in agreement with predictions of Li and Atick (1994), we find that vertically oriented neurons develop with decreased binocularity compared to horizontal orientations.
I-6. Analysing fixations using latent Gaussian fields

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Although eye movements are often described as arising from one of the simplest decision mechanisms, they sometimes reflect fairly sophisticated behaviour and are not trivial to predict (Schutz et al., 2011). One important aspect of eye movement sequences is naturally fixation locations—i.e., where people choose to look. Several factors are often at work, because where people look will depend on what information they need, on what the stimulus is, but also on things less directly relevant to the analysis: for example, the common bias for central locations (Tatler and Vincent, 2009). To understand the strategies at work, one must be able to somehow separate these different factors. We formulate a framework based on techniques borrowed from Functional Data Analysis (Ramsay and Silverman, 2005) and Spatial Statistics (Moller et al., 1998). We use Latent Gaussian Fields to describe conditional fixation distributions, adapting the Logistic Gaussian Process of Lenk (1988). To introduce some regularity we assume that fixation distributions do not vary completely freely but are functions of some known variables, based on the stimulus or on trial history. The use of log-additive decompositions lets one separate out the various factors at work. We show that our framework is extremely useful for the analysis of saliency in natural images. It is customary to analyse the role of low-level saliency by focusing on the properties of regions that are empirically salient, i.e. regions that subjects often look at. However, we know that people tend to fixate the same locations regardless of what the image is, and make small saccades rather than large ones. The implication is that not all fixations signal the same level of intrinsic saliency. Using a dataset collected by Kienzle et al. (2009), we illustrate how intrinsic saliency can be inferred using our framework.

I-7. Semantic organization of a neural population codebook and accurate decoding using a neural thesaurus

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Noise in neural circuits, from synaptic unreliability to variable responses of neurons to repeated stimuli, determines how neural populations encode information. The noisy nature of the code implies that to decode neural population activity patterns we must understand which activity patterns are similar and which are different—in terms of the information they carry. This is especially important for decoding responses of large populations since the number of potential activity patterns is exponentially large, and most patterns are rarely seen. To characterize the “semantic” organization of the codebook of large neural populations, we learned a “thesaurus” for the responses of a neural population. We defined the similarity of population activity patterns (words) $R_i$ and $R_j$, as the similarity of the distributions over stimuli that may elicit them, $P(S|R_i)$ and $P(S|R_j)$. These distributions were estimated using Bayes’ rule from the encoding dictionaries, $P(R|S)$, which were inferred from repeated presentations of a large set of stimuli. We learned the similarity between code-words of large groups of retinal ganglion cells, presented repeatedly with artificial and naturalistic movies. Because of strong “noise correlations” in large populations, and to overcome sampling issues, we used maximum entropy models for $P(R|S)$. We found that the population codebook is organized in clear clusters of words with similar meanings. Importantly, the codebook organization...
I-8. Internal model estimation for feedback control in brain-computer interfaces

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The motor system effortlessly plans and executes sophisticated movements despite sensory feedback delays and non-stationary motor plant dynamics. Behavioral studies suggest that internal models of the plant are central to motor control, but neurophysiological evidence of such models has been limited. We developed a probabilistic framework for extracting a subject’s internal forward model of the motor plant from recorded neural activity. We applied our framework to brain-computer interface (BCI) experiments, where a rhesus monkey acquired visual targets with a BCI cursor. Cursor velocity was linearly decoded from spike counts recorded with a 96-electrode Utah array implanted in motor cortex. Using only the recorded neural activity, visual feedback, and target locations, we extracted the subject’s internal forward model and its predictions—the subject’s internal estimates of the cursor position at each 30ms decoder time step. Inferred internal state estimates reveal that the subject often believed the BCI cursor was moving straight to the target, even when the actual cursor did not. Across 20 BCI experiments, these models explain roughly 50% of angular errors between cursor movement direction and cursor-to-target direction. BCI is an attractive paradigm for investigating motor control because it provides experimenters the opportunity to monitor activity of all neurons that drive the prosthetic plant, to define plant dynamics as linear and low-dimensional, to observe all relevant sensory feedback, and to design task goals. While we are also interested in developing assistive BCI systems, our immediate goal is developing a statistical framework for basic scientific studies of the neural basis of motor control and learning. By enabling quantitative identification of internal models and comparison of identified models at multiple time points, we expect to gain insight into the neural mechanisms that drive internal model formation and adaptation.

I-9. Circuit- and systems-level contributions to successful memory retrieval in the hippocampus

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Two critical problems plague neural implementations of recurrent auto-associative memory networks, such as area CA3 of the hippocampus. First, as stressed by Fusi et al (2005), synapses only have limited dynamic ranges. Memory thus has a palimpsest character, with traces degrading as new patterns are stored. Second, synapses sharing pre- or post-synaptic partners are significantly correlated (Song et al., 2005). This oft-ignored fact severely complicates recall, as the information stored in a synapse can only be interpreted correctly in light of the strengths of other synapses to the same neuron. Here, we suggest systems- and circuit-level solutions to these problems in the context of the hippocampus. First, since traces degrade over time, pattern age needs to be considered for successful recall. Age is a form of unfamiliarity, a quantity that is known to be reflected in the
activity of a subpopulation of perirhinal neurons. We show that a dual system, combining the hippocampus (for recollection) and perirhinal cortex (for familiarity) can provide an efficient solution for this problem (Savin et al., 2011). Second, at the circuit level, (approximately) optimal retrieval dynamics predict a close link between CA3 synaptic plasticity and homeostatic mechanisms reported in this region (Zhang & Linden, 2003), and stabilization from feedback inhibition. Homeostatic mechanisms also compensate for the inter-synaptic correlations. Overall, our results provide an unifying view of various aspects of hippocampal circuitry, offering high-level solutions for synapse-level concerns.

I-10. How plastic is the “slow speeds prior”?

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Perception is commonly viewed as a form of Bayesian inference, where noisy or ambiguous sensory evidence (“likelihood”) is combined with expectations (“prior”) about the world. A well-known example of such prior is that our visual system expects that objects are static or move slowly rather than quickly. This “slow speed” prior was postulated because it could elegantly explain a number of perceptual biases. Interestingly, those biases affect not only the perception of speed but also the direction of motion. For example, the direction of a line whose endpoints are hidden (as in the “aperture problem”) or poorly visible is more often perceived as being perpendicular to the line than it really is—an illusion consistent with expecting that the line moves more slowly than it really does. Is this prior rigid or plastic? We asked two groups of subjects to report the direction of a field of parallel lines that moved either perpendicularly or obliquely to their orientation, as we varied stimulus contrast and duration. One group was exposed, during a “training” phase, to high speeds (8 deg/s), the other to lower speeds (4 deg/s) and the experiment was conducted over 5 sessions on consecutive days. Consistent with previous studies, initial perception of motion direction was biased towards perpendicular judgments at low contrast for both groups. However, for the high-speed group, the initial bias gradually diminished until the illusion reversed and direction was most often perceived as being oblique. This suggests that systematic exposure to high-speed stimuli can change the prior towards favouring higher speeds. Our results can be accounted for by the Bayesian model of Weiss et al (2002), when extended to allow the speed prior to have a nonzero mean. In the best-fit model, the mean increases approximately linearly across experimental sessions.

I-11. Hamiltonian Monte Carlo sampling and oscillatory activity in V1

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Bayesian computations have been implicated in a range of cognitive phenomena but their neural underpinning remains unknown. In order for the brain to implement Bayesian inference it needs to represent probability distributions over features of the environment. One way to achieve such a representation is to use a temporal sequence of activities in a network of neurons to represent stochastic samples from the distributions (Fiser et al, 2010). While this approach can account for a wide range of stimulus-dependent changes in neural response variability and co-variability in the visual cortex (Orban & Lengyel, 2011), it has been incomplete at least in two aspects. First, it accounted only for variability across trials and over long time scales (>50ms), and second it left the key imple-
mentational level question unanswered: what kind of neural circuit dynamics may be able to implement sampling? Here, we investigate a form of neural dynamics that can generate samples from probability distributions that are appropriate for V1 (Schwartz & Simoncelli, 2001). These dynamics amount to a deterministic approximation to a class of stochastic sampling schemes, Hamiltonian Monte Carlo (Neal, 1996), and are readily implementable by standard E-I networks (Wilson & Cohen, 1972). We demonstrate that these deterministic dynamics can effectively approximate stochastic sampling on time scales relevant to neural computations and give a functional interpretation to inhibitory interneurons as representing useful “auxiliary” variables to speed up the convergence (in distribution) of the sampler. The model accounts for several short-time scale physiological phenomena, including the time scale of decorrelation of membrane potential traces and the increased dominance of high-frequency oscillations during evoked compared to spontaneous activity. Our results also suggest that particular forms of neural synchrony may simply be signatures of sampling from special cases of noise correlations and modeled within the same framework.

I-12. Sparse and expansive representations in network models of associative memory

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Several brain areas exhibit expansive transformation of signals in which the downstream population is much larger than the number of incoming axons. Often, these transformations result in a neural overcomplete and sparse representation. Examples are visual representations in V1, granule cell layer in cerebellum, and odor coding in piriform cortex. Dimensionality expansion enhances the memory capacity and facilitates classification of activity patterns by downstream readouts. ICA theories (Olshausen and Field, 1996; Bell and Sejnowski, 1997) and Compressed Sensing theories (Bruckstein et al., 2009; Coulter et al., 2010) have highlighted the advantage of sparse representations of inherently sparse signals. However, the computational advantage of sparseness in cases where the represented signals are dense is unclear. Here we address this issue by analytical and numerical investigations of a feedforward associative memory network containing an intermediate layer with sparse neuronal activity (Baum et al., 1988; Kanerva, 1988). Weights are learnt by versions of Hebb rules. We ask: (1) is sparseness advantageous even when the memory representations at the input and output layer are dense? (2) how does the functionality of sparse representation depend on the pattern of synaptic projections from the input layer? To answer these questions, we evaluate the role of dimensionality expansion and sparseness in memory capacity and pattern completion. Our theory shows that capacity is increased with increasing size of hidden layer. Pattern completion or error correction in the memory recall are controlled by the degree of sparsity (fraction of active neurons) in the intermediate layer, with best error correction achieved at limit of low sparsity. Importantly, sparse coding is not beneficial if synaptic projections are random. Incorporating Hebbian recurrent connections is studied. Our theory delineates the respective computational benefits of dimensionality expansion and sparse coding in neural memory systems. Implications for odor coding in piriform cortex are discussed.

I-13. A computational role for noise in the cortex

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Spike trains in the cortex are noisy, irregular and asynchronous (Shadlen and Newsome, 1998). Although the dynamical mechanisms responsible for generating this noise are known, what is not known is why it's there. We
show here that it makes at least one computation—orientation selectivity—robust. Dynamic balancing of strong excitatory and inhibitory synaptic input has been identified as the predominant source of spike train noise (van Vreeswijk and Sompolinsky, 1996). This balancing is dynamically robust, shielding cortical networks from pathological network dynamics in which neurons never spike or spike incessantly. Accurate tracking of cortical input and temporal differentiation have been proposed as computations that exploit balanced network dynamics (van Vreeswijk and Sompolinsky, 1996; Barrett and Latham, 2011). However, noise is an undesirable property in those computations, and would seem to be an undesirable property in many others. We investigate the computational role of cortical noise by quantifying the ability of a balanced network to perform orientation selectivity - a simple computation in which the orientation of a visual stimulus is estimated from network activity. We do this analytically by calculating linear Fisher Information (Barrett and Latham, 2010). We find that information (averaged over stimulus contrast) is largest when a network is balanced. This result is surprising because we would expect noise associated with balanced networks to reduce information. Indeed, it does, but across only a narrow range of contrasts. This exemplifies a performance-stability trade-off: the cost of high performance is a lower operating range. The trade-off arises because while dynamic balance adds noise, it also maintains the network in a highly informative state. It thus provides computational stability, just as it provides dynamic stability. Furthermore, we find, at least in our model, that the contrast invariance of orientation tuned cells is a signature of this computational stability.

I-14. Quadratic networks for invariant perceptual discrimination

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Many perceptual tasks require fine discrimination between similar stimuli in the presence of nuisance, or hidden, parameters. An example is a 2AFC between an oriented bar presented at an angle $\theta$, and a similar bar rotated clockwise or anti-clockwise (at an angle $\theta \pm \delta \theta$). Importantly, the angle $\theta$ varies from trial to trial, so that the discrimination must be invariant to $\theta$. It has long been realized that a single layer neural network, which linearly weights incoming spikes from sensory neurons, inevitably fails for some values of $\theta$. Thus, single layer networks are unsuitable for discrimination that involves invariance to a hidden variable. Previous work has shown that training a two-layer perceptron network resulted in suboptimal performance even in the limit of a large hidden layer. Thus, it remained unknown what is the minimal neural architecture required for performing such a task in a Bayes-optimal manner. We consider a decoder that generates decisions by thresholding a quadratic function of input spike counts. We prove that (1) surprisingly, with suitable choice of parameters, the quadratic decoder performs optimally on the orientation task; (2) the result extends readily to an arbitrary discrimination task between similar stimuli, with invariance to one or more hidden variables, and; (3) Bayes-optimality is achieved if the number of possible independent values of the hidden variable is not greater than the number of sensory neurons. In addition, we show that a two-layer feed-forward perceptron network can compute the quadratic based decision to arbitrary precision, and close to optimal performance can be achieved with remarkably small number of hidden units. Taken together, these results provide constructive proof that a simple neural architecture can perform complex nonlinear invariant discrimination tasks in a Bayes-optimal manner. We consider several applications, including motion detection in a patch of a natural visual scene.
I-15. Significance of graph theoretic measures in predicting neuronal network activity

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One of the most prominent patterns of activity observed in developing cortical neuronal networks in vitro is network-wide spontaneous bursting (Wagenaar et al. 2005). In this work, we study computationally the spontaneous emergence of bursts and the effect of network structure on burst shape and frequency. Recent computational structure-function approaches show the effect of, e.g., second-order connections (Zhao et al. 2011) and degree distribution widths (Roxin 2011) on activity patterns. We aim to study a wider set of graph-theoretical measures using networks with identical in-degree distributions. We apply a biophysically plausible point-neuron model of a cortical cell (Golomb et al. 2006). The model network consists of a small (N=100) number of neurons, both excitatory pyramidal neurons and inhibitory interneurons. A model of short-term depression (Golomb and Amitai 1997) is used for glutamatergic synapses. The activity simulation is run over a wide set of classes of network structure. To quantify the structure of the network, we consider graph theoretical measures such as clustering coefficient, geodesic path length, node-betweenness and occurrence of different motifs. We restrict to unweighted bidirectional graph representation, hence the synaptic weights between the neurons are uniform. We study the significance of different graph theoretic measures using a prediction framework: How well can a bursting property, such as burst duration or frequency, be estimated using various measures of structure as attributes? We show that the prediction of bursting properties is improved by taking one or more of the aforementioned measures as prediction attributes. It is best improved when the prediction is based on the clustering coefficient or occurrence of the most highly connected motifs. We confirm the results using a noise-driven LIF model with short-term depression (Tsodyks et al. 2000). We conclude that the significance of measures of clustering is prominent compared to other measures of structure.

I-16. Sequences and the emergence of continuous attractor networks

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It has been long hypothesized that both spatial navigation in hippocampo-entorhinal circuits and parametric working memory in various cortices are the product of a continuous attractor structure in the underlying recurrent networks. Continuous attractor networks are recurrent networks whose patterns of synaptic efficacies depend on the distances between neurons in some “feature space.” In such networks, neurons preferentially excite others having similar coding properties, such as overlapping receptive fields. The resulting “bump” attractors are sub-populations of neurons that respond to similar stimuli. While this model explains many experimentally observed features of neural activity, there is little direct evidence for or against such a synaptic organization. Moreover, a plausible mechanism for the creation and maintenance of continuous attractor networks is not well-understood. In contrast, robust sequences of neuronal activation have been experimentally observed in hippocampus and several neocortical areas. We suggest a simple mechanism by which robust sequences of neuronal activation, such as those observed during hippocampal sharp waves, can lead to the formation of continuous attractor networks. We have found that, in the presence of a natural Hebbian learning rule, a pair of short temporal sequences leads to a pattern of synaptic weights that is characteristic of continuous attractor networks. Moreover, the resulting network exhibits 2-dimensional “bump” attractor dynamics. This behavior also emerges for networks that are formed from many sequences, with bump attractors evident in 2-dimensional slices of a higher-dimensional
organization of neurons. Remarkably, the resulting bump attractor dynamics reinforce the established pattern of synaptic weights. We propose that robust sequences of neural activity and continuous attractor networks are not only compatible, but may be a part of the same mechanism as they mutually reinforce each other.

**I-17. Short-Term Memory Capacity in Recurrent Networks via Compressed Sensing**

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Characterizing the memory capacity of neural circuits is vital to understanding the performance of tasks such as working memory. In particular, critical questions recently raised in the literature include the effects of network size, connectivity pattern and natural signal statistics on the ability of a neural circuit to encode temporal memories in transient dynamics. Recently, results from compressive sensing (CS) have indicated that the memory capacity of a linear neural circuit could exceed the number of neurons when the temporal signals are sparse (i.e., having few non-zeros) [White et al., 2004, Ganguli and Sompolinsky, 2010]. In this work we perform a full CS analysis of the memory capacity of a neural circuit for general inputs that have sparse coefficients in a known basis (a model for many natural signals [Olshausen and Field, 1996]). Using a model similar to [Ganguli and Sompolinsky, 2010], our results 1) provide signal recovery guarantees for the exact linear network dynamics with no approximations; 2) provide guarantees for every temporal sequence sparse in any basis (not average performance), where the characteristics of the basis have well-defined effects; and 3) quantify the dependence of the memory capacity on properties of the neural connectivity pattern. Our analyses (based on the restricted isometry property [Candes, 2006]) demonstrate that the memory capacity can far exceed the number of neurons, and illustrate the magnitude of this excess in two distinct cases: 1) the perfect recovery of finite-length signals that are within the capacity of the circuit, and 2) the recovery error for signals that are beyond the capacity of the circuit (possibly infinitely long), with an exponential forgetting factor in the circuit. These results point to the existence of an optimal signal length (for a given network) that minimizes the joint recovery error due to un-recalled signal and recall errors.

**I-18. Norepinephrine, neural gain, and “first one wins” network dynamics**

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Norepinephrine is thought to increase neural gain (i.e. responsivity to input). We use neural network simulations to show that high neural gain causes network output to reflect only the earliest-processed aspect of the input, and prevent a slower convergence process that integrates multiple aspects of the input. For instance, consider the stimulus “C[]T”. The global resemblance of the stimulus to the word CAT favors perception of the middle letter as an A, whereas the actual shape of the middle letter favors perception of an H. With low neural gain the network integrates these two conflicting aspects and outputs A and H with similar probabilities. In contrast, with high gain the output mainly reflects the shape of the middle letter, which is processed more quickly than the global pattern, and thus the network “perceives” an H. This effect can be inverted if prior attention is directed to the word CAT, in which case the word representation is active first, and thus, high neural gain biases the network towards the letter that completes the word (A). We present experimental evidence that supports our theory. We designed 52 letter-
morphs (such as []) and placed each one in a letter string so that it may complete a word depending on the letter that is perceived. Subjects were asked to report which letter they saw while we recorded their pupillary dilation, an inverse measure of norepinephrine activity. In accordance with the simulation results, mean pupil response was positively correlated across subjects with perception of the letter that completes the word. Furthermore, when prior attention was directed to the word through priming (e.g. by showing a semantically related word such as DOG immediately before C][T), we found the inverted result. Namely, mean pupillary dilation was negatively correlated with word completion.


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Neural networks in various brain areas exhibit both recurrent and feedforward organization. It has often been observed that many of the functions attributed to recurrent networks can in fact also be accomplished by networks with strictly feedforward architecture. This raises a natural question: what functions of recurrent networks can not be accomplished by feedforward ones? We address this question by examining the coding properties of networks. For a given network, the (combinatorial) neural code consists of all subsets of neurons that can stably co-fire in response to an external input. Given a neural code (i.e., a set of neural activity patterns), there are natural topological invariants that can be computed from the code’s combinatorial structure. It has previously been shown that these invariants match topological features of the represented stimulus space if the neurons have convex receptive fields (Curto & Itskov, 2008). These invariants thus capture meaningful properties of the stimuli being represented by the network. Remarkably, we find that neural codes of recurrent networks are capable of realizing any topological type (homotopy type), whereas two-layer feedforward networks can only generate neural codes with highly restricted topology. In particular, neural codes of excitatory two-layer feedforward networks correspond to stimulus spaces that are topologically trivial (contractible), with all topological invariants vanishing. We conclude that recurrent networks may be necessary for representing stimulus spaces that do not have these highly restricted topologies.

I-20. Diffusion of nodal sodium channels can restore function in multiple sclerosis

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Long-range communication in the CNS and PNS is mediated by myelinated axons. We are interested in the engineering design principles of this wiring. In multiple sclerosis these axons demyelinate, which increases the attenuation of action potentials (APs) between Nodes of Ranvier, leading to propagation failure. In healthy myelinated axons, thousands of Nav1.6 channels cluster at the nodes of Ranvier were they regenerated APs. In a similar manner, almost all K+ ion channels are mechanically attached to the nodal or paranodal regions of the axon, to stabilise the resting potential. However, during demyelination, K+ channels lose their attachment, diffusing freely along the membrane of the demyelinated region, whereas Nav1.6 channel remain constrained to the nodes of Ranvier. Once the K+ channels diffuse away, the membrane potential cannot be sufficiently stabilised by leak conductances and Na+ channel noise produces a persistent subthreshold depolarisation (consistent data (Waxman (2006)) - which increases resting metabolic cost of these axons. We predict that if Nav1.6 channels were free to diffuse along the demyelinated axon, their positive feedback could help decrease the effects of de-
myelination and re-establish AP propagation. To test this hypothesis, we simulate a stochastic model, based on experimental data from mammalian PNS. The healthy axon models reliably conducts APs. We simulate multiple sclerosis by increasing gradually the capacitance and leak conductance of one internode. The axon increasingly fails to conduct action potentials, reproducing the predicted pathology. Finally, we allow Na+ channels to diffuse from one node along the demyelinated internode. The axon is once again able to propagate action potentials, suggesting pharmacological disruption of Na+ channel anchors as a possible drug target. We hypothesise that this effect relies on the stochasticity of Na+ channels that allows the axon to fire despite the very low channel density when diffused across the membrane.

I-21. Perceptual grouping and figure-ground segregation arising from short-term plasticity in a spiking network

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The segmentation of visual scenes is a fundamental process of early vision, but the underlying neural mechanisms are still unclear. Both theory and neurophysiology data point to the importance of temporal correlations in neural activity. Here we extend previous work on a mean firing rate model of figure-ground segregation (Sporns et al., PNAS 88:129-33), and develop an equivalent spiking network that displays similar behaviors. This network has dense local excitatory connections between motion-responsive neuronal units arranged in a retinotopic array. Synapses in the network are modified by both long-term spike-timing dependent plasticity and by a model of short-term changes in synaptic efficacy. The network is presented with a visual stimulus of waffle-like texture elements, where some of these elements move coherently together and in anti-phase to the rest. In humans, this stimulus produces the perception of a diamond shaped figure oscillating against a textured background. In our model, temporal correlations between spike trains of neurons whose receptive fields cover figure elements enable the grouping together of those elements into a perceptual whole. Short-term synaptic plasticity is shown to be critical for the development of such temporal correlations.

I-22. The multi-class tempotron: a neuron model for processing of sensory streams

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Neurons operate in continuous time. To understand how neurons transform high-dimensional streams of input spikes into continuous sequences of output spikes is a central challenge of neuroscience. Recently, spike-based computational studies of neuronal systems function have advanced through the tempotron family of supervised learning rules. However, because of its binary decision rule (spike vs. ~no spike) the applicability of the tempotron to neuronal processing has remained of limited scope. Here we introduce a new principle that generalizes the tempotron from a binary to a multi-class decision rule, allowing for any number of output spikes to be set as the desired response. We analytically compute the resulting gradient descent learning rule for a leaky integrate and fire neuron with reset. To test the multi-class tempotron we mimic streams of sensory features by randomly concatenating segments of frozen Poisson spike trains drawn with replacement from a fixed pool. The tempotron can quickly learn to report the presence of a specific target feature within such sequences. Note that this is accomplished by only providing the number of occurrences of the target feature in each training trial. No temporal information is given. In an even more difficult task, we use a weighted linear sum of the frequencies of multiple target features as desired output. Astonishingly, the neuron readily performs a regression and starts signaling each of the targets with the appropriate number of spikes. Using these principles, we have successfully trained...
neurons to report with high fidelity spoken digits within connected speech. Also here no segmentation of the training data was required. The multi-class tempotron is an important generalization of the original model and strongly boosts its applicability to spiking models of neuronal systems including sensory processing streams, spike count modulated tuning curves and multi-layer networks.

I-23. Biologically plausible learning of sparse-coding dictionary in a neural network

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Many natural signals can be represented as linear combinations of a few feature vectors chosen from an over-complete dictionary (Olshausen & Field, 1996, 1997). Such sparse representation strategy is likely used in the brain because neuronal activity is often sparse (DeWeese & Zador, 2006, Lewicki, 2002). Moreover, training a sparse-coding network on natural images by updating synaptic weights using a local Hebbian-like results in feature vectors similar to receptive fields of V1 neurons (Olshausen & Field, 1997). However, existing models of dictionary learning (Olshausen & Field, 1997; Mairal et al., 2010) activate a learning rule only after the network activity converges to a sparse representation. Such learning paradigm seems biologically implausible because it would be difficult for synapses to know when the transient period of activity ends and a sparse representation is found. This becomes particularly problematic for sensory systems, which face continuously varying stimuli rather than static stimulus presentations. Here, we considered a biologically realistic learning paradigm where synaptic update proceeds simultaneously with the transient neural activity. Specifically, we modeled dictionary learning in the reciprocal neural network by alternating activity updates with the local Hebbian-like update of synaptic weights, which was derived from stochastic gradient descent. Activity updates combine the gradient step and linear-thresholding step reminiscent of biological neuron response function (Yin et al., 2008), which is needed because of the non-differentiability of the L1 norm. Simulating the network activity in response to prewhitened natural image patches, we find feature vectors similar to receptive fields of simple cells in V1. Therefore, a sparse-coding dictionary can be learned in a reciprocal neural network, in a biologically plausible manner with a Hebbian-like learning rule operating continuously in time. Our result support sparse representations as a model of neural computation in the brain.

I-24. Embodied Exploration

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Computational modeling of exploration has largely focused on its role in the acquisition of external rewards. In contrast, the field of Psychology, through studies of human and animal behavior, has emphasized that exploration is largely driven towards learning as a primary objective and is not secondary to external reinforcement. We have developed an information theoretic model of learning-driven exploration in Controllable Markov Chains (CMCs). CMCs are discrete, stochastic systems in which state-transitions depend both on the current state and on a control variable set by an active agent. Through Bayesian inference we demonstrate here: 1) How an agent can best model the inherent dynamics of its world from previously collected data alone and 2) How an agent can predict the amount of information a future observation will carry towards improving its internal model. The ability to predict such future information gain allows an agent to guide its exploration of the world yielding efficient learning. An
innate tendency in humans and animals to seek out information may have been selected for during evolution by the generalized utility such information offers the organism towards accomplishing arbitrary tasks. Accordingly, in CMCs, we show that efficient explorers are better able to use their learned world models to accomplish a range of goal-directed tasks. While our framework is derived for discrete systems, we demonstrate that they can be applied to modeling continuous systems such as manipulation of a weighted pendulum. Revealing how action strategies shape the flow of information over time provides a new dimension to the study of active learning. It has applications in the design of autonomously learning robots and brings insight to an array of human behaviors. We conclude by offering preliminary results extending our work to the problem of predicting human gaze attention.

I-25. Critical exponents derived for neuronal avalanches in alert non-human primate

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The theory of criticality provides important insights into the organization of complex systems. Experimental and theoretical advances in the study of neuronal avalanches (Beggs and Plenz, 2003; Petermann et al., 2009) suggest that the cortex operates at criticality. These conclusions are based on power laws that govern avalanche dynamics and optimization principles found experimentally in line with predictions for critical dynamics (Shew et al, 2009, 2011). However, a clear proof of criticality includes the demonstration of typical critical behaviors, i.e. divergence of specific heat, C, and susceptibility, chi, the phase transition of an order parameter, M, and the characterization of critical exponents, based on which critical dynamics can be categorized into different universality classes. Here, we examined critical behaviors and derived critical exponents for the first time for neuronal avalanches. Neuronal avalanche dynamics were identified based on ongoing local field potential activity in premotor cortex from two alert macaque monkeys during rest. The probability of avalanche patterns was analyzed to identify the critical thermodynamic temperature, Tc, under which the system reaches criticality. To this end, we used the single histogram method (Ferrenberg and Swendsen, 1988; Tkacik et al., 2009) to infer the system's behavior at various temperatures. We found that the temperature T0, under which the actual recordings were taken, was very close to Tc. Near T0, C and chi diverged, i.e. exhibited peaks with unbounded increase in amplitudes when system size increased, and M went through a phase transition. Using finite size scaling, we computed several critical exponents, including alpha, beta and gamma, which were consistent with Rushbrooke's law: $\alpha + 2\beta + \gamma = 2$. Our results provide strong evidence that neuronal avalanches are a signature of cortical dynamics at criticality, and potential explanation for recent experimental findings that the brain is extremely sensitive to small external perturbations (Houweling and Brecht, 2008).

I-26. Functional Connectivity of the Neural Integrator in Larval Zebrafish

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The oculomotor integrator generates eye position signals by integrating, in the sense of calculus, velocity inputs from the saccadic, optokinetic and vestibular systems. Most models propose that integration results from network interactions, the pattern of which remains unknown. Here we use two-photon calcium imaging to measure
the dynamics of integrator neuron activity and infer functional network connectivity. We first find that following saccades, the network's population activity (as assessed by the singular value decomposition) contains three significant modes, which can be explained by a connectivity matrix containing as few as three non-zero eigenvalues. We next compared this activity pattern to that following a constant-velocity optokinetic ramp, and found that the activity patterns generated during these two behaviors occupied significantly different volumes of state space. Specifically, following saccades, the most persistent cells were located at the most medial, ventral, and caudal positions, whereas following optokinetic stimulation, the most persistent cells were located at the most medial, ventral, and rostral positions. In addition, cells with larger spontaneous responses following saccades were in more rostral positions whereas cells with larger optokinetic responses were located in more caudal positions. Network modeling shows that this reversal of gradients in the rostro-caudal direction is consistent with 1) a pattern of input where the most rostral cells receive stronger saccadic inputs and the most caudal cells receive stronger optokinetic inputs, and 2) a pattern of functional connectivity within the integrator network dominated by localized connections arranged in a symmetric, chain-like organization. Together, these results demonstrate how a single network can use its multiple modes of activity to differentially process inputs arriving along separate pathways.

I-27. Dynamic grouping in neuronal networks by inhibition induced neuronal excitability transitions

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Neurons fall into different neuronal excitability types \cite{1,2}: While type I neurons integrate and support arbitrarily long inter-spike-intervals, type II neurons show resonance and start firing with a non-zero frequency. Here we show that across a large number of conductance-based neuron models (including Wang-Buszaki, Connor-Stevens) an increase in leak conductance induces a transition from type I to type II neuronal excitability. We prove that the bifurcation structure of this transition is organized by a degenerate Bogdanov-Takens-cusp bifurcation point of co-dimension 3 \cite{3} which implies a switch from type I to type II for the spiking dynamics, a transition from integration to resonance near spike threshold, as well as a region of bistability of resting and regular spiking dynamics. We confirm these predictions experimentally for different neurons using dynamic patch clamp recordings to artificially change the leak conductance. Interestingly, the neuronal excitability type can also be switched dynamically via activation of shunting synapses, which we mimicked experimentally by bath application of GABA. These results imply that inhibitory cells can dynamically control the neuronal excitability type of postsynaptic neurons and as a consequence their synchronization properties. In particular, we show both analytically and numerically that inhibition can separately synchronize several coexisting sub-populations of excitatory neurons. Moreover, the maximal amount of synchrony in the network can be efficiently regulated by dynamically forcing the neurons into the region of bistability. In conclusion, inhibition-induced dynamic neuronal excitability switching provides a mechanism for flexible and activity controlled dynamic formation of synchronized neuronal cell assemblies. \cite{1} A. L. Hodgkin, J. Physiol. 107, 165 (1948). \cite{2} E. M. Izhikevich, Dynamical Systems in Neuroscience, MIT Press (2007). \cite{3} F. Dumortier, R. Roussarie, J. Sotomayor, and H. Zoladek. Bifurcations of Planar Vector Fields, Springer (1991).
I-28. Phase coherence of field potentials facilitates prediction of single-trial outcome in a memory task

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The reset of neuronal oscillations has been associated with both short-term memory recall (Rizzuto et al. 2003) and error-related signals (Cavanagh et al. 2009). We investigated this phenomenon using human local-field potential (LFP) data measured during a classic “memory” matching card game. We found that the LFP response differed during correct (matching) and incorrect (non-matching) trials. In many cases, this difference was robust enough to classify new single trials as either correct or incorrect. Moreover, using wavelet analysis, we found that the delta-band phase rivaled the full LFP signal as a classifier. This appears to be possible due to an increase in inter-trial phase coherence after the presentation of the stimulus. While this increase was present during both correct and incorrect trials, we found that the incorrect trials reached maximum coherence later than the correct trials. An analysis of the full wavelet transform results revealed increases in coherence at frequencies up to 8 Hz and increases in power above 30 Hz, although the specific responses varied by brain region and for correct and incorrect trials. Sometimes the increase in coherence appeared to coincide with an increase in power; this may indicate that the increase in coherence is due to an evoked response, rather than phase resetting. To test this, we calculated the correlation between power and coherence over all frequencies during the presentation of the stimulus. We found no significant correlation in the hippocampal delta band or in the delta band of the amygdala during correct trials. This implies that, in these cases, coherence at low frequencies is not due to an evoked oscillation and may be indicative of phase resetting. In general, our study elucidates the importance of low-frequency phase for single trial decoding and examines the possibility of phase resetting as an important mechanism in mesiotemporal lobe function.

I-29. Two modes of phase-amplitude coupling in human cortical electrical dynamics under general anesthesia

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Understanding the role of rhythmic oscillations in the organization of cortical electrical dynamics is a fundamental aim in systems neuroscience. Rhythmic activity across widely separated frequency bands appears closely coordinated during active behavior and in reduced states of consciousness such as sleep or general anesthesia (GA), yet no unified framework for such coordination has emerged. To address this we induced GA using propofol under experimentally controlled conditions in normal human volunteers, while continuously recording cortical activity via 64-channel electroencephalogram (EEG) and monitoring instantaneous level of arousal via a behavioral task. Following loss of consciousness we observed robust phase-amplitude coupling between two low-frequency bands with prominent power spectral peaks (slow oscillation, 0.1–2 Hz; alpha band, 8—14 Hz). This cross-frequency
I-30. Retinal adaptation and invariance to changes in higher-order stimulus statistics

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Adaptation in the retina optimizes the encoding of natural light signals into sequences of spikes sent to the brain. However, adaptation also entails computational costs: adaptive code is intrinsically ambiguous, because output symbols cannot be trivially mapped back to the stimuli without the knowledge of the adaptive state of the encoding neuron. It is thus important to learn which statistical changes in the input do, or don’t, invoke adaptive responses, and ask about the reasons for potential limits to adaptation. To address the issue of retinal adaptation to statistical properties of the light intensity distribution, we first analyze theoretically the adaptation process that would maximize information transfer from the retina to the brain, and find how noisy spiking retinal ganglion cells should change their encoding properties when the stimulus distribution changes. Then we compare the theoretical result to the properties of the salamander retina by measuring experimentally the retinal ganglion cell responses to controlled changes in the second (contrast), third (skew) and fourth moments (kurtosis) of light intensity distributions of spatially uniform temporally independent stimuli. We choose the skew and kurtosis of our stimuli to cover the range observed in natural scenes. We quantify adaptation in the ganglion cells by studying two-dimensional linear-nonlinear models that can capture well the retinal encoding properties across all stimuli. We find that the retinal ganglion cells adapt to contrast, but show remarkably invariant behavior to changes in higher-order statistics. This invariance is demonstrated both by insignificant changes in the inferred linear filters across the skewed / kurtotic stimuli for each cell, as well as the ability of non-adapting models to predict well the firing rate and generalize across stimulus classes. We further show why the neural code can maintain a high information rate despite changes in skew and kurtosis without dynamic adaptation.
I-31. Inhibition in mouse IC affects the rate code but not the timing code when processing vocalizations

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Inhibition is well known to shape responses to sensory stimuli. In the auditory system, it shapes frequency response curves and responses to complex stimuli. Here, we examined how inhibition affects response to vocalizations in mouse inferior colliculus (IC). We studied two cases in awake mice: normal auditory processing (control) and auditory processing after pharmacological blocks of inhibition (test, application of bicuculline and strychnine to block GABA A and glycine receptors). As previously reported, we observed that the overall spike rate tended to increase when inhibition was blocked. More surprising to us was the finding that the temporal precision of the neural representation was essentially unchanged after blocking inhibition. To explain these findings, we hypothesized a mechanism analogous to the iceberg effect in vision: there is an underlying continuous driving potential, and inhibition controls the effective threshold for spike generation (or scale of the driving potential). Specifically, we distributed the sample of recorded cells into three main classes, depending on the way they responded to test vocalizations: 1) Cells that responded only when inhibition was blocked; 2) Cells that were very selective for a few specific stimuli; and 3) Cells that responded distinctly to a variety of stimuli. All classes responded with increased rate when inhibition was blocked. Class 1 was not analyzed any further. Class 2 did not change its selectivity substantially, so most of the statistical and information-theoretic methods we used did not register any difference between conditions apart from rate changes. Most of the subsequent analysis refers to Class 3, in which rate changes but not significant other coding changes were found.

I-32. Hierarchical generalized linear models of dendritic integration and somatic membrane potential

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Accumulating evidence suggests that dendritic trees play a crucial role in single-neuron information processing. While dendritic integration is currently studied experimentally and using compartmental or cable-theoretic models, there exists no simple, analytically tractable, and canonical mathematical model for dendritic processing. Poirazi et al. (2003) suggested that the thin dendrites of pyramidal neurons may be viewed as a “two-layer neural network” in which a weighted sum of the synaptic inputs to each dendrite is passed through a dendrite-specific sigmoidal nonlinearity before being globally summed to yield the somatic membrane potential. However, their approach focused only on static inputs and output and a particular subclass of dendrites of a particular subclass of neurons. We developed a data-driven model of dendritic integration by building hierarchies of generalized linear models (GLMs), which have previously been successfully applied to modelling the stimulus-dependent spiking behavior of sensory neurons (Pillow et al., 2008). Our hierarchical GLM model generalizes previous work by (1) representing the dependence of a cell’s somatic membrane potential on arbitrary spatiotemporal inputs to its dendrites, rather than only static inputs, and (2) flexibly inferring the appropriate hierarchy of GLMs from experimental data, rather than assuming a priori the number of layers and particular identification of synapses with subunits. We demonstrate the success of a maximum likelihood fitting procedure on synthetic data from single-dendrite and two-layer networks. In subsequent work, we validate our fitting procedure on synthetic data from GLM hierarchies of more than two layers. We also explore the success of our framework in modeling synthetic data from compartmental models and data from glutamate-uncaging experiments produced by the labs of Michael Häusser, Judit...
Makara, and Szabolcs Káli. In doing so, our method allows us to assess how “functional” morphology, that is the GLM hierarchy inferred from electrophysiological data, relates to anatomical morphology.

**I-33. Structure-preserving model reduction of the passive and quasi-active neuron**

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We use a Krylov subspace projection method to construct a reduced model of the passive and quasi-active neuron which accurately captures the membrane potential at the spike initiation zone (SIZ) using a system of dramatically reduced dimension (3-5%). Unlike previous neuronal reduction techniques (Kellems et al. 2009), the reduced model retains the RC and RLC circuit structure of the passive and quasi-active neurons, providing a biophysical interpretation for the input/output map of the reduced neuron. Furthermore, the model retains the spatial specificity of inputs within the dendritic tree, rendering it to be a useful tool for examining dendritic computations both numerically and conceptually. The reduced model is robust to instability and resonance and captures the neuron's resonant frequency. Inputs into each reduced compartment are filtered by the columns of the reducer matrix, whose null space determines the set of inputs causing the SIZ to be blind to an input at any given dendritic location. The same reduced model is effective for injected and synaptic inputs into the passive neuron, and we compare the latter case, which has nonlinearities through sublinear summation, to a related bilinear reduction technique (Phillips 2003). The reduced model is accurate for the general dendritic tree, and we present two examples of the reduction of morphologically accurate neurons: the lobula giant movement detector (LGMD) and the CA1 pyramidal neuron. Each dendritic location in the LGMD corresponds to a location on the locust eye, and reducing a neuron in which space is well understood while retaining the neuronal structure may help to elucidate the dendritic computations performed in the LGMD. The CA1 neuron receives inputs locally on the dendrite through the Schaffer collaterals and distally through the perforant path, and the reduced model can be used to examine the role of dendrites in integrating these two distinct inputs.

**I-34. Using dimensionality reduction to explore muscle synergies and torque encoding during insect flight**

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A central challenge in understanding motor control, particularly during complex rhythmic behaviors like flight, is decoding the specific features of body dynamics controlled by a changing motor command. We recently discovered that the main downstroke muscles powering flight in the hawkmoth, Manduca sexta, are modulated by optomotor feedback to produce turns in response to left-right visual motion. This is surprising because these muscles receive only a single action potential for each wingstroke. The animal controls torque in part through precise timing modulation of these spikes. Here we investigate how to identify the control authority encoded in changes in peripheral motor signals. The goals of our study are 1) to extract, with as few dimensions as possible, the features of torque controlled by spike timing and 2) to test whether the timing of each of the left and right muscle's spike have independent contributions to controlling torque or function as a single control channel. We constructed spike triggered ensembles (STEs) of yaw (turning) torques and extracted the dominant features using singular value decomposition (SVD) of the STEs and a new approach applying partial least squares (PLS–Krishnan, A. et al., 2011) to extract features that best capture task-relevant variation. The PLS analyses capture the feedback
controlled components of torque in only one or two features, while the general SVD analyses typically required five or more. Torque features are comparable to the within-stroke torque measured previously from a dynamically-scaled model of a flying insect (Fry, S. et al., 2003). In most individuals, the timing difference between the muscles alone best explains the torque features, indicating that these two muscles work together in a functional synergy for control. Finally, including the left-right timing difference from the previous wingstroke significantly improves the models' explanatory power indicating significant history dependence.

I-35. Retinal metric: a stimulus distance measure derived from population neural responses

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Retinal ganglion cells transmit information about the organism's visual environment to the brain using a population neural code that consists of combinations of spikes and silences. If this code is to efficiently represent the environment, different stimuli should reliably elicit different population responses. It has been shown, however, that this is not true for single neurons, which produce distinguishable responses only when the stimuli differ along a small number of directions in the stimulus space, but not otherwise. It is thus unclear whether a neural population uses the diversity of neural sensitivities to distinguishably represent all possible stimuli, or whether it is inherently able to discriminate much better between some pairs of stimuli than between others. We recorded simultaneously from 100 neurons in the salamander retina to measure the population responses to repeated presentations of temporally random and spatially uniform stimuli. From this data we built the stimulus-dependent maximum entropy model for the population and used it to construct a corresponding "retinal distance" function between arbitrary pairs of stimuli. In contrast to previously used choices for the distance measure in the space of stimuli, the retinal distance tells us precisely how distinguishable, given the noise in population neural responses, a pair of stimulus clips is to the retina, thus placing bounds on any downstream decoding layer. We find that the retinal distance strongly deviates from Euclidean, and indeed from any distance with a static metric. For a given stimulus trace, we are able to create ensembles of similar stimuli that are distinguishable from the given one to within a prescribed level of discriminance of the response, and we identify which snippets are well constrained by the retinal response and which are not. This has important consequences for decoding and understanding of the neural code in the retina.

I-36. Bayesian spike-triggered covariance and the elliptical LNP model

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An important problem in computational neuroscience is to estimate the (typically low-dimensional) space of stimulus features that affect a sensory neuron's response. One popular method uses the first two moments of the spike-triggered stimulus distribution: the spike-triggered average (STA) and the spike-triggered covariance (STC). However, these estimators have not previously been formulated within an explicit probabilistic encoding model. Here we provide that formulation, clarifying the conditions under which STA/STC estimates are optimal, and pointing to several useful model-based generalizations. Specifically, we show that the STA and STC provide an
asymptotic maximum-likelihood estimate when the nonlinearity of a Linear-Nonlinear-Poisson (LNP) neuron takes the form of an exponentiated quadratic and the stimuli are Gaussian. We can therefore connect the STA and STC to the likelihood of an explicit probabilistic encoding model, making it straightforward to: (1) consider the same likelihood when stimuli are non-Gaussian, resulting in consistent and efficient feature space estimation with non-Gaussian stimuli; and (2) introduce priors and perform Bayesian estimation of neural feature spaces. We illustrate these extensions using a smoothing prior on filters, which substantially improves performance on multi-dimensional feature spaces. We also describe an empirical Bayes method for automatically selecting the feature space dimensionality (i.e., the number of filters), which avoids nested hypothesis testing or cross-validation. Finally, we extend the model to accommodate an arbitrary elliptically-symmetric nonlinear response function, resulting in a more powerful and flexible model for low-dimensional neural responses. We validate these methods using neural data recorded extracellularly from macaque primary visual cortex.

I-37. Using a doubly-stochastic model to analyze neuronal activity in the visual cortex

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Sensory neurons encode information probabilistically: repeated stimulus presentations elicit variable firing. This variability is often described using a cascade model, in which spikes arise from a Poisson process whose rate is a deterministic function of the stimulus. However, it has recently been shown that time-dependent rate variability is a wide-spread phenomenon in cortex (Churchland et al 2010, 2011). Consequently, the Poisson noise model commonly underestimates the variability of visual cortical recordings, which can lead to systematic errors in inferring neuronal characteristics. We measured responses to a variety of stimuli in visual cortex in anesthetized and alert monkeys. The fluctuations in neural responsiveness that typically occur over the timescale of these experiments are significantly greater than predicted by a Poisson model—estimated Fano factors as high as 10 occur in the acute preparation. We propose a doubly stochastic model, in which the stimulus-driven firing rate is modulated according to a stimulus-independent gamma-distributed random variable. This fluctuating rate generates spikes according to a Poisson process. Fitting the resulting mixture of Poisson processes to neural data reveals that the model is statistically superior for all neurons, and therefore provides an improved framework for analyzing neuronal tuning. The framework offers two further advantages over existing methods. First, it provides a natural means of estimating and tracking fluctuations in responsiveness (state changes) that occur during the course of an experiment. Second, it offers an efficient and accurate estimate of the upper bound on discrimination performance that can be supported by each neuron. Application of this new method can substantially improve the analysis of neuronal data, both in fitting explicit models and in assessing the limits of neuronal performance.

I-38. A feedback error learning approach to online-adaptive decoding for dynamic prosthetic arm control

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Dynamic neural decoders for prosthesis control will allow the user to anticipate the necessary task forces and to command the prosthesis accordingly. Because the user is faced with many different dynamic contexts in the course of her day, it is important that the neural decoder be capable of adapting to the new contexts without requiring an explicit recalibration session. In this work, we present an online-adaptive, hybrid neural decoder that is capable of improving task performance when placed in novel dynamic scenarios. The hybrid neural decoder estimates “intended” arm positions/velocities and joint torques from recent MI activity Suminski et al. (2011). The decoded torque is interpreted as a feed-forward control signal, while the decoded position and velocity are interpreted as references signals for a proportional-derivative (PD) feedback controller. The arm is commanded with a weighted contribution from each of the feedback and feed-forward components. We extend this work by adapting the torque decoder as it is being used to command an arm in a random target reaching task. Inspired by the Feedback Error Learning model of Kawato and Gomi (1992), we interpret position errors (differences between actual and decoded position) as 1) an error that must be corrected immediately through the PD controller and 2) an estimate of recent errors made by the torque decoder. We use this latter error signal to drive a quasi-supervised learning process that alters the parameters of the torque decoder. Through a simulation study, we show that the adaptive decoder improves performance over a fixed decoder under two novel scenarios: 1) the corruption of the original torque decoder parameters with zero-mean Gaussian noise, and 2) the introduction of a curl field. In both scenarios, the adaptive decoder outperforms the fixed decoder over time in both relative time-to-target and relative path length.

I-39. Inferring eye position and saccade direction from populations of LIP neurons

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A central problem in systems neuroscience is how multiple signals jointly encoding the state of the world are inferred from responses of neuronal populations. It has been shown that the eye position and saccade direction signals are jointly encoded by single neurons in the lateral intraparietal cortex (LIP) of macaques. However it is still unclear how these signals are represented at the population level. Using Bayesian inference, we predicted eye position and saccade direction from the population activity of LIP neurons, and found that both signals were combined more accurately than predicted by the product of their error distributions (“optimal combination”). This suggests a neuronal population code that reliably transmits information by combining signals, and falls comfortably within the framework of gain fields. We also found that a small subset of neurons yielded decoding accuracies similar to entire populations, and that different neuronal subsets were recruited for eye position and saccade direction predictions. This shows a sparse and selective neuronal code. The final eye position could be decoded well before the movement, presumably by combining the current eye position and the eye movement plan. The accuracy of the eye position and saccade direction decoding signals both peaked after the saccade, suggesting a strong memory signal representing past states and actions respectively. Such retrospective signal can be used for learning or monitoring. The onset of the decoding accuracy differed for the two signals. For the saccade direction signal, this onset was 100 ms before the saccade, hinting at corollary discharge signals. For the eye position, the onset was 100 ms after the saccade, suggesting either slow corollary discharge or proprioception. Taken together, our findings show that cortical computations can untangle jointly encoded signals by inferring them with distinct temporal signatures and from distinct neuronal population subsets.
I-40. Adaptation to spectro-temporal correlation in the primary auditory cortex

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Sounds stemming from the same object—be it a human voice, an animal vocalization, or a running brook—contain characteristic correlations in their structure across spectro-temporal channels. The temporal modulation across spectral channels, denoted here by the correlation coefficient (r), forms an important cue for sound encoding. In this study, we examined neuronal mechanisms in the primary auditory cortex, which serve to encode r. Using chronically implanted multi-tetrode microdrives, we recorded responses of neurons in the primary auditory cortex (A1) of awake rodents to acoustic stimuli with varying r between 0 and .97. The mean firing rate of neurons driven by the stimulus increased with r. We also quantified changes in neuronal spectro-temporal receptive field (STRF). The temporal width of the excitatory lobe of the STRF increased with r. This is consistent with the efficient coding hypothesis, by which neurons adjust the dynamic range of their responses to match the stimulus. We next quantified the timecourse of adaptation to r. We presented a stimulus, consisting of a sequence of 2 second long segments that alternated between r of 0 and 0.9, and recorded neuronal responses to 300 repeats of this sequence. Firing rates of neurons exhibited adaptation to the transition from high to low r over 400ms. This adaptation was differential between neurons preferring high r and those preferring low r. Changes in firing rate were accompanied by changes in temporal and spectral width of the STRF. This study demonstrates a novel form of adaptation to the temporal statistics of complex sounds, suggesting that A1 neurons modulate their response properties to match the temporal dynamics of incoming signals.

I-41. Decision-making and attention in a sampling-based neural representation

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According to the sampling hypothesis, the activity of sensory cortex can be interpreted as drawing samples from the probability distribution over features that it implicitly represents. Perceptual inference is performed by assuming that the samples are drawn from an internal model that the brain has built of the external world (Fiser et al 2010). We explore the implications of this hypothesis in the context of a perceptual decision-making task and present three findings: (1) Because the simple generative model for typical experimental stimuli does not match the rich internal model of the brain, the psychophysical performance is below what is theoretically possible based on the sensory neurons’ responses. This can explain why previous studies have found that surprisingly few sensory neurons are required to match the performance of the animal, and why traditional decoding models need to invoke ad-hoc “decision noise” (Shadlen et al 1996) when pooling the responses of all relevant sensory neurons. (2) We show that in the sampling framework typical 2AFC tasks induce higher correlations between neuron pairs supporting the same choice, than between those contributing to different choices - as has previously been observed empirically (Cohen & Newsome 2008). (3) We demonstrate that, given the limited number of samples in a trial and a reward structure that is strongly concentrated on particular parts of the sampling space, expected reward is maximized by sampling from a probability distribution other than the veridical posterior (for a related, but parametric, idea see Lacoste-Julien et al 2011). Based on these findings we propose that the brain actively adapts the posterior distribution to account for (1) and (3), and that this adaptation is closely related to the cognitive concept of attention. Using this interpretation of attention, we replicate existing neurophysiological findings and make new predictions.
I-42. Attention, Information, Normalization and Correlations

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Enhanced visual attention leads to improved behavioral performance in a range of perceptual tasks. Previous neural models have argued that the observed improvement in performance is due to a combination of gain modulation at the single-cell level and divisive normalization at the population level. However, these prior models were based on the assumption that response variability is independent across neurons in the population, both in the presence and absence of attention. This assumption is problematic because neuronal variability is correlated in vivo and these noise correlations are known to change when attention is engaged. Indeed, a recent study found that noise correlations were significantly decreased when attention was engaged during an orientation discrimination task, and that this decrease in noise correlations accounted for the majority of attention-related improvements in behavior. Here we investigate the properties of a biologically plausible neural network model of visual attention in the context of an orientation discrimination task. Building on our previous work on analytically quantifying Fisher information in realistic networks of spiking neurons, we analyze the link between attention-related changes in network connectivity, noise correlations and Fisher information. In such networks, there is no guarantee that an increase in gain implemented via a mechanism such as divisive normalization will increase information. We found however that an increase in the strength of feedforward connections between the LGN and V1 can increase Fisher information, thus improving behavioral performance. Moreover, this change also decreases pairwise noise correlations in V1 and V4 in a manner consistent with experimental findings. This work is the first neural theory of attention that can simultaneously account for the pattern of correlations found in cortex, the behavioral improvement observed with attention, and the gain modulation induced by divisive normalization.

I-43. Short-term memory with balanced excitation and inhibition based on derivative feedback control

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Persistent patterns of neural activity that last long after the offset of a stimulus are thought to be the neural substrate for short-term memory. Because the observed decay of persistent activity in memory circuits is much slower than the typical decay time constants associated with synaptic or intrinsic neuronal dynamics, it has been suggested that network interactions must be used to prolong the duration of persistent activity. Most often, these network interactions have been assumed to mediate positive feedback between neurons that supports a long-lasting reverberation of activity. However, most positive feedback models do not naturally fit the architecture of working memory-storing structures in neocortex that have been suggested to exhibit a close balance between excitation and inhibition. Furthermore, these models are highly non-robust against commonly studied perturbations in network connectivity. Here, we suggest that synaptic interactions in networks with balanced excitation and inhibition can provide a negative derivative feedback that detects drifts in activity and sends a corrective feedback to the system. We construct a network with excitatory and inhibitory populations in which a derivative-like feedback arises naturally when excitation has strength equal to inhibition but has slower kinetics. We show that our networks maintain a continuum of stable firing rates even in the presence of intrinsic input-output nonlinearity. These memory networks operating in this balance regime are robust against many commonly studied perturbations to synaptic weights that grossly disrupt the performance of persistent activity circuits based on positive feedback. Specifically, in response to uniform increases in synaptic excitation, synaptic inhibition, or intrinsic neuronal gains, there is minimal decay or instability in persistent firing. Furthermore, we show that spiking network models implementing derivative feedback generate persistent firing with Poisson-like statistics. This work suggests a new
paradigm for short-term memory storage based upon a balanced network with cortical-like architecture.

I-44. Selective Allocation of attention is crucial in setting a capacity limit in visual short-term memory

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Temporary storage of information in visual short-term memory (VSTM) is a key component of many complex cognitive abilities. However, VSTM is highly limited in capacity. We used a multiple-item color change detection task to probe the limits of VSTM in macaque monkeys. Consistent with previous reports, we found that as the number of items in the memory increased, subjects' performance significantly decreased. We measured the precision of memory representations by parametrically varying the similarity between sample and test colors. For all array-sizes, subjects were less likely to detect the change in trials with similar sample and test colors, compared to trials with highly discriminable colors. We modeled the probability of subjects reporting a change as cumulative Gaussian function and used this to estimate the precision of VSTM representations. We found that as the number of items increased, the precision of representations, significantly decreased. Additionally, we found that shifting attention to one of the items increased that item's precision at the expense of the remaining items. Determining the precise neuronal mechanisms of how selective allocation of attention gives rise to variable precision representations is crucial in understanding the fundamental nature of the capacity limit in VSTM. To determine the neuronal basis of the decrease in precision, we recorded single unit activity from the lateral prefrontal cortex and focused on the effect that adding a second item into VSTM had on neuronal representations. We found that neuronal tuning broadened with the addition of a second item to memory. However, when attention was focused on one of the items in the array, neuronal tuning sharpened to a degree comparable to the tuning for a single item. These results point to a significant involvement of attention in controlling the fidelity of the contents of VSTM.

I-45. Dynamic networks in frontal cortex support the cognitive flexibility to switch between rules

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Complex, goal-directed behavior depends on the ability to flexibly switch between “rules” that define the correct behavior in a given context. Neuropsychological and human imaging studies suggest the frontal cortex is key to this flexibility. To understand its neural mechanisms, we recorded from two frontal regions, dorsolateral prefrontal cortex (PFC) and anterior cingulate cortex (ACC), while monkeys switched between two rules. PFC neurons played a leading role in rule-switching, encoding the cued rule and switch before ACC neurons. Different sub-networks within PFC supported each rule, synchronizing at beta frequencies (19-40 Hz) during task execution. The sub-network supporting the more-dominant rule also showed preparatory alpha synchronization (6-16 Hz) during the competing rule, suggesting a suppressive mechanism. These results support a primary role for PFC in cognitive flexibility with different rules supported by different synchronous PFC sub-networks.
I-46. A winner-take-all mechanism of decision rule discrimination by the supplementary eye field

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In the absence of an explicit instruction, rules learned from experiences can guide a decision of whether to initiate or withhold a movement. How the brain encodes a rule that connects a set of sensory inputs to a motor output is not well understood. Previously we identified two complementary populations of neurons in the supplementary eye field (SEF) of macaque monkeys that differentially modulate the firing rate during categorization of a motion direction in a rule-based decision making task that required the animals to either track a moving target using a smooth pursuit eye movement or inhibit the movement to maintain fixation. Whether the SEF neurons increase activity to select the agonist rule that guides a categorical decision, or decrease activity to deselect the antagonist rule remained unclear. Here we show that the SEF neurons predominantly deselect the antagonist rule prior to the selection of the agonist rule, and do so at a faster rate when the motion direction invokes the antagonist rule more certainly. Mutual inhibition between a pair of integrators, one that instantiates movement initiation and the other that instantiates movement inhibition, account for the predictive deselection of the antagonist rule. The results suggest that an inhibitory interaction between two complementary populations of neurons is a prerequisite for discrimination of categorical decision rules by the SEF.

I-47. How prior probability influences decision making: A unifying probabilistic model

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How does the brain incorporate prior probabilities of stimuli into decision making? Two apparently contradictory models have been suggested: (1) a model that adds an offset to a decision variable, implying a static effect of the prior (Carpenter et al., 1995, Dorris & Munoz, 1998, Gold et al., 2008), and (2) a model that dynamically weights the influence of the prior on the decision variable (Hanks et al., 2011). The additive offset model can successfully predict behavioral data when discriminating between two low contrast stimuli but is inconsistent with recent data from a random dots motion discrimination task where the prior probability of motion direction is manipulated (Hanks et al., 2011). The drift diffusion model has been popular as a model for the random dots task but to fully account for the experimental data, one is forced to invoke ad-hoc assumptions such as an urgency signal and a time-varying influence function for the prior. We present a normative framework for decision making that incorporates prior knowledge in a principled manner. The additive offset model and the dynamically weighted prior model both emerge naturally when decision making is viewed within the framework of partially observable Markov decision processes (POMDPs). We show that the ad-hoc assumptions utilized in the drift diffusion model are unnecessary: the urgency signal emerges naturally in the form of a collapsing deadline and the time-varying effects of the prior on decision arise directly as a consequence of reward maximization. By fitting model parameters to the psychometric function in the neutral prior probability condition, we are able to predict both the psychometric function and reaction times for a new prior probability for motion direction. The predictions of our normative model are consistent with experimental data reported by Hanks et al. (2011).
I-48. Semi-Markov models of the molecular psychophysics of brain stimulation reward

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Brain stimulation reward (BSR) has long been recognized as offering the best platform for quantitative psychophysical analyses of the nature of preference and choice. Particular illumination has been cast on effects of the value of the reward (i.e., the strength of the stimulation in the medial forebrain bundle) and the work requirements (i.e., the price, or the length of time a lever must be pressed) to get those rewards. However, theoretical accounts of these studies have been restricted in two ways: by being algorithmic rather than computational, and thus not offering a normative account, and by offering a molar rather than a molecular characterization of the subjects’ choices, assessing overall rates of pressing rather than the detailed temporal topography of choice. We extend a semi-Markov model of appetitive vigour (Niv et al, 2007) to address both lacunae. In the model, subjects can receive rewards from BSR or from leisure, and make stochastic, approximately optimizing choices of both whether to work or to rest, and for how long to do so. In an average reward setting, they pay an automatic opportunity cost for the time they allocate. We show that when the benefit of leisure increases non-linearly with leisure duration, it is possible to model in a qualitative manner many molecular features of choices. In particular, when the value of work exceeds that of leisure then the subjects will pre-commit to working for the whole price; furthermore, the distribution of leisure bouts post-reinforcement is roughly exponential with short means for high payoffs, gammas with means possibly exceeding the trial duration for low payoffs, and bimodal with short and long modes for medium payoffs.

I-49. Neuronal activity in anterior cingulate cortex predicts susceptibility to distraction

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The oft-cited “conflict monitoring” model of dorsal anterior cingulate cortex (dACC) function predicts increased neuronal activity in the presence of competing response options that predicts success in adjusting behavior. This model is based on research conducted in human subjects however, and no study of single-unit dACC function in macaques has observed conflict-like signals. The present study utilized a social distraction task, which adds potent, variable-onset images of faces to a simple visually guided saccade task, to generate a behavioral model of endogenous control in the presence of distraction. A significant proportion of neurons within dACC signaled the presence of distractors by increasing firing rate. Further, increased firing in response to the distractors predicted slower reaction times. Finally, pre-task firing rates in an overlapping population of cells predicted distractibility on subsequent trials, indexed by saccade deflections away from ideal trajectories, independent of recent reward, error, or distraction history. This study provides the first evidence for conflict signals in the macaque and the first single-unit characterization of conflict and endogenous control in the dACC. It remains unclear whether the distractor responses in these cells represent response conflict per se or a potentially evolutionarily older system for endogenous control.
I-50. Cortico-basal ganglia computations in controlled decision making: an extended diffusion model analysis

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The antisaccade task has widely been used to research cognitive functions such as response inhibition and executive control. While the Prefrontal Cortex (PFC) is generally associated with cognitive functions, more recently, a prominent role of the Basal Ganglia (BG) in these processes has been established. We have recently linked detailed dynamics within a neural circuit model of PFC-BG interactions to higher level computations summarized by an extension of the Ratcliff drift-diffusion model (DDM). The model consists of a two-staged drift-process: in the prepotent phase, the drift-process evolves towards responding to the salient but erroneous stimulus direction; after a delay (i.e. time of cognitive control; tcc), the cognitive control mechanism reverses the drift-process to exert controlled responding. This basic pattern gives rise to fast errors and slow correct responses, as observed empirically in the antisaccade task. This model provides two crucial advantages over traditional analysis that uses the mean reaction time (RT) and accuracy: (i) the model takes the complete RT distribution of correct and erroneous pro and antisaccade trials into account; and (ii) if fitted to data, it allows inference of cognitive latent variables underlying response inhibition and executive control, such as strength of bottom-up saliency (i.e. prepotent drift-rate), speed of cognitive control (i.e. tcc and cognitive control drift-rate) and response threshold – all of which have been linked to distinct cortico-basla ganglia mechanisms. We present the feasibility of this method by fitting the model to antisaccade data from a large healthy population and compare the results to parameter fits of a patient population. Finally, we discuss other areas of application for our model such as the flanker and Simon task.

I-51. The importance of being slow: Extreme-value theory of cognitive representations.

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The activity of neural circuits depends on a multitude of biological processes, and its dynamics is characterized by a spectrum of timescales spanning a few orders of magnitude. Whereas fast processes are suitable for reflexive responses, much slower timescales are needed for cognitive functions. It is currently unknown how neural dynamics adjusts to perform “slow computation”, such as memory and decision-making. How do we make decisions based on the evidence accumulated for seconds or hours? To address this issue, we develop and test a new hypothesis based on the mathematical concept of extreme value and the operation of maximization. We assume that neural dynamics can be described by a given set of timescales, determined by diverse biological processes affecting neural activity. Any given process impacts some neural populations and not others; therefore the dynamics of each population is characterized by a different subset of timescales. When engaged in slow cognitive tasks, in order to slow down the dynamics, each population becomes dominated by the longest (maximum) timescale in its own subset. As a consequence, the maximum timescales sampled across different neural populations follow a specific, universal distribution, the Extreme-value distribution. We tested this prediction by analyzing neural activity in the cortex of primates performing a matching pennies task, where long integration timescales are required to generate unpredictable decisions. We found that the timescales of neural responses follow the Extreme-value distribution across neurons. In addition, the timescales of behavioral responses also follow the Extreme-value distribution, albeit on a different temporal scale. These results point to a new interpretation of the dynamics of neural activity and the behavior observed in “slow” cognitive tasks. Extreme-value theory may serve to generate and test new hypotheses on the neural representations and mechanisms underlying cognitive functions.
I-52. Executive control and arbitration in reinforcement learning

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There is considerable evidence that decisions are influenced by separate competing processes. Recent work suggests these influences can be formalized computationally as different algorithms for reinforcement learning (RL): ‘model free’ strategies for repeating reinforced actions (associated with the striatal dopamine system), which are generally computationally simple and easily implemented, and more computationally demanding deliberative ‘model-based’ planning methods. However, little is known about how the brain solves the problem of arbitrating between multiple decision systems. We investigated whether the expression of difficult model-based RL over simpler model-free RL might involve executive control mechanisms studied in other areas of human cognitive neuroscience. To address this question, we compared the performance of human subjects (N=48) on an RL task and a standard test of executive control. The RL task was a sequentially structured MDP that permits distinguishing model-based and model free contributions to learning by their different consequences for trial-by-trial adjustments in action preferences (Daw et al., Neuron 2011). We tested whether the degree of these influences, assessed by regressing recent rewards on choices, was related to individual differences in executive control, measured by the reaction time penalty for suppressing an incongruent color-naming response in a Stroop task. As expected, evidence for both model-free and model-based influences on choices was observed at the group level in the RL task (mixed logit regression, ps < .01), but with individual variability in their degree. Comparing tasks, a lower Stroop penalty (better executive control) was associated with a greater influence of model-based RL (ps < .05). This result was robust to attempts to rule out less specific sources of covariation, such as motivation. These results suggest that the executive control system contributes to model-based RL or its expression, perhaps by permitting deliberative planning to be undertaken even in the face of preponent, model-free influences.

I-53. Natural grouping of neural responses reveals spatially segregated clusters in prearcuate cortex

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A fundamental challenge in studying the frontal lobe is to parcellate this cortex into “natural” functional modules despite the absence of topographic maps, which have proven so helpful in more primary areas. Here we show that unsupervised clustering algorithms, applied to large-scale recordings from prearcuate gyrus, reveal spatially segregated sub-networks that remain stable across contexts and have different physiological signatures. We recorded from 96-channel microelectrode arrays while two monkeys discriminated the direction of motion in a dynamic random dot display and reported the perceived motion direction by a saccadic eye movement. Looking for natural groupings of neurons based on the similarity of their response variation across the entire recording session, we discovered that the recorded area consists of at least two spatially segregated regions: one closer to the arcuate sulcus whose responses are tightly correlated with choice and reaction time, and another more medial and rostral that is less predictive of choice and reaction time. Our finding suggests that area 8r is not homogenous, but divides naturally into two smaller sub-networks. Importantly, these sub-networks are easily detectable during all trial epochs including the inter-trial interval, and surprisingly, are defined better by “common noise” within the areas than by task-evoked responses. The “noise” signal that drives the spatial clustering is temporally broadband...
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over at least three orders of magnitude (.01-17 Hz). Our results demonstrate a powerful new tool for parcellating the cerebral cortex into sub-networks by objective classification of simultaneously recorded electrophysiological activity. Our parcellation process works well on ‘spontaneous’ neural activity, and thus bears strong resemblance to the identification of “resting state” networks in fMRI data sets. In the future, it will be important to determine whether the spontaneous “noise” activity we are recording is in fact the neural basis of the fMRI resting state signal.

I-54. Neural threshold for patch leaving decisions in posterior cingulate cortex

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Deciding when to leave a depleting resource and move on to a new one is a ubiquitous problem faced by foraging animals and web-searching humans alike. The Marginal Value Theorem (MVT; Charnov 1976) of behavioral ecology dictates that the optimal time to leave a patch occurs when the instantaneous resource intake rate falls below the average for the environment. Animals as diverse as bees, fish, birds, monkeys, and humans behave in accordance with the MVT, suggesting convergent evolution of decision mechanisms implementing the algorithm for solving the patch-leaving problem. In a prior study, we showed that the primate brain implements this algorithm via a rise-to-threshold process (Hayden et al., 2011). Specifically, neurons in anterior cingulate cortex (ACC) respond phasically each time monkeys choose to stay in a patch, these responses grow with increasing time in a patch, and monkeys abandon the patch when neuronal responses reach a fixed threshold. When travel times between patches are increased, the firing rate threshold for leaving increases and monkeys stay longer in each patch, consistent with the MVT. Here we test the idea that the posterior cingulate cortex (CGp) encodes the threshold for patch-leaving. ACC and CGp are strongly and reciprocally connected. Further, firing rates of CGp neurons vary tonically across multiple decisions, and slow variations in neuronal activity therein predict both exploration behavior and distractability. We recorded from 28 cells in CGp in monkeys performing our foraging task. We found that CGp neurons respond to each decision to stay in a patch and these responses grow as monkeys continue to forage in the patch, just like neurons in ACC (Figure 1). Consistent with our hypothesis, we found that mean firing rates of CGp neurons varied with travel time between patches (Figure 2). Such signals may set the threshold for leaving a patch.

I-55. Trial-by-trial perceptual learning during odor category decisions: Value, uncertainty and dopamine

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Choices in a sensory discrimination task need not be influenced by reward history after asymptotic performance has been reached. However, even after extensive training in a binary odor mixture categorization task, rats continue to show a form of learning that depends on the history of rewards received on recent trials. The magnitude of this ongoing learning is proportional to the difficulty or uncertainty associated with the stimulus—the distance from
the 50/50 mixture categorization boundary—on the preceding trial. We hypothesize that this learning is the result of dopamine (DA) dependent reinforcement learning (RL). To test this hypothesis, we first changed ratio of rewards for correct choices to test sensitivity to reward. When we manipulated the reward ratio in blocks, subjects learned to bias their choices towards the larger reward, consistent with an RL-like learning process and implying that choice functions depend not only on stimuli but on choice values. We then manipulated the DA learning pathway using the DA D2-like agonist quinpirole. Systemic quinpirole injection (i.p., 0.1 mg/kg) sessions were compared with alternating saline injection sessions. Quinpirole produced a systematic increase in trial-by-trial learning effect independent of prior stimulus difficulty, consistent with the involvement of DA. Average performance and odor sampling times were not statistically different from control sessions. We are now performing localized pharmacological manipulations to test the involvement of the olfactory tubercle, a ventral striatal DA target downstream of the primary olfactory areas, in this learning process. We hypothesize that on-going RL in this task reflects a source of irreducible uncertainty in the sensory representation that causes continuing learning near the category boundary and that constant increases in DA cause positive reward prediction errors that are attributed primarily to the prior choice. We suggest an extension of the standard RL model to account for these effects.

I-56. Generic and stimulus-dependent value signals are encoded in human ventromedial prefrontal cortex

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In order to facilitate decisions to be rendered between different kinds of goals it has been suggested that the brain may encode the value of diverse goal-stimuli within a common currency (Berns and Montague, 2002). However, the neural computations underlying the implementation of a common currency are currently not well understood. In a previous study (Chib et al., 2009), we showed that a region of vmPFC in humans had overlapping correlations with the value of three different classes of economic goods: sums of money, food items, and trinkets (books, DVDs). However the nature of the encoding of the goal-value signal remains unaddressed: goal-values could be encoded in a generic manner indifferent as to goal identity, or alternatively, goal-values could be represented in a category specific manner, whereby distinct yet spatially intermingled patterns depict the value of different classes of good. To discriminate these possibilities we used multivariate pattern analysis techniques on fMRI data acquired from human participants performing a paradigm similar to that used by Chib et al. 2009. Our results support the existence of both a generic distributed goal-value code on the medial wall where activity patterns differentiate high vs. low values irrespective of the good category, as well as for a category-specific goal-value coding mechanism on the medial orbital surface, in which different distributed patterns of voxels encode for the value of each class of good but do not generalize to the others. To the best of our knowledge, this is the first evidence for signals in the human brain that encode both the value and identity of a stimulus in a combined representation. Such a signal could form the basis of an input into a decision comparator for the purpose of rendering a decision over specific goals on the basis of their respective values.
I-57. Spatial heterogeneity in visual perception; a new conceptual framework for translation invariance.

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The identity of an object is a fixed property independent of where it appears, and an effective visual system should capture this invariance. However, we have reported that the perceived gender of a face is strongly biased toward male or female at different locations in the visual field (Afraz et al, CB, 2010). The spatial pattern of these biases was distinctive and stable for each individual. Identical neutral faces looked different when they were presented simultaneously at locations maximally biased to opposite genders. A similar effect was observed for perceived age of faces. We measured the magnitude of this perceptual heterogeneity for four other visual judgments: perceived aspect ratio, orientation discrimination, spatial-frequency discrimination, and color discrimination. The effect was sizeable for the aspect ratio task but substantially smaller for the other three tasks. We also evaluated perceptual heterogeneity for facial gender and orientation tasks at different spatial scales. Strong heterogeneity was observed even for the orientation task when tested at small scales. In a new set of experiments, we show that it is possible to induce new gender-biased locations in the visual field following \textasciitilde 1 hour of exposure to a face that orbited the fixation point continuously while morphing back and forth from female to male. Based on these results and previous work, we formulate a new conceptual framework for the problem of translation invariance. In the new framework, the traditional view that translation invariance is achieved through the large receptive fields of neurons in the higher brain areas is challenged. Instead, we suggest that translation tolerant perception depends on adequate sampling of the visual signal by neurons that are calibrated together (at a temporal scale as short as one hour) based on visual cues such as spatio-temporal continuity of the stimulus.

I-58. Visual Object Classification is Consistent with Bayesian Generative Representations

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The ability to learn and distinguish categories is essential for human behavior, and the underlying neural computations are actively investigated (Freedman, 2011). Taking a normative view, we can relate categorisation to the distinction between generative and discriminative classification in machine learning. Generative approaches solve the categorization problem by building a probabilistic model of how each category was formed and infer then category labels. In contrast, the discriminative approach learns a direct mapping between input and label. Recent work (Hsu and Griffiths, 2010) shows human classification is consistent with discriminative and generative classification depending on conditions. We hypothesize that humans employ generative mechanisms for classification, when not encouraged otherwise. To test this we exploit a counterintuitive prediction for generative classification, namely how the discrimination boundary between two classes shifts if one category’s distribution is revealed to be broader during learning. We trained N=17 subjects to distinguish two classes, A and B in two tasks (two Persian-characters, armadillo-horse stick-drawings). The classes in each task were parameterized by two scalars; objects for each class are drawn from Gaussian parameter distributions, with equal variance and different means (class “prototypes”). Next, subjects classify unlabelled examples drawn between the classes, so we can infer their discrimination boundary. This process is then repeated but includes training data for class A, which lie
far away from B. Counter-intuitively, generative classification predicts a shift of the discrimination boundary closer to B. Conversely, discriminative classifiers will show either no shift of the boundary or a shift of the boundary away from class B. Our results show that categorization in both tasks is consistent with generative and not discriminative classifiers, as classification boundaries shifted towards B for both tasks in all subjects. Our experiments provide an ideal framework for neurophysiological and imaging investigations of the underlying neural mechanisms.

I-59. Event timing in associative learning: From biochemical reaction dynamics to behavioral observations

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Associative learning requires a neural coincidence detector that modifies a behavioral output according to the relative timing of the relevant external events. Spike timing-dependent plasticity (STDP) has been proposed to serve this purpose at the millisecond time scale. Olfactory conditioning experiments in fruit flies show the same bimodal characteristics as STDP – but on a time scale that is three orders of magnitude larger (Fig A). Attempts to explain this phenomenon through classical STDP (Drew and Abbott, PNAS 2006) are not compatible with electrophysiological characteristics of the fruit fly olfactory system. We here present an alternative approach that is based on biochemical as well as behavioral data: Fruit flies trained with an odor that precedes electric shock subsequently avoid this odor (punishment learning); if, on the other hand, shock precedes odor, the odor is approached later on (relief learning). In the model, an odor-induced Ca(2+) signal and a shock-induced dopaminergic signal converge in the Kenyon cells during learning, synergistically activating a Ca(2+)-calmodulin-sensitive adenylate cyclase (AC), which triggers the synaptic plasticity underlying the conditioned odor avoidance (Fig B). AC thus acts as a molecular coincidence detector between shock and odor. Using a mathematical model of the signaling cascade we can quantitatively explore this biochemical property of AC and demonstrate that it indeed can generate the effect of event timing on associative learning. Systematic parameter variations and theoretical analysis shows that the model framework is robust with respect to parameter changes and model variants. Beyond its applicability for classical olfactory conditioning in fruit flies, the AC coincidence detector may thus also serve as a basic computational motif in various other associative learning systems.

I-60. Bridging the gap: A third time-scale between plasticity and homeostasis?

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Recurrent cortical circuits are plastic and their activity dynamics are stable. Most network models fail to incorporate both of these features because the mechanisms for potentiation and depression are intrinsically unstable and lead either to run-away potentiation and epilepsy-like network states, or silent networks with no activity at all. To ensure stable, “healthy” dynamics, potentiation and depression have to be tightly balanced. Experimentally, a large variety of homeostatic mechanisms that control this balance have been characterized, and consequently
deployed in theoretical models. Still, there are only few examples of plastic recurrent network models that exhibit stable long term behavior. Why? We answer this question, using a mean field approach, where we limit our analysis to BCM type learning rules. We show that stability is achievable, but comes with strict temporal requirements. For plausible network and plasticity parameters we find that the stabilizing mechanism has to act on a time-scale of seconds to minutes rather than hours as most homeostatic mechanisms indicate. We verify these findings in simulations of spiking neural networks subject to a triplet-STDP learning rule. Here the homeostatic mechanism takes the form of a sliding threshold that regulates the ratio between potentiation and depression. Similarly to the analytical results, the circumstances in which spontaneous background activity can be stable in the presence of plasticity require threshold sliding on the time scale of minutes. Our results show that plasticity control has to be constantly adjusted on a time-scale of minutes, whereas the typical time-scale for homeostasis is in the order of hours. These findings suggest that there should be a third time-scale between the one of plasticity and homeostasis that preserves network stability. We discuss these findings in regard to recent experimental findings.

I-61. The incorporation of new information into prefrontal cortical activity after learning new tasks

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Humans and nonhuman primates have the ability to learn complex new tasks. This ability requires new information to be integrated into neural systems that already support other behaviors. To study how task learning changes neural representations, we analyzed single unit recordings from the prefrontal cortex (PFC), a brain region important for task acquisition and working memory, before and after monkeys learned to perform two new behavioral tasks. A population decoding analysis of the PFC firing rate activity revealed that there was a large increase in task-relevant information, and smaller changes in stimulus-related information, after training. This new information was contained in dynamic patterns of neural activity, with many individual neurons containing the new task-relevant information for only a short period of time in each trial in the midst of other large firing rate modulations. Additionally, examining data from dorsal and ventral PFC separately revealed that stimulus information could only be decoded with high accuracy from dorsal PFC, while task-relevant information was distributed throughout both areas. These findings help reconcile the controversy about whether PFC is innately specialized to process particular types of information, or whether its responses are completely determined by task demands, by showing there is both regional specialization within PFC that was present before training, as well as more widespread task-relevant information that is a direct result of learning new tasks. The results also show that new information is incorporated into PFC through the emergence of a small population of highly selective neurons that overlay new signals on top of patterns of activity that contain information about previously encoded variables, which gives new insight into how information is coded in neural activity.

I-62. Sequence Learning in Primary Visual Cortex

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Stimulus-specific response potentiation (SRP, Frenkel et al. 2006, Cooke and Bear 2010) is a robust form of experience driven plasticity characterized in the mouse primary visual cortex by a dramatic increase in the mag-
nitude of visually evoked potentials (VEPs) following repeated exposures to sinusoidal gratings. This response potentiation is highly specific for grating orientation, spatial frequency and contrast, is NMDA dependent, occludes and is occluded by thalamocortical LTP and is rapidly reversed by local cortical infusion of a peptide that inhibits PKMζ. Sharing attributes and mechanisms with classical LTP, SRP seems to serve a form of perceptual learning that allows neurons in the visual cortex to recognize familiar spatial visual stimulus patterns. Here we present evidence that the visual cortex can also learn to recognize and predict familiar sequences of spatial stimulus patterns presented with specific temporal organizations. Similar in some respects to SRP and LTP, our data indicate that expression of this learning is based on divergent mechanisms and suggest an unanticipated role for intracortical circuits. While previous work implicates hippocampal involvement in the acquisition of temporal sequences, this is the first clear evidence showing that sequence learning can occur in a primary sensory region and may provide a new and easily accessible system for mechanistic investigations into the coding and recall of sequentially ordered memory.

I-63. BMI learning results in highly precise cell-specific coherence in corticostriatal networks

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For any given cognitive task, our nervous system must coordinate the activity of large ensembles of individual neurons across distant cortical sites. However, the ways in which distinct neuronal ensembles can coordinate their activity and communicate effectively remains a key problem in neuroscience. Recent theories have proposed that coherent oscillations across neural ensembles could serve as the substrate for selective coordination between cells and the development of functional cell assemblies. Here we show that coherence develops between primary motor cortex and the dorsal striatum over the course of learning in a novel neuroprosthetic task. Rats learned to volitionally modulate activity in primary motor cortex while receiving auditory feedback about neuronal activity levels to guide performance. Strong coherent interactions developed between the two regions in low frequency bands as learning progressed. Importantly, this coherence was specific to task-relevant cells, despite them being intermingled with non-task-relevant cells. The phase offset of this coherence closely matches estimates of the corticostriatal conduction delay measured using intracortical microstimulation, suggesting that the developing interactions are timed with high precision between the two regions. In addition, spikes from primary motor cortex were followed by a consistent phase in the dorsal striatum, suggesting that network feedback reinforces this synchrony. Together, these results suggest that highly precise coherence develops during learning in task-relevant neuronal populations, and further, that entrainment of oscillatory activity serves to synchronize large-scale brain networks and facilitate communication across neuronal populations.

I-64. Dendritic processing underlying temporal integration

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In neural integrators, transient input signals are mathematically accumulated into sustained neuronal activity. Nu-
merous models of temporal integration have been proposed. Some depend purely on recurrent synaptic feedback within a population of neurons. Others instead rely on regenerative currents within the dendritic compartments of individual neurons that may yield propagating wavefronts of elevated calcium or stationary plateaus resulting from voltage bistability. Here we aimed to discriminate between these proposed mechanisms by imaging the dendritic activity of oculomotor integrator neurons during behavior. We loaded integrator neurons of the larval zebrafish with Oregon green BAPTA-1 AM through bolus injection into the caudal hindbrain. Recordings of the soma showed the expected optokinetic, saccadic, and fixation sensitivity; recordings in the neuropil showed a mixture of these signals with spatial heterogeneity at the few microns scale. We then targeted selected somata using a micropipette containing Alexa 594 dextran, electroporated, and visualized the dendritic morphology of the targeted neuron while imaging calcium dynamics. During optokinetic tracking we found along numerous dendritic branches of a given cell distinct hotspots of activity that were $1 - 5 \mu m$ long and separated by at least $2 \mu m$. Activity in the hotspots were generally correlated with somatic activity, but also exhibited some heterogeneity. These data, although early, do not seem consistent with models proposing propagating waves of elevated calcium. To explore possible mechanisms underlying these observed response patterns, we have developed a conductance-based network of spiking neurons with dendritic subunits containing voltage-dependent currents capable of generating hotspots. The network integrates its inputs and exhibits heterogeneous dendritic outputs consistent with experimental observations. Overall, these experiments and modeling provide a rare case in which the role of individual dendritic subunits can be directly connected to network function and animal behavior.

I-65. Loom sensitive neurons link computation to action in the Drosophila visual system

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Many animals extract specific cues from rich visual scenes to guide appropriate behaviors, such as navigation and collision avoidance. The complexity of these visual signals requires neural circuits to link particular patterns of motion to specific behavioral responses. In flies, the lobula complex, the third neuropil of the optic lobe, is thought to underlie such motion processing. This complex comprises two ganglia, the lobula and the lobula plate, and contains a diverse array of cell types. While the visual response properties of many of these cells remain unknown, electrophysiological studies of specific subsets of lobular neurons, including lobula plate tangential cells and small target motion detector neurons, have described cells that become tuned to specific patterns of movement through the integration of local motion cues. However, in no case has the activities of identified neurons in the lobula complex that are tuned to a particular pattern of motion been demonstrated to be critical to trigger the specific behavioral response appropriate to that signal. Here we examine both the visual responses and behavioral role of a group of genetically identified neurons in the Drosophila lobula complex, the Foma-1 neurons. We found that these cells are tuned to detect looming stimuli, visual motion signals generated by an object on a direct collision course with the fly. Such stimuli elicit escape behaviors from flies, allowing them to avoid imminent collisions. Using genetic tools to silence and activate these neurons, we demonstrate that these cells are necessary for normal responses to looming stimuli, and that their activation is sufficient to trigger an escape response, even in the absence of visual input. Thus, these neurons serve as a nexus that integrates specific motion cues and triggers the escape response in this sensorimotor pathway.
I-66. Identifying the neural initiation of a movement

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The preparation of voluntary movements takes time (Rosenbaum, 1980), suggesting that such actions depend on sequentially readying and then executing a motor plan. When these two phases are separated by a delay, neurons in the motor cortex often modulate their firing during both, indicating that the cortical circuits involved in the two computations overlap. Thus, to start the movement, the cortex must switch from a preparatory mode to an executory one. Is the moment of this switch evident in the neural firing? Reasoning that the switch should manifest as a change in computational dynamics, we fit a “hidden switching linear dynamical system” model (Petreska et al., NIPS, 2011) to multi-neuron data from macaque dorsal premotor (PMd) and primary motor (M1) cortices, recorded as the animal performed delayed reaches. Modelling the spike trains alone—without reference to external events—we could indeed see a trial-specific change in dynamics in both areas that appeared to anticipate initiation of arm movement. The change in M1 tended to follow that in PMd (mean shift = 36±0.13 ms), and its estimated timing on each trial was more tightly correlated with the beginning of movement (cross-validated $r^2 = 0.70±0.03$) than was the estimated change in PMd (cross-validated $r^2 = 0.51±0.06$). It has been suggested that movements are triggered when population firing reaches a threshold. If so, then applying a similar threshold to the recorded population might better predict movement onset. In fact, no matter how we estimated or thresholded firing rates, this approach could explain no more than 0.37±0.02 of the reaction-time variance. Thus, we conclude that the neural initiation of movement is better identified with a change in estimated circuit dynamics than with the crossing of a firing-rate threshold.

I-67. How does pacemaking in the globus pallidus affect striatal microcircuits?

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The basal ganglia (BG) are a collection of highly interconnected forebrain nuclei that network the cortex, thalamus and brainstem and are critically involved in action-selection and reward-based learning. The circuit structures underlying this functionality are poorly understood, but likely involve coordinated activity in cell assemblies across the BG. The globus pallidus (GP) is a hub of this network, containing GABAergic projection neurons that innervate all of the BG. Most GP neurons are spontaneously active yet their firing is desynchronized, providing independent inhibitory pacemaking throughout the BG. Here we use transgenic mice, optogenetics, and viral synaptic tracing to define the physiological properties and anatomical topography from a single class of genetically defined GP neurons. We focus on projection from the GP to the striatum, the major input nucleus of the BG. Recordings from acute brain slices demonstrate that GP neurons expressing the calcium binding protein parvalbumin are spontaneously active around gamma frequency and selectively innervate two types of striatal interneurons with different synaptic properties. Thus while inhibitory projections from the striatum heavily innervate the GP and are sufficient to pause GP pacemakers, these pacemakers indirectly affect striatal output by differential modulation of two types of local interneurons. Are these synaptic loops between the GP and striatum “closed” or “open”?
In other words, is the function of these projections more akin to feedback or horizontal inhibition? We are using retrograde viral tracing from the two classes of GP-connected striatal interneurons to determine the topography of these synaptic loops.

I-68. Spike time-dependent plasticity can organize a recurrent network to generate grid cell responses

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There are many competing models of possible mechanisms underlying grid cell activity, but none explain how the complex networks assumed in such models could arise through development and plasticity. We present a biologically plausible model for the formation of the grid cell network with periodic spatial neural responses. Further, the network develops the ability to path integrate. Our model uses an asymmetric spike time-dependent plasticity (STDP) rule applied to an initially unstructured network of spiking neurons that receive different speed-modulated head-direction inputs and also receive randomly assigned place cell-like inputs. As the animal explores its spatial environment, the STDP rule causes neurons firing at short time-lags – i.e. neurons receiving similar place inputs – to become recurrently connected. This produces a center-surround structure in the weights, if, for visualization, the neurons are rearranged topographically according to their place inputs. At the same time, the STDP window enhances connectivity between neurons receiving similar direction inputs. This enhancement induces slight asymmetries in the network weights based on the direction tuning of the cells. The end product – an asymmetrically shifted center-surround weight structure – produces grid-like activity patterns in the neural population. The asymmetries drive movements of the population activity pattern in proportion to animal velocity, which enables path integration. The mature network displays the low-dimensional continuous attractor (CA) dynamics of models (Fuhs & Touretzky, 2006; Burak & Fiete, 2009) that successfully predict many features of the grid cell response. The simplicity and plausibility of this developmental model should lay to rest critiques about the complexity of wiring assumed in CA models. The model explains why the mature network need not be topographic, and generates predictions about inputs to and maturation of responses in the grid cell network during development (Wills et al., 2010; Langston et al. 2010).

I-69. Which edge probabilities reveal long-range horizontal connections in visual cortex?

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Anatomically the long-range horizontal connections in superficial V1 appear highly complex but densely clustered. This clustering, plus the cortical organization revealed by optical imaging, implies an order to their structure. Under the assumption that they are involved in boundary inference, we seek to understand this order functionally. Informally, the logic is that edge pairs, triples, ... and so on will “wire” together provided they occur together in natural images. The question is: what is the smallest order of edge statistics that predicts the known long-range horizontal connection statistics. There exists a literature on pairwise statistics, but this only agrees in the mean with existing population data; different models build on this, such as the association field, make incorrect predictions about the variance. We extend edge statistics to triples in a large natural image corpus. Because the underlying probability distribution is high-dimensional (for our experiments, e.g. 20 pixels x 20 pixels x 10 orientations = 4,000 dimensions) we develop a non-linear dimensionality reduction technique to reveal where the probability mass concentrates. In brief, we find that third-order statistics are necessary to predict the mean
and variance of excitatory long-range horizontal connections, but inhibitory connections are more uniform. This asymmetry agrees with physiology. Contingency table tests confirm statistical validity.

I-70. What kinds of local motion signals are present in naturalistic movies?

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Extraction of motion from visual input plays an important role in many visual tasks, such as separation of figure from ground and navigation through space. Motion analysis begins with the extraction of local motion signals. Several kinds of local motion signals have been distinguished based on mathematical and computational considerations (for example, Fourier and non-Fourier), but little is known about their prevalence in the real world. Here we address this by examining the strength of each kind of local motion signal in naturalistic movies. To approach this question, we first note that all local motion signals are characterized by correlation in a slanted spatiotemporal region. Specific different kinds of local motion signals correspond to specific region shapes and orders of correlation. Fourier motion, for example, corresponds to pairwise correlation in two checks, arranged on a slant in space-time. Non-Fourier motion, as identified by Chubb and Sperling (1988), corresponds to motion of a simple feature, such as an edge or a luminance change, independent of the sign of that feature. This is equivalent to a fourth-order correlation in a spatiotemporal parallelogram. A third kind of local motion signal, “glider motion” (Hu et al., 2010) corresponds to third-order correlation within a spatiotemporal triangle. Thus, the prevalence of local motion signals in natural scenes can be estimated by determining the extent to which these correlations are present in spacetime patches of binarized movies. We apply this technique to several Hollywood movies. The results show that all three kinds of motion signals are present. The proportions are relatively constant across movies, but from scene to scene, different kinds of motion signals predominate. This suggests that the different kinds of motion signals are non-redundant, and raises the possibility that the different kinds of motion signals occur in distinct contexts.

I-71. Sparse coding neurons encode individual vocalizations in complex auditory scenes

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Many animal species communicate with one another vocally, often in a distracting acoustic background. Although psychophysical experiments and everyday experience suggest that the brain filters background sounds to focus on a single vocalization (“the cocktail party effect”), the neural correlates of this ability remain unclear. Here, we experimentally characterize a putative neural mechanism for extracting important signals from complex sensory scenes. We trained songbirds to behaviorally discriminate among vocalizations presented in a distracting acoustic background and we recorded from individual neurons at multiple stages of the auditory pathway. We found that the neural representation of vocalizations transformed from a continuous and redundant code in early auditory areas into a sparse and distributed code in later regions of the auditory system. In contrast to continuous firing neurons, sparse coding neurons were better at extracting individual vocalizations from a distracting background, commensurate with psychophysical findings. Sparse coding neurons extracted vocalizations from auditory scenes at higher levels of background sound; retained a noise-invariant spike-train pattern in the presence of low background sound; and abruptly stopped firing when the background reached a critical threshold. Using electrophysiology, pharmacological manipulations and simulations, we characterized a simple neural circuit of fast excitation and delayed and recurrent inhibition that transforms a continuous input into a sparse output.
This same circuit also shuts down during auditory scenes with high levels of background sound, consistent with physiology.

I-72. A normative theory of Weber’s law

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A diverse array of studies have shown that discrimination thresholds for sensory variables are often proportional to the stimulus magnitude, a phenomenon known as Weber’s law. Typical explanations invoke a finely tuned combination of a nonlinear neural representation and noise in neural responses. For instance, one such explanation assumes that neural responses are sensitive to the logarithm of the sensory variable (or the ratio of sensory variables) corrupted by noise with fixed variance. We propose a purely computational explanation for Weber’s Law which does not require an appeal to internal representation or noise. Rather, it arises purely from the statistical nature of the problem faced by the brain. For example, imagine having to estimate the number of items in a scene. If we treat the items as blobs of activity in feature maps, the total sum of the activity provides a numerosity estimate. If the variability within the feature map is independent, the variance of the estimate scales with the mean numerosity, in violation of Weber’s Law which predicts that the variance scale with the square of the mean. However, the independence assumption is problematic because activity in such maps is likely to be scaled by global parameters which vary from trial to trial such as the overall luminosity in the image or the level of attention. The presence of such global scaling parameters correlates neural activity in such a way that the variance of the total sum scales with the square of the mean, thus yielding Weber’s law. We argue that this simple intuition can be generalized to more complex situations by showing that optimal inference in scale mixture models such as the Gaussian Scale or Gamma-Gamma mixture models precisely replicate Weber’s Law when the variance of the scale parameter is large enough.

I-73. Efficient coding of visual motion signals in the smooth pursuit system

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Performance in sensorimotor behaviors guides our understanding of many of the key computational functions of the brain: the representation of sensory information, the translation of sensory signals to commands for movement, and the production of behavior. Eye movement behaviors have become a valuable testing ground for theories of neural computation because the neural circuitry has been well characterized and eye movements can be tightly coupled to cortical activity. Here we show that smooth pursuit eye movements, and the cortical sensory signals that mediate them, demonstrate the hallmarks of efficient coding. Barlow proposed that neurons adapt their sensitivity as stimulus conditions change in order to maintain efficient coding of sensory inputs. Evidence for efficient coding of temporal fluctuations in visual contrast has been observed in the retina, thalamus, and visual cortex. We asked whether adaptation to stimulus variance generalizes to higher cortical areas whose neurons respond to features of visual signals that do not drive adaptation in the periphery and whether such adaptation impacts performance of visually-driven behavior. Specifically, we studied the impact of adaptation to dynamic fluctuations in motion direction on smooth pursuit. We recorded eye movements of monkeys pursuing moving targets with an added stochastic perturbation. We found that the amplitude of the linear filter that relates eye to target movement rescaled in proportion to target motion variance, consistent with the efficient coding hypothesis.
Steps in target motion variance create a transient decrease in the information capacity of pursuit behavior (either a low to high variance transition or vice versa). To test whether the adaptation to motion variance arises in the visual system, we recorded single units in the middle temporal cortical area (MT). The linear component of MT neuron responses (e.g. spike-triggered average stimulus) also rescales with target motion variance consistent with the effect on pursuit.

I-74. Stereotyped and diverse computations in third order olfactory circuits

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Summary: Understanding central odor representations is of fundamental importance to neuroscience. However, basic principles of higher order olfactory processing remain poorly understood. In vertebrates and invertebrates, secondary olfactory neurons project to multiple distinct third order areas. It has been proposed as a basic principle that these anatomically distinct areas are functionally specialized such that they fall into two broad categories: those that perform primarily associative computations and underlie olfactory learning capabilities, and those that perform stereotyped computations and mediate innate olfactory behaviors. While the “associative” areas have received considerable attention, the “stereotyped” areas have received less scrutiny. In fact, there exists little physiological evidence for this sort of stereotypy in any animal. Here we describe sensory representations in the lateral protocerebrum, a putative “stereotyped” area in the olfactory system Drosophila melanogaster. We describe two different computations that are performed by anatomically distinct and genetically identifiable types of third order neurons that reside in this area. Using in vivo whole cell electrophysiology combined with genetic labeling, we demonstrate that indeed, the computations performed by both of these neuron types are stereotyped across individual flies. Moreover, using dual whole-cell recordings, we show that the feedforward connectivity that underlies these computations is also stereotyped across individuals. In particular, each of these neuron types receives direct input from specific second-order neurons residing in identified olfactory glomeruli. Having identified presynaptic partners for our third order neurons, we describe the transformation of odor representations as they travel into this higher brain region. We compare and contrast connectivity and transformations for these two neuron types and show that while one type appears to simply sum direct excitatory inputs from multiple glomeruli, the other combines direct excitation with strong indirect inhibition. We propose a functional role for each computation and describe our preliminary work on testing our proposals.

I-75. Sensation of a “noisy” whisker vibration in rats: Psychometric and neurometric analysis

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We have devised a delayed comparison task for rats; they discriminate between two stimuli delivered to their whiskers. The rats learn to position their snout in a nose hole such that their head is stationary and their right-side whiskers are firmly in contact with a plate that delivers motion along the anterior-posterior axis. Each stimulus is a sequence of position values drawn from a truncated Gaussian distribution with standard deviation denoted as S. The first stimulus is called “base” (defined by S1) and the second stimulus “comparison” (defined by S2). In the standard protocol, the duration of the base and comparison stimuli both are 400ms. By considering trials with S1 fixed while S2 spans a range of values, we construct psychometric curves. Performance is above 75%
correct when the Standard Deviation Index (STDI) defined as the absolute value of |S1-S2|/(S1+S2)—is larger than 0.1. It has been debated how sensory systems accumulate stimulus information over time. To investigate this, we varied the duration of the comparison stimulus: 200, 400, or 600ms. The rats’ performance improved for longer comparison stimuli, suggesting that for stimuli with a probabilistic structure, evidence can be accumulated over time. A preliminary analysis of neuronal activity from anesthetized rats provides support for a simple model where (i) both firing rate and spike count are correlated with the stimulus position standard deviation S; and (ii) differences in both firing rate and spike count could be decoded to allow comparison of the base and comparison stimuli in 400ms condition. The change in performance as a function of variable stimulus duration suggests that firing rate is a better candidate than spike count as the decoded feature, in contrast to previous studies.

I-76. Neural processing of social signals in the medial amygdala

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All animals must recognize conspecifics to carry out social interactions that ensure individual survival and the transmission of genes to subsequent generations. In many species, signals essential for guiding social interactions are communicated by the emission and detection of specific chemical cues. Rodents rely heavily on the vomeronasal system (VNS) to guide innate behaviors including: predator avoidance, territorial defense, mating, and parenting. An important goal is determining how sensory signals transduced by the vomeronasal organ (VNO) are transformed to elicit adaptive behaviors. Recent studies have revealed the molecular logic within the sensory epithelium of the VNO by which different vomeronasal receptors extract biological information: including sex, species, and physiological status, about animals in the immediate environment. This information is processed by subsequent nuclei of the VNS including the accessory olfactory bulb (AOB) and the medial amygdala (MeA). At present, little is known about how sensory information is processed within this serial network or how this information is used to guide adaptive behaviors. We recorded the electrophysiological activity of single units using a novel anesthetized preparation in order to reveal the sensory representation in the MeA. These experiments demonstrate a set of emergent properties not present in the VNO or AOB including: the topographical segregation of sensory responses into distinct subnuclei of the MeA, a sharpened representation of the sensory stimulus space, and the emergence of sexual dimorphic responses to reproductively relevant cues. We believe that these changes reflect an important stage in the translation of sensory cues into adaptive behavior. Indeed, these sexually dimorphic responses are not present in juvenile animals or in mice with perturbed sex-steroid signaling. Taken together, these results offer new insights regarding how the VNS processes social cues and provide a new avenue to investigate how differences in neural circuitry lead to individual differences in behavior.

I-77. Summary statistics in auditory perception

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Sensory signals are transduced at high resolution, but their structure must be stored in a more compact format. We hypothesize that time-averaged sound statistics form a perceptual code used by the auditory system to summarize the acoustic structure of natural sounds. To explore this hypothesis, we generated synthetic sound stimuli
using a recently developed model of auditory texture representation (McDermott & Simoncelli, 2011). The synthesis procedure shapes samples of noise to have the same summary statistics as a target sound (despite having a completely different acoustic waveform), matching the moments and pair-wise correlations of simulated cochlear channel envelopes and their modulation bands. We conducted experiments with excerpts of five-second signals synthesized to have the same statistics as a real-world sound texture (rain, fire, etc.). The summary statistics of different excerpts were variable when the excerpts were short, but converged to the statistics of the full-length signal as the excerpt length increased. We first presented listeners with excerpts from two signals with distinct statistics, asking them to judge whether the excerpts arose from the same sound source. Performance improved with excerpt duration, presumably because the summary statistics that differentiate different sound types are more accurate for longer excerpts. We then presented excerpts of two different exemplars synthesized from the same summary statistics, and asked listeners to judge whether these were identical. Performance in this task was good for short excerpts but paradoxically declined with duration, even though the longer sounds contain more information to support discrimination. The results can be explained by supposing that listeners represent sounds with time-averaged statistics, such that discrimination of two sounds becomes difficult as their summary statistics converge to the same values. Such statistical representations produce good categorical discrimination, but limit the ability to discern fine-grained temporal detail.

I-78. The neural representation of behaviorally relevant acoustical sequences

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Sensory events unfold in time, and the relative positioning of events is particularly important in speech and language perception. Vocal production in songbirds, a model for human speech production and perception, shows temporal structure at multiple hierarchical levels, including sequencing of ethologically relevant auditory objects (motifs), and European starlings are sensitive to this structure when using song to identify other starlings. Responses in mammalian auditory cortex can be modulated by earlier acoustical events, but it is unclear whether these long timescale (800+ ms) response dependencies reflect learned statistical properties of the environment. To explore the neural representations of learned sequences, we trained starlings on an operant conditioning task in which the only relevant information available to solve the task were transitions between motifs. We show that starlings can discriminate between strings of motifs based solely upon transition statistics, independent of motif identities. Subject performance covaried with trial difficulty. In the face of ambiguity, performance is consistent with accumulating evidence from individual transitions during the presentation of a string and differentially weighing learned transition cues. Importantly, this training protocol establishes behaviorally meaningful transitions (associated with either reward or no reward, or are non-diagnostic) which can then be used to explore the neural representation of behaviorally meaningful sequences, independent of representations of individual motifs. After birds reached criterion performance, we recorded extracellular single units and local field potentials from a region in the starling forebrain analogous to auditory cortex. We find that approximately half of recorded units in NCM show sensitivity to motif transitions (i.e., responses during the second motif in a pair are modulated by both the first and second motif), indicating that sequence information is represented in the spiking response. Further analyses explore the extent to which behaviorally meaningful transitions are represented by spiking and local field potential activity.

I-79. Feedback from retinal ganglion cells to the inner retina

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Feedback from retinal ganglion cells to the inner retina
Retinal ganglion cells are thought to be strictly postsynaptic within the retina. They carry visual signals from the eye to the brain, but do not make chemical synapses onto other retinal neurons. Nevertheless, they do form gap junctions with other ganglion cells and with amacrine cells in the inner retina. This provides a possible route for ganglion cell signals to feed back into retinal circuitry via electrical connections. To investigate this issue, we electrically stimulated the optic nerve emerging from an isolated salamander retina. Simultaneously we presented visual stimuli and recorded the firing of many ganglion cells using a multi-electrode array. Here we report that optic nerve shock has pronounced effects on the activity of retinal ganglion cells. In absence of a visual stimulus, the optic nerve shock produced immediate antidromic spikes (at a delay of \( \sim 1 \) ms) followed by a period of enhanced firing (10s of ms) and a suppression of firing on longer time scales (100s of ms). However, the proportion and time course of the two effects varied greatly among ganglion cells. These modulations were largely eliminated by blocking gap junctions pharmacologically, suggesting that the feedback pathways from ganglion cells involve electrical synapses. By pairing the nerve shock with visual stimulation, we encountered a rich set of changes in the light response. Both the gain and the kinetics were affected, in either direction, and at various delays from the optic nerve shock. Thus it appears that ganglion cells are actively involved in visual computations rather than merely collecting postsynaptic signals from the inner retina. Several feedback pathways seem to contribute, accounting for the diversity of affected response patterns. Taken together, these results suggest that the principal neurons of the retina do participate in a recurrent circuit, much as has been demonstrated elsewhere in the brain.

I-80. Evidence for a class of dLGN neurons with extra-strong classical surrounds in the awake rat

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Classical center-surround antagonism in the early visual system is thought to serve important functions such as enhancing edge detection and increasing sparseness. The resulting image representation depends upon the relative size and strength of the center and surround of each neuron. Surround strength has been measured in the retina, dorsal Lateral Geniculate (dLGN), and primary visual cortex (V1), mostly in anesthetized preparations. Response properties in the dLGN differ in awake and anesthetized conditions, however (Alitto et al, 2011). We revisit the center-surround architecture of dLGN neurons in the un-anesthetized rat. We report the spatial frequency tuning responses of \( N = 68 \) neurons and fit these tuning curves to a classic difference-of-Gaussians (DOG) model of the spatial receptive field. We find that some dLGN neurons in the awake rat have weak surrounds, but the majority have well balanced center and surround weights. Surprisingly, a substantial fraction of neurons have a stronger surround than center. Within the space of DOG models, strong surrounds were necessary and sufficient to explain the bimodal tuning curves we observed in spatial frequency tuning data of these cells. These results indicate that prior measurements of the classical surround obtained from measurement in anesthetized preparations may be an underestimate.

I-81. Probing mechanisms of contrast adaptation in retina with modeling of synaptic currents and spikes

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Nonlinear processing in retinal ganglion cells has been implicated in a variety of response properties important
for natural vision, including adaptation to stimulus contrast and the generation of temporal precision. Here, we use nonlinear modeling applied to in vitro recordings from mouse retinal ganglion cells (RGCs) to understand how nonlinear response properties are derived from RGC synaptic input and computations within each neuron. RGCs were recorded both in cell-attached mode (spikes) and whole-cell voltage-clamp mode (excitatory synaptic currents), and later classified using dendritic stratification. We focus on off-alpha RGCs, which strongly adapt to contrast, and additionally have transient synaptic currents not explained by standard linear-nonlinear cascade modeling. A more complex nonlinear model applied to both synaptic currents and spikes reveals that both the effects of adaptation and precision can be largely explained by a nonlinear “suppression” that is delayed relative to the neuron’s excitatory input. Furthermore, this suppression can be predicted by a simple two-parameter synaptic depression model acting on the modeled excitatory inputs. Such a description of contrast adaptation is an alternative to gain control models based on feedback from contrast sensors in the retina, and works as follows. Synaptic depression generates transient responses at high contrast, but has a much smaller effect at low contrast, when there is much less depletion of synaptic resources. The resulting contrast-dependent modulation of synaptic depression contributes to familiar changes in processing at high contrast: lower gain and faster temporal filtering. Furthermore, modeling describes how these effects of adaptation are accentuated through interaction with spike generation. The resulting nonlinear processing in the retina appears to be amplified in downstream areas and fundamentally shapes the information used by the rest of the visual system.

I-82. Decorrelation of retinal response to natural scenes by fixational eye movements

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Fixational eye movements are critical for vision since without them the retina adapts fast to a stationary image and the entire visual perception fades away in a matter of seconds. Still, the connection between fixational eye movements and retinal encoding is not fully understood. To address this issue, it was suggested theoretically that fixational eye movements are required to reduce the spatial correlations which are typical for natural scenes. By analyzing a model of retinal ganglion cells, which are the only cells that send axons from the retina to the brain, it was shown that the spatial correlation between ganglion cells is significantly reduced when fixational eye movements are present. These reduced correlations can yield a compact representation of the visual information when it is sent to the brain. The goal of our study was to put this theoretical prediction under experimental test. Using a multi electrode array, we measured the response of the tiger salamander retina to movies which simulated two types of stimuli: fixational eye movements over a natural scene and flash followed by static view of a natural scene. Then we calculated the cross-correlation in the response of the ganglion cells as function of receptive fields distance. We found that when static natural images are projected, strong spatial correlations are present in the neural response due to correlation in the natural scene. However, in the presence of fixational eye movements, the level of correlation in the neural response drops much faster as function of distance which results in effective decorrelation of the channels streaming information to the brain. This observation confirms the prediction that fixational eye movement act to reduce the correlations in retinal response and provides better understanding of the contribution of fixational eye movements to the information processing by the retina.
I-83. The role of nonlinear phase processing in photoreceptors

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Fly photoreceptors transform visual information into graded voltage responses and shape the first neural image in the retina. It is well known that photoreceptor responses to naturalistic stimuli are nonlinear (van Hateren 1997) whereas Gaussian white noise (GWN) stimuli linearize the response (Juusola 1994). Using a nonlinear photoreceptor model with integrated gain control, which accurately predicts Drosophila photoreceptor responses over a wide range of light intensities, we demonstrate that nonlinear phase processing plays a crucial role in linearizing photoreceptor responses to GWN stimuli. By exploiting the recently developed concept of Nonlinear Output Frequency Response Functions (Lang 2007) we were able to decompose the photoreceptor responses into linear, second- and higher-order responses, allowing us to characterize their relative contribution to the overall photoreceptor response in time as well as in the frequency domain. We show how the magnitude and phase of the nonlinear generalized frequency response functions are tuned such that GWN stimuli do not elicit a nonlinear response. In contrast, the nonlinear component of the response is stronger to stimuli patterns which exhibit a high degree of phase coherence. We find striking evidence that the photoreceptor’s nonlinear responses correlate highly with a local phase congruency measure, which is widely used for edge detection in image processing. Finally, we propose a simple circuit by which local phase coherence information encoded by the nonlinear component of the photoreceptor response can be extracted from the overall photoreceptor response.

I-84. Humans integrate motion information using noise adaptive filters

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Visual processing of motion requires mechanisms that can calculate the temporal derivative of location. If information is perfectly noise-free it is possible to use an instantaneous estimate of the derivative. But the natural environment presents us with stimuli that have a wide range of signal-to-noise ratios (SNR). In the presence of noise an instantaneous derivative measure becomes unreliable and it is necessary to smooth over time in order to generate an accurate estimate. However, in a causal system, increasing integration time comes at the cost of increasing the lag between the input to the system and its output. Therefore, an optimal system would dynamically modulate its integration time in response to changes in the SNR of the incoming information. Motion perception has classically been modeled as a set of fixed spatio-temporal filters applied by neurons in early visual cortex. We propose a variant of this motion-energy model that uses filters that adapt their spatio-temporal integration as a function of the SNR of the stimulus. We tested the adaptive filter model of motion processing in humans by fitting our model to both psychophysical and EEG data. The high temporal resolution of EEG allowed us to measure how quickly neural responses followed changes in motion coherence. We found that neural responses were faster for stimuli with a high SNR, consistent with an adaptive system. In the psychophysical task we measured participants’ thresholds for detecting sinusoidal oscillations of motion direction (“wiggles”). We found that participants’ sensitivity to high oscillation rates increased as stimulus SNR increased. Both the EEG and the psychophysical results demonstrate that neurons in early visual areas change their integration time in response to the statistical reliability of the visual stimulus.
I-85. Adaptive sampling of visual stimuli in cortical neurons

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Neurons in the visual system have been characterized for decades using predefined sequences of stimuli that sample a limited portion of sensory space. Ideally, it should be possible to adaptively modify the stimuli for each individual neuron to explore larger portions of stimulus space in a “closed-loop” manner (i.e. the stimuli are modified based on the response of the neuron). We have tested different approaches of adaptive stimulus sampling on responses of single neurons in the visual cortex (area V1) in cat. At this time, one of the most successful approaches is a Particle Swarm Optimization (PSO) algorithm that optimizes sequences of spatiotemporal noise pixels. The PSO is a population based technique in which particles move around in a search-space to locate the optimum. Social interactions among particles (and the history of individual particles) are then used to update the particles positions. In our case, a particle represented one sequence of spatiotemporal pixels and the search-space was the entity of the luminance values of all pixels. The PSO algorithm was able to optimize stimulus sequences to drive strong and reliable responses in both linear and nonlinear cortical neurons. Preliminary results suggest that the optimization is remarkably restricted in cortical space (i.e. neighboring V1 neurons that were just a few hundred microns away from the optimized neuron did not show robust increases in firing rate during the optimization process). Taken together, adaptive sampling provides a powerful approach to optimize white noise stimuli for single V1 neurons with linear and nonlinear receptive fields. Our preliminary data suggests that this optimization can be remarkably restricted in cortical space, providing new insights into the amount of redundancy in the visual cortex. Support: NIH Grant EY02067901 and EY05253 [1] Kennedy J, Eberhart R (1995) Particle swarm optimization. Neural Networks 4:1942-1948

I-86. Presaccadic modulation of visual responses in area V4 measured simultaneously across cortical layers

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Visual and saccade preparation-related representations converge in extrastriate cortex, yet little is known about how these signals are integrated within neocortical microcircuits. Specifically, how does the representation of top-down visual and bottom-up saccadic information differ between cortical layers? To address this issue, we recorded simultaneously from all cortical layers of macaque area V4 during a task involving saccades to receptive field stimuli. The behavioral paradigm was designed to isolate in time the onset of saccadic and visual signals in V4. The electrode arrays consisted of single shafts with 16 recording sites each spaced 150µm apart (Plexon, Inc.). We recorded spiking activity and local field potentials from each of the 16 sites simultaneously. In order to record from different layers in the same cortical “column,” we inserted the electrode arrays into V4 perpendicularly to the cortical surface, confirmed by measured RF alignment. To determine the laminar positions of the recording sites, we used current source density analysis, which allowed identification of four distinct functional layers. Similar to previous studies, we find that the visual responses of V4 neurons are significantly enhanced by the preparation of saccades to RF stimuli. In addition, this novel recording approach allows us to examine the laminar pattern of presaccadic modulation including differences in the magnitude and timing of these modulations across all layers within the cortical column. These data comprise a fundamentally novel view of the interaction between feedforward and feedback visual information in the neocortex of awake, behaving animals.
I-87. Predicting functional connectivity in primary visual cortex

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The responses of neurons in primary visual cortex to repeated presentations of the same stimulus are highly variable. Much of this variability is shared across neurons. The structure of shared variability is called functional connectivity which is usually measured by the correlation coefficient, or noise correlation. The strength and origin of noise correlations are hotly debated. We asked how these and other factors work together in determining noise correlations, and established their relative importance. Further, we asked whether simple and complex cells differ in their functional connectivity. Since noise correlations can depend on firing rate purely due to a threshold non-linearity, we had to separate the contributions of firing rate and linearity of spatial summation as measured by the F1/F0 ratio. We did so in two ways: first, by regressing noise correlations onto a comprehensive set of potential factors, thereby taking interactions into account. Second, we used the Dichotomized Gaussian Model (DGM) which removes firing rate effects caused by rectification. We analyzed spike trains 31,412 pairs. The resulting regression model is a compact description of the structure of noise correlations and explains ~60% of the variance (cross-validated). We find that noise correlations grow with firing rate, which is their strongest determinant. The next strongest determinants are proximity in cortex and similarity of orientation tuning. In addition, we find a clear effect of the pair’s F1/F0 ratio: complex cells are more noise correlated than simple cells. The DGM strongly reduces the effect of firing rate modulation. It confirms all other findings. We conclude that firing rates are most predictive for noise correlations, and that their effect is largely due to simple rectification. We also find that complex cells are more noise correlated and generally more variable in their response, probably because they participate more in the network activity.

I-88. Visual cortex learns novel representations under anesthesia

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The activity of neural populations has the tendency to adapt to the statistics of the environment [Berkes et al., 2011, Sotiropoulos et al., 2011]. Here we explore the adaptation of neuronal responses to visual stimuli in cat area 17 under anesthesia. Repeated exposure to a set of images (26 letters and 8 digits) changed the response properties of the neuronal population (63 units) such that stimulus classification steadily improved over time. We applied linear and non-linear classification methods (see [Nikolic et al., 2009]) to investigate the presence of stimulus-related information in the spiking activity of neuronal ensembles across several hours-long recording sessions (1700 trials). The classification performance of letter identity based on short integration intervals (20ms) of evoked responses reached up to 25% correct (chance level = 3%). Most importantly, the performance improved gradually with the amount of stimulus exposure and was not accounted for by fluctuations in spike rate. Next, we increased the difficulty of the task by performing a classification which relied on the detailed representation of stimulus features. A 12x12 array of readout neurons was trained to reconstruct the original stimulus based on the population activity within a single 20 ms window. The readouts were able to generalize across stimuli and could reconstruct letters omitted from the training set. Most interestingly, however, during later trials in the experiment, the spiking patterns of the spontaneous population activity began replaying the activity evoked by previously shown stimuli. The results suggest that efficient visual discrimination of familiar stimuli is achieved partly through separation of neuronal representations already at the level of the primary visual cortex. Also, these newly learned representations seem to be reactivated spontaneously. Given that the experiments were
performed under anesthesia, this process is likely to involve local mechanisms independent of attention and conscious control.

I-89. Co-variability of spontaneous synaptic excitation and inhibition in visual cortex

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Spontaneous activity may be a signature of neural circuitry, is modulated by behavioral state, and affects stimulus encoding and synaptic plasticity. Here we estimate the co-variability of spontaneous synaptic excitation and inhibition in the pentobarbital-anesthetized rat visual cortex. We measured synaptic currents at various membrane potentials with in vivo whole cell voltage clamp recordings. Assuming an isopotential neuron with linear current-voltage relation and ergodic spontaneous activity yields a quadratic relation between synaptic current variance and membrane potential whose coefficients are excitatory and inhibitory conductance covariances. Fits of the observed synaptic current variances to the quadratic relation provide 90% confidence lower limits for the cross-correlation coefficient, averaged across the population, of $0.2 \pm 0.1$ (std). The upper limits for the cross-correlation coefficients are sensitive to the assumed reversal potential and thus only weakly constrained. We estimate stronger upper limits to the cross-correlation coefficients by further assuming that the synaptic currents are filtered Poisson processes. This assumption is consistent with the observed synaptic currents consisting of distinct events whose inter-event intervals were approximately exponentially distributed. Across neurons the excitatory Poisson rate of a neuron was 2.7 times greater than its inhibitory Poisson rate. We estimate the maximum cross-correlation given a greater excitatory than inhibitory rate via a model in which the inhibitory rate is entirely due to a filtered Poisson process that is also a source of the excitatory rate, with the remainder of the excitatory rate provided by an additional independent filtered Poisson process. The maximum cross-correlation coefficient is unity when excitatory and inhibitory rates are equal, and decreases as a power law function of the excitatory to inhibitory rate ratio. An excitatory to inhibitory rate ratio of 2.7 corresponds to a maximum cross-correlation coefficient of 0.6. The greater excitatory rate suggests that inhibitory neurons spike less frequently or more synchronously.

I-90. Model-based analysis of 3D surface representations in human visual cortex

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Neurons sensitive to binocular disparity are widespread in visual, temporal and parietal cortices. Human fMRI suggests that dorsal visual areas are particularly engaged by stereoscopic stimuli, but what do these areas encode? We test responses to an important 3D property, surface slant. We set out to distinguish representations of slant from lower-level stimulus covariates such as local disparities or edges. We measured fMRI responses while participants (n=8) viewed random dot stereograms depicting slanted planes ($\pm 7.5$ to 52.5 deg in 15 deg steps) in a blocked design. We developed a cross-correlation voxel similarity measure to evaluate fMRI responses in regions of interest in the visual cortex. Specifically, we correlated the vector of voxel responses evoked by a given slant with those evoked by other slants, testing for similarity/dissimilarity between slants. We further compared responses in control conditions that addressed changes in (i) overall disparity (disparity control) and (ii) changes in projection size (spatial control) that result from rotating surfaces in depth. To evaluate the computations performed in different visual areas, we developed a model that comprised five detector mechanisms: (1) filters tuned
to disparity; (2) disparity edge-detectors; (3) disparity gradient detectors; (4) units tuned to retinotopic extent; and (5) units responding to size. We then used model responses to different slants as regressors for the empirical cross-correlation matrices. We show that fMRI responses to slanted surfaces are gradually transformed in the dorsal visual pathway, from representations of edges in early (V1, V2) cortex to responses reflecting disparity gradients in V3A. Further, V3A responses are highly similar when the same slant is depicted, irrespective of changes in edge locations or disparity range. Our results suggest that surface slant is encoded in intermediate portions of the dorsal visual hierarchy, suggesting a potential locus for neuronal computations that underlie slant perception.

I-91. Inferred functional circuitry in a microcolumn of cat visual cortex

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We attempt to elucidate the circuit structure of a single cortical microcolumn by simultaneously recording units from all layers of cat visual cortex and fitting probabilistic models to this data. While much research has gone into the anatomical basis of connectivity between laminae, we focus on functional circuit structure inferred from activity evoked by visual stimulation. We analyze how circuits are dynamically remapped in response to grating and natural movie stimuli by fitting Ising models to pairwise correlations between units. In particular, we focus on the question of whether gamma oscillations in response to preferred stimuli are accompanied by changes in the functional connectivity. Recordings were made from anesthetized cat area 17 using 32-channel laminar silicon probes, simultaneously recording from 33 single units with spikes binned at 10ms. Because Ising models of this size are computationally challenging to estimate by maximum likelihood, we use Minimum Probability Flow learning, which is a novel estimation method that circumvents the need to compute the computationally expensive partition function. To alleviate the problem of overfitting in high-dimensional models with limited data, we applied L1-regularization to the parameters. The result of this model fitting procedure is a coupling matrix that describes all pairwise interactions between units. The coupling terms of this matrix reveal excitatory interactions between layers II/III and V/VI. Cross-correlation analysis is consistent with elevated gamma activity sharpening this coupling. Inhibitory interactions are more specific and can be tracked to putatively identified inhibitory interneurons. Additionally, there are global patterns of excitatory connections within layers II/III and V/VI as well as inhibition within layer V. This result is in agreement with the anatomically defined canonical microcircuit with strong excitatory connections from layer III to layer V as well as feedback connections back onto layer III.

I-92. Precise decoding of dynamical motion from a large retinal population

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Retinal ganglion cells perform several non-linear computations on moving objects. However, it is unclear how the representation of moving objects is distributed across the entire population of ganglion cells. To address this issue, we recorded a large (100-200) population of ganglion cells with a large, dense array, while displaying a bar animated with random, Brownian motion. The position of the bar could be reconstructed from retinal activity with very high precision using a linear decoder taking a large population of cells as input. Reconstruction using a
second order decoder did not lead to a significant improvement in quality. We estimated the decoding error as a function of both bar position and trajectory frequency. We found the minimal error to be below the average spacing between pairs of cones for a broad range of frequencies, indicating that the decoding performance was in a regime of hyperacuity. This high precision was made possible thanks to the large number of cells recorded: performance increased with the number of cells used for decoding, slowly reaching a plateau of high correlation between real and estimated trajectories ($r=0.9$) towards 70 cells. We estimated the mutual information between real and estimated stimulus trajectories for subsets of cells with different sizes. For up to 10 cells, the mutual information estimated this way could be predicted by summing the mutual information obtained for each cell individually, indicating there was little redundancy between them. However, for larger groups, a significant and increasing redundancy was found. These large-scale recordings showed that the cells did not carry the information about a moving object independently. Rather, they conveyed redundant information, and accumulating a large number of these redundant cells was necessary to decode precisely the stimulus trajectory.

I-93. Dealing with sequential dependencies in psychophysical data

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Psychophysical experiments are the standard approach for quantifying functional abilities and properties of sensory systems, and for linking observed behaviour to the underlying neural mechanisms. In most psychological experiments, human observers or animals respond to multiple trials that are presented in a sequence, and it is commonly assumed that these responses are independent of responses on previous trials, as well as of stimuli presented on previous trials. There are, however, multiple reasons to question the ubiquitous assumption of “independent and identically distributed trials”. In addition, it has been reported that inter-trial dependencies are pronounced in behaving animals (Busse et al, 2011, J Neurosci). These observations raise two central questions: First, how strong are sequential dependencies in psychophysical experiments? Second, what are statistical methods that would allow us to detect these dependencies, and to deal with them appropriately? Here, we present a statistical modelling framework that allows for quantification of sequential dependencies, and for investigating their effect on psychometric functions estimated from data. In particular, we extend a commonly used model for psychometric functions by including additional regressors that model the effect of experimental history on observed responses. We apply our model to both simulated data and multiple real psychophysical data-sets of experienced human observers. We show that our model successfully detects trial by trial dependencies if they are present and allows for a statistical assessment of the significance of these dependencies. We find that, in our datasets, the majority of human observers displays statistically significant history dependencies. In addition, we show how accounting for history dependencies can lead to changes in the estimated slopes of psychometric functions. As sequential dependencies are presumably stronger in inexperienced observers or behaving animals, we expect that methods like the ones presented here will become important tools for modelling psychophysical data.
I-94. Diverse Network Representations of Risky Decision-Making in mPFC

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The medial prefrontal cortex (mPFC) is critical for decision making involving cost/benefit evaluations. Recent studies in rodents suggest that decisions involving risky outcomes engage the mPFC to integrate information about changing reward probabilities in order to update value representations. However, the neural mechanisms underlying this form of decision-making are largely unknown. To investigate this issue we used a task that consisted of 4 discrete blocks of trials in which a response on safe lever always delivered one food pellet, whereas a response on risky lever delivered four food pellets with decreasing probability (100, 50, 25, 12.5%) as blocks of trials progressed. Rats trained on the task were then implanted with 16 drivable tetrodes bilaterally into the mPFC. From the unit recordings we generated population instantaneous firing rate (iFR) vectors and using various statistical methods we evaluated the distinction between clusters of points in the N-dimensional space (where N=number of recorded units). Individual mPFC neurons displayed behaviorally correlated discharge patterns in response to a number of distinct aspects of the task, including large/risky vs. small/safe lever presses and reward epochs across trial blocks. At the population level we reliably observed distinct network activity states when animals were making risky decisions under the different probabilities of risk. These network states displayed adaptive encoding in that they became more distinct from one another as the relative difference in risk increased. This analysis reveals that mPFC networks are not encoding pure representations of risky lever reward probability levels but rather are forming relative representations of probability that indicate the size of the changes in probability over multiple blocks. While the mPFC tracks diverse aspects of behavior, in this case PFC ensembles employed an adaptive and relative encoding scheme for rewards that could guide behavior in situations with changing reward probabilities.

I-95. How criticality of visuo-motor control behaviour depends on task objective.

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When humans perform closed-loop control tasks like standing upright or balancing a stick, their behavior exhibits spatiotemporal scaling suggesting operation close to a critical point. Prominently, control errors during balancing are power-law distributed. A possible explanation is self-tuning of the control system to a critical point due to the annihilation of local information by adaptive predictive control. A simple model based on this principle was shown to reproduce many experimental findings. This model makes several predictions, including that the underlying neuronal control system continues to be adaptive even when the controlled system itself is stationary. This seemingly irrational behavior is caused by the controller trying to eliminate local random trends in its interaction with the controlled system over short time scales close to its reaction time. We performed virtual balancing experiments to test the theoretical predictions. Most notably, we found the subjects’ behavior to be dramatically dependent on the utilized reward function. The existing model was found to be an excellent description for subjects trying to minimize mean squared controller-target distances. Given a different reward function, subjects displayed other solutions to the balancing problem that have not been reported before. Some of these solutions which do not exhibit power-law fluctuations can be explained by simple modifications to the existing model. Our results
provide important constraints for possible neuronal implementations of visuo-motor control.

I-96. Maximum entropy models of social behavior reveal high-order interactions in groups of mice

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Social behavior is often quantified from measurements of how an animal interacts with one other animal of its own kind, and not in the context of a group. However, the behavior of groups as a whole, and of individuals within a group, may arise from complex network of dependencies among them. We studied small groups of freely behaving mice in an ethological relevant environment, whose behavior was automatically tracked for several days with high temporal and spatial resolution. To uncover the underlying social interaction network of groups of animals, we built mathematical models of the joint activity patterns of the members of the group. We found that the location of a mouse in the arena, was significantly correlated and informative of the location of the other mice. Moreover, when predicting the location of a mouse the information that was gained from the locations of the other mice was synergetic when they were viewed as a group. We used a maximum entropy framework to model the distribution of mouse configurations, where the state of each animal was given as one of 10 locations in the arena. The maximum entropy model in this case is a generalized Potts model. We found that a pairwise maximum entropy model could account for less then 60% of all correlations among the mice; the third order model, explain 90% of the correlations or more. We then used the interaction terms in the generalized Potts model to construct a social interaction map between the mice. Finally, in spite of the variability in the interactions when we compared groups of mice with environmental or genetic variations we found that groups with similar backgrounds clustered together in terms of their distribution of states.

I-97. A retinotopic systems identification method reveals parallel visual streams in the fruit fly

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Figure tracking—the acquisition and pursuit of objects superimposed on a background—is a requirement of all high performance visual systems. One example of this behavior is the frontal fixation of vertical edges by flies in a rigid tether. While it is known that flies process panoramic motion cues along an Elementary Motion (EM) stream that computes coherent motion by correlating luminance measurements on the retina in space and time, we demonstrate that while figures may produce EM cues, flies employ a second, EM-independent figure motion (FM) subsystem to saccade toward and smoothly track visual figures. We show that (i) the two systems extract different information from a single time varying visual input; (ii) their characteristics vary differently across the visual field; (iii) the FM system superimposes saccadic turns upon smooth pursuit; (iv) the two systems in combination are necessary and sufficient to predict the full range of figure tracking behavioral capabilities, including those that...
generate no EM cues. The technical advance that enables this analysis is a non-stationary white noise based systems identification tool known as a SpatioTemporal Action Field (STAF). In the same way that a SpatioTemporal Receptive Field (STRF) is a piecewise linearization of the dynamics of a single cell’s membrane potential to stimuli confined to discrete locations within its receptive field, the STAF assigns a linear filter to each retinotopic position describing the flies’ steering effort perturbations in EM or FM optic flow. This analysis and the conclusions drawn by it expand the classical model that fly visual tracking is based solely on signals encoded by elementary motion detectors. In addition, the ability to perform system identification in a retinotopic manner constitutes a computational phenotype through which mutants with abnormal neural circuitry can be compared.

I-98. Odor detection vs. mixture categorization: crucial differences in behavioral and learning strategies

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In the visual system, multiple streams of information are processed in parallel by specialized channels to solve different problems. In olfaction, the problem of detecting the presence of a low concentration of an odor and the problem of distinguishing closely related odors make very different demands, but specialized neural processing strategies have yet to be identified. In order to address this issue, we studied odor detection and categorization in parallel in the same animals, using tasks that are identical except for the relevant stimulus parameters. Here we show that while most aspects of the behavior remain identical between tasks, two critical differences can be identified. First, we found that, whereas odor sampling times increased substantially when odor concentrations approached detection threshold, they remained almost constant as odor mixtures became closer to the category boundary. This was true even for categorization at threshold concentrations. We hypothesize that in odor detection, accuracy is limited by stimulus uncertainty, whereas in odor mixture categorization accuracy is limited by variability in the mapping of the stimulus to the response, which must be learnt by the subject on a trial-by-trial basis. Given this hypothesis, we investigated whether ongoing learning has a different influence on the choice strategy of the animals in detection and categorization. In both tasks there was a clear trial-by-trial updating of the animal’s choice function. However, whereas in mixture categorization choice bias increased with difficulty of the previous trial as well as the outcome, in odor detection this bias was dependent only on choice side and outcome. Thus, a detailed comparison of odor categorization and detection revealed differences in strategies both at the level of behavior (odor sampling time) and learning (trial-by-trial updating). These observations suggest differences at the neurophysiological level that can be tested by simultaneous recordings.

T-44.

II-1. Efficient coding of natural images and movies with populations of noisy nonlinear neurons

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Efficient coding provides a powerful principle for explaining early sensory processing. Most attempts to test this principle have been limited to linear, noiseless models, and when applied to natural images, have yielded localized oriented filters (e.g., Bell and Sejnowski, 1995). Although this is generally consistent with cortical representations, it fails to account for basic properties of early vision, such as the receptive field organization, temporal dynamics, and nonlinear behaviors in retinal ganglion cells (RGCs). Here we show that an efficient coding model that incorporates ingredients critical to biological computation – input and output noise, nonlinear response functions, and a metabolic cost on the firing rate – can predict several basic properties of retinal processing. Specifically, we develop numerical methods for simultaneously optimizing linear filters and response nonlinearities of a population of model neurons so as to maximize information transmission in the presence of noise and metabolic costs. We place no restrictions on the form of the linear filters, and assume only that the nonlinearities are monotonically increasing. In the case of vanishing noise, our method reduces to a generalized version of independent component analysis; training on natural image patches produces localized oriented filters and smooth nonlinearities. When the model includes biologically realistic levels of noise, the predicted filters are center-surround and the nonlinearities are rectifying, consistent with properties of RGCs. The model yields two populations of neurons, with On- and Off-center responses, which independently tile the visual space. As observed in the primate retina, Off-center neurons are more numerous and have filters with smaller spatial extent. Applied to natural movies, the model yields filters that are approximately space-time separable, with a center-surround spatial profile, a biphasic temporal profile, and a surround response that is slightly delayed relative to the center, consistent with retinal processing.

II-2. Optimally adapting heuristics: humans quickly abandon the constant bearing angle strategy

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Animals ranging from dragonflies through teleost fish to humans all intercept moving targets using the same strategy of adjusting their speed so as to hold the angle pointing towards their target constant over time. This constant-bearing-angle strategy has been suggested as a fundamental visuomotor heuristic and as an instance of Darwinian intelligence that overcomes the need for complex and expensive computations involving multiple sources of uncertainty. We consider the task of intercepting a moving ball for which many previous studies have shown that humans use this constant bearing angle strategy. Here we manipulated the observation function in a virtual reality setup so as to change the uncertainty of the balls position parametrically. Specifically, the contrast of the ball changes as a function of the heading angle towards the ball along the subject’s momentary trajectory. Subjects adjusted their interception strategy within an average of 26 trials and were consistently able to catch these balls. To gain insight into the adopted new interception strategy, we setup two approximate optimal control models, which know the observation function. In one case, an iterated signal dependent linear-quadratic-Gaussian controller was modified to handle non-linear observation models. The second approach utilizes a Monte Carlo sampling of smooth trajectories of increasing complexity in a low dimensional parameter space. These analyses show that the ideal actor modifies its trajectories by executing controls that increase information gain, and that these changes mirror human behavior. Thus, we provide evidence that humans quickly abandon the constant bearing angle strategy in favor of more informative action sequences, if this allows catching moving targets more reliably. The constant-bearing-angle-strategy is not an invariant heuristic of Darwinian intelligence as humans employ near-optimal information seeking actions that violate the constant bearing angle strategy, but produce less uncertainty in the interception.
II-3. The simultaneous silence of neurons explains higher-order interactions in ensemble spiking activity

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Sparseness is a major characteristic of the spiking activity of neuronal populations [1,2]. Neurons are often simultaneously inactive with a probability greater than expected if neurons fired independently [1]. A complete description of ensemble neuronal activities, however, remains a challenging problem. While higher-order interactions (HOI) are typically introduced to capture the sparse activities [1,2], inclusion of combinatorial HOIs into a probability model is problematic [2]. This is because the model can easily over-fit the data even in small networks. An unnormalized model was proposed in [2] aiming at capturing sparse HOIs in a large network, but this approach makes statistical interpretations obscure. In the present work, we suggest adding to the classical log-linear model (LLM) a single HOI parameter that introduces a specific global interaction favoring sparse spiking activities. This parameter describes the extent to which all neurons are simultaneously inactive more/less frequently than expected from their firing rates and pairwise correlations (if the parameter is added to a pairwise LLM). We applied these models to parallel spike data of subsets of 4-10 neurons (out of 138) reconstructed from calcium imaging of a hippocampal CA3 pyramidal cell layer. Compared to independent and pairwise LLMs, adding a single additional parameter dramatically improved the goodness-of-fit. The fitted sparsity values were positive, indicating that neurons tended to be inactive together. This means that the addition of the single HOI parameter successfully captured positive pairwise and negative triple-wise interactions observed in many CA3 neurons. This work suggests that seemingly complex HOIs can be explained by the simultaneous inactivation of many neurons. [1] Ohiorhenuan et al. Nature(466), 617-621, 2010. [2] Ganmor et al. PNAS(108), 9679-9684, 2011.

II-4. Neural representations that are good for both generalization and discrimination

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How do we tell whether a neural representation is good or bad? The answer depends on the input statistics, the task at hand and the readout. Previous work, mainly in early sensory areas, focused on the amount of information about a stimulus contained in the neural representation. Here we took a different perspective and evaluated a neural representation by considering the dynamics of a generic cortical circuit. This approach led us to test the classification performance of a linear readout from a population of input neurons that encode a few different noisy sources of information. Our analysis revealed that input neurons have to respond to mixtures of the information sources in order to enable classification. One efficient way to achieve these response properties is to mix different sources of information with randomly connected neurons (RCNs). Under the assumption that the output neuron reads out the RCNs, we derived a formula for the classification performance of noisy inputs (generalization error). The performance depends on the “discrimination factor”, expressing how much the population activity changes when only one of the information sources is altered; and on the “generalization factor”, expressing the change when none of the sources are altered, but different noisy versions are presented. Specifically we explored the effect of the population coding level on the tradeoff between these factors, and show that a coding level of about 0.1 is optimal for many different cases. The advantage of optimal coding is greater for higher levels of noise...
in the inputs. Our results provide a possible explanation for the abundance of mixed selectivity found in neural recordings, and for the coding level observed in many areas. Furthermore, we provide a prescription to measure components of the generalization-discrimination tradeoff from neural data. Funding: DARPA SyNAPSE. Gatsby, Kavli and Sloan-Swartz Foundations.


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 Hierarchical models of visual cortex based on the HMAX/Neocognitron model have reported state-of-the-art accuracy on object classification tasks using natural still imagery. More recent work has started to explore the role of sparse representations in these models, using feature dictionaries learned from the data. This work has mostly focused on whole image classification, applied to standard datasets such as CalTech256, which provides \sim 100 human-labeled example images for each of 256 image object categories, with a total dataset size \sim 1 Gpixel. Much larger image and video datasets are now becoming available, which raise questions about how to learn from mostly unsupervised data streams where any given frame of video may contains hundreds of objects drawn from thousands of object categories (involving object detection as well as classification), presented at data rates of several Gpixels/min for high definition video. We describe new work exploring semi-supervised methods for learning representations of video sequences of natural scenes. Our methods are based on learning over-complete feature dictionaries that capture texture, color and motion, with local pooling to provide invariant representations of image patches while allowing reconstruction of the original image. Our model then uses this unlabeled representation to learn the natural background classes in these video sequences. We describe how to add supervised learning of additional foreground categories that may represent a relatively rare but behaviorally important component of the external environment. This type of multiple-category clustering algorithm can be learned using fast, online methods, and supports high-level description of the scene and learning of high-level relationships between foreground and background object categories, which can further enhance object recognition rates. We demonstrate our models using high performance implementations of our algorithms on public domain video datasets.

II-6. Implicit representation of high-dimensional stimulus distributions

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Our sensory stimuli are ambiguous, and behavioral experiments show that we often use probabilistic information in our judgments and decisions. Recent work in neural probabilistic codes posit that marginal probabilities are encoded variously in individual neural activities or distributed across neural populations. In both these cases it remains unclear how our brains could represent the exponentially high-dimensional joint probability distributions of complex stimuli. Here we show that sparse posterior distributions can be represented implicitly using surprisingly little information, scaling nearly linearly with the dimensionality of the stimulus. In typical conditions, a sensory scene is ambiguous but this ambiguity is limited to a tiny fraction of all possible stimuli. This is for two reasons: first, our prior expectations over stimuli is highly restrictive, and second, our sensory evidence is usually consistent with only a small subset of stimuli with any appreciable prior probability. Under normal conditions this makes the posterior distributions very sparse. Recent results in the field of compressive sensing prove that sparse images can be represented accurately with surprisingly few measurements. We adapt these results to compressing
not images but rather probability distributions over images, specifically binary images in this study. We find that with sufficiently limited ambiguity, the most probable configurations in the complete posterior distribution are implicitly but accurately encoded in a small number of local marginal probabilities. These results suggest that the brain may not need to explicitly represent any unwieldy, high-dimensional probabilities in order to capture the relevant probabilistic information. This information is also captured effectively by random marginals, the marginal distributions of random combinations of stimulus inputs. We discuss how random marginals provide a novel interpretation of the complex feature conjunctions observed in receptive fields of high-level neurons.

II-7. Fano factor constancy and scale-invariant sampling in recurrent networks with probabilistic synapses

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Neuronal activity in cortex is variable both spontaneously and during stimulation. This variability has the remarkable property that the Fano factor of the neuron's spike counts (variance/mean) is constant over broad ranges of their firing rates, a property that we call “Fano factor constancy”. Realistic neuronal networks models in the balanced regime do not lead to Fano factor constancy over broad ranges of firing rate unless their parameters are fine-tuned, posing a problem. What mechanism could lead to Fano factor constancy? One well-documented source of variability in cortex is synaptic noise. However, whether synaptic noise can lead to the observed properties of neuronal variability is currently unknown. Here we show that realistic neuronal networks of spiking neurons endowed with probabilistic synaptic release naturally generate constant Fano factors over several orders of magnitude in the neurons’ firing rate. The mechanism does not require fine tuning of the network parameters, but rather it arises naturally from the amplification of the synaptic noise and the neuronal spiking threshold. Probabilistic synaptic release naturally leads to information loss. Then, what could be the role of this form of variability? We show that synaptic noise allows sampling the states of the network and, furthermore, that the Fano factor constancy property implies that the state-sampling dynamics obeys a scale-invariant rule: if the input drive to the network is scaled by some factor, the probability of visiting the states of the network remains constant. Therefore, synaptic noise might not only be the responsible for the type of variability found in cortex, but it also might endow cortical neurons with crucial computational properties to solve inference problems with ambiguous information.

II-8. On the precision of sensory encoding in visual search

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The neural encoding of visual stimuli is typically noisy. In many visual tasks, a stimulus is not presented in isolation but is part of a set. We ask whether set size affects the encoding precision (inverse variance) of a stimulus, and whether encoding precision is identical among individual items within a set. The existing literature is inconsistent about the effect of set size on precision, even for simple stimuli. Many visual search studies report that precision is constant with set size, but visual short-term memory studies typically report that it decreases. This has led to the suggestion that memory might be a key factor (Palmer, 1993). In the search studies, however, non-target items were all identical to each other (homogeneous distractors), whereas the memory studies used heterogeneous stimuli. Therefore, an alternative hypothesis is that the decrease in precision is caused by stimulus heterogeneity (Wilken and Ma, 2004). To disentangle both factors, we asked subjects to detect a target among heterogeneous distractors in a task without or with a memory component. In the pre-cue condition, a target orientation was presented before viewing a search display. In the post-cue condition, the order was reversed, requiring subjects...
to memorize the entire search display. Using an ideal-observer model, we found that noise increases with set size in both conditions, suggesting that distractor heterogeneity is the critical factor. The data also allow us to examine whether encoding precision at a given set size is constant or variable. Traditionally, encoding precision is thought to be constant given the stimuli and experimental conditions. We tested a new model in which precision is itself a random variable, fluctuating across trials and items. We found that precision is indeed variable. Together, these results offer a new perspective on the precision of sensory encoding in visual search.

II-9. Neural implementation of Bayesian inference using efficient population codes

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Experimental evidence suggests that human judgments of many perceptual attributes are consistent with Bayesian inference, in which noisy sensory measurements are combined with prior knowledge to obtain estimates. How does the brain represent and utilize prior probabilities to achieve this computation? Recent work has shown that a population vector decoder can approximate a Bayes Least Squares Estimator (BLSE), if one assumes a neural population with tuning curves proportional to the likelihood, and preferred stimuli sampled from the sensory prior (Shi & Griffiths 2009; Fischer & Pena 2011). Here, we examine and derive more precise conditions under which this can hold. We assume sensory variables are encoded with a heterogeneous neural population optimized for transmission of sensory information, subject to limitations on the number of neurons (N) and the total average spike rate (R). This encoder implicitly represents the sensory prior in the distribution of preferred stimuli, and is consistent with experimental data for a variety of sensory modalities and attributes (Ganguli & Simoncelli 2010). Given this encoder, we derive a novel decoder to approximate the BLSE. Similar to the population vector, it computes weighted averages of the preferred stimuli. However, the firing rates are not used directly as weights, but are first convolved with a linear filter then exponentiated. The decoder is neurally plausible, and requires knowledge only of the preferred stimuli and a fixed filter, and not the prior or tuning curves (Jazayeri & Movshon 2009). Simulations demonstrate that it outperforms the standard population vector, and converges to the true BLSE as N increases. In a low signal-to-noise regime, the decoder outperforms a BLSE operating on a resource-matched homogeneous population. We conclude that in a regime where resources are limited, neural representations optimized for transmitting information enable neurally plausible decoding that can utilize implicit prior information to perform Bayesian inference.

II-10. Change detection as probabilistic inference under variable resources

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Visual short-term memory (VSTM) is generally believed to have a fixed, discrete capacity of about four items. This belief is largely derived from experiments in which observers detect whether a change occurred between two successive displays containing multiple items. Here, we introduce a different conceptualization of change detection, namely as a form of optimal probabilistic inference under limited resources. We assume that the internal representation of each item is noisy, with a level of precision that is determined by the amount of resource allocated to the item. A previous idea (Shaw 1980) has been that resource is spread equally over all items (fixed-precision,
We make the novel proposal that the amount of resource—and therefore precision—varies from item to item and trial to trial, possibly due to attentional fluctuations (variable-precision, or VP, model). On each trial, the model observer uses the internal representations of the stimuli to compute the probability that a change occurred. We conducted a set of change detection experiments in which we varied magnitude of change, number of items, and stimulus reliability. Besides testing the discrete-capacity, FP, and VP models, we considered variants of the FP and VP models in which the observer performs suboptimal probabilistic inference, due to incomplete knowledge about item-to-item precision and/or by using an alternative rule for integrating evidence across items. We found that among the 16 resulting models, human behavior was best described by the one in which precision is variable, observers have complete knowledge of variations in precision, and use the optimal integration rule. Our results not only provide strong evidence that VSTM resource is continuous and variable rather than discrete and fixed, but also suggest that neural populations encode precision for each item on each trial, and use this information in subsequent computation.


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To survive, animals must not only detect changes between visual scenes but also localize them. Despite its ecological importance, change localization remains underexplored. Here, we use change localization as a novel paradigm to compare models of visual short-term memory (VSTM). Subjects sequentially viewed two displays containing N ellipses each, separated by a 1-second blank. Exactly one ellipse changed its orientation between the displays, and subjects reported the location of this change. This is an N-alternative forced-choice task. We found significant effects of set size and change magnitude on proportion correct (see figure). Established discrete-capacity models claim that VSTM consists of a small number of discrete chunks of resource. Here, we instead introduce a set of continuous-resource models based on the assumption that each item is encoded in a noisy way. The precision of encoding could either be independent of N (“flat”) or inversely proportional to N (“1/N”). In addition, precision could be constant for given N (fixed precision, FP), or vary across items and trials (variable precision, VP). In these models, to make a decision, observers compute the posterior distribution over the location of the change based on the noisy internal representations of the items. The FP models have one free parameter, all others two. We found that the 1/N VP continuous-resource model describes human observers’ behavior very well (R²=0.99), and outperforms both the discrete-capacity models and the alternative continuous-resource models. This indicates that precision is variable across items and trials, and on average inversely proportional to N. Variability in encoding precision may be explained by top-down mechanisms such as attentional modulation. Our findings suggest that VSTM is limited by a continuous and variable resource, and establish change localization as a suitable paradigm for further study of these limitations.

II-12. Phase precession in a network model of entorhinal cortex stellate cells without external pacemaker

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Stellate cells in layer II of the medial entorhinal cortex exhibit place-specific firing in-vivo. Their firing fields are arranged on a spatial hexagonal lattice, generally referred to as grid. Grid-field activity is accompanied by os-
cortical oscillations of the local field potential (LFP) in the theta band (≈10 Hz). The theta phase of single spikes thereby decreases with the distance traveled in the field, a phenomenon called phase precession. Stellate cells have been characterized as type II oscillators with a subthreshold resonance in the theta range. As such they are considered to be pacemakers. It is unclear how spiking of such putative pacemaker neurons would be able to precess in phase relative to a self-generated oscillation. Based on a recent model of phase precession in the hippocampus (Geisler et al. 2010 Proc. Natl. Acad. Sci. U.S.A. 107: 7957), we developed a theory on how this paradox can be resolved. For the hippocampus model, the core idea is that the limited spatial extent of the firing fields ensures that the sum of all synaptic currents, i.e., the LFP, is a little slower than the firing frequency of the individual cells, hence leading to phase precession. Here, we show that extending this idea to grid fields is not straightforward since the periodicity of the grid fields generally destroys the phase coordination. Moreover, the original model strongly relies on a compression parameter with entirely unclear mechanistic origin. Our simulations show that the type II property of stellate cells is instrumental in synchronizing small cell groups and thereby accounts for theta oscillations and phase precession. Direct excitatory coupling between the stellate cells, indirect inhibitory coupling via a gamma-oscillating network of interneurons, or both could mediate phase coordination. The compression index follows as a natural consequence of the self-organization of firing phases.


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A key function of brains is undoubtedly the abstraction and maintenance of information from the environment for later use. Neurons in association cortex play an important role in this process: during learning these neurons become tuned to relevant features and represent the information that is required later as a persistent elevation of their activity. It is however not well known how these neurons acquire their task-relevant tuning. Here we present a biologically plausible neural network model based on reinforcement learning that explains how neurons learn to represent task-relevant information in delayed response tasks. Reinforcement Learning (RL) provides a formal framework for learning action sequences with delayed rewards. Our learning scheme implements a Temporal Difference (TD) learning algorithm, SARSA(λ). The neural network model consists of a layer of sensory neurons, a second layer of association neurons and finally a layer of motor neurons. The association layer contains memory units that have persistent activity allowing the network to solve the state aliasing problem in delayed response tasks. Each motor neuron tries to predict the Q/Action-Value of its associated action, and a stochastic Winner-Takes-All competition biased by the predicted values determines the action that is executed. Motor neurons have feedback connections to the association layer, and an interaction of feedforward and feedback activation from the winning motor neuron lays down synaptic tags on those synapses that were involved in the decision. Synaptic plasticity is determined by the product of tag strength and a globally released neuromodulator that reflects the TD error. We can show that on average the updates are equal to a variant of the Error-Backpropagation algorithm. The model can explain tuning of neurons as observed in area LIP (lateral intraparietal cortex) in (1) saccade/antisaccade tasks; (2) categorization tasks; and (3) probabilistic classification tasks.
II-14. Modeling and analysis of rhythm generation mechanisms in excitatory neural networks

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The mechanisms generating neural rhythmic activity that persist after blockade of synaptic inhibition remain poorly understood. Experimental studies in thick slices from neonatal mice containing the pre-Botzinger Complex (pre-BotC) identified two types of pacemakers and proposed two intrinsic neuronal bursting mechanisms that may contribute to rhythm generation: one based on the persistent sodium current (INaP), and the other involving calcium (ICa) and calcium-activated, nonspecific cationic (ICAN) currents. Only the INaP-dependent bursting mechanism has been found in the pre-BotC within thinner slices from neonatal rats. Both these mechanisms were also suggested to contribute to the generation of rhythmic activity in the isolated spinal cord. However, an involvement and relative roles of these mechanisms in the operation of rhythmogenic excitatory networks within the brain stem respiratory and spinal cord locomotor central patter generators are still under debate. Studies of the effects of pharmacological blockers of INaP and/or ICAN on the network bustling activity and its characteristics have shown inconsistent results. In this theoretical/modeling study we have investigated rhythmogenic mechanisms in a population of excitatory neurons with INaP, ICa and ICAN conductances randomly distributed within the population. We incorporated in the model and investigated the possible roles of Na+/K+ pump, IP3-dependent intracellular calcium release, and mutually excitatory synaptic interactions within the population in generation of population bustling activity. We have demonstrated that such population can operate in several regimes of oscillatory bursting activity, which can be dependent on INaP and/or ICAN, or independent of both. The particular oscillatory regime critically depends on general neuronal excitability and the number of neurons involved, which may vary with the size of the slices studied experimentally. This may provide explanations for the different rhythmogenic mechanisms inferred to operate under various experimental conditions.

II-15. Fluctuations in attractor networks

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Noise correlations, which can provide information about functional connectivity between neurons and significantly alter estimates of the information carried in neural populations, are of burgeoning interest in neuroscience with the advent of simultaneous in-vivo recordings from multiple neurons. However, the theory of fluctuations in neural networks – essential for interpreting such measurements – has not kept pace. Rate-based models provide only an approximation to the mean firing rate, ignoring fluctuations. Going beyond this mean field is often handled in an ad hoc manner. We present a theory of fluctuations in general, non-linear recurrent neural networks of Poisson neurons with rates given by their time-varying synaptic inputs. The theory uses a path integral approach, enabling a systematic and analytic evaluation of fluctuation effects beyond mean field. For concreteness and comparison with existing work, we consider (continuous) attractor networks. The path integral mean-field theory gives the standard rate-based result for a given attractor network, while allowing us to compute noise correlations as a function of network connectivity, the effects of such fluctuations on the mean rates of neurons, the loss of persistence of states on the attractor through diffusion, and the effects of input correlations on the rates and correlations of network neurons. We illustrate these results in a simple 1-dimensional ring-attractor network.
that underlies models of visual orientation tuning. Finally, our results are instrumental for accurately estimating
the Fisher Information in population codes, because they specify the actual correlations that will be present in
network models of population tuning. We show that, surprisingly, although neural correlations grow vanishingly
small in increasingly large networks, their contribution to Fisher Information remains finite. We also show that this
effect cannot exist in the corresponding Mutual Information, and thus contribute to growing evidence that Fisher
Information is a flawed proxy for information.

II-16. A neural system for motor planning and control
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Two ideas [1] have resurfaced in motor control that, if validated experimentally, should strongly constrain neu-
nral network modeling efforts. The first [2] proposes that the “pre-movement” state of motor cortex codes “peri-
movement” neural activity and behavior – but not any particular task-level variable like the end-point of a reach.
The second idea [3] states that the motor system is not a static controller but an optimization machine that gener-
ates motor programs online for new task contexts. We demonstrate a novel neural system that synthesizes these
two ideas. For the first idea, we design a perceptual working memory (PWM), related to Pollack’s RAAM [4]. It
takes in a stream of sensory measurements s(t) and produces at each time point a code C(t) that compresses
the history s(0), ..., s(t). The PWM is recursive in that it works by jointly compressing s(t) and the previous code
C(t-dt) to make C(t). At time t, C(t) provides an enriched representation of the state of the body. C(t+T) for some
future time t+T, represents a proposed future trajectory that the body can undergo. Thus, it predictively codes
the neural activity that will occur during movement. To implement online optimization, a planning circuit samples
possible codes C(t+T). A controller receives C(t) and C(t+T) and propagates motor outputs to a forward model
to produce predicted sensory measurements, which are compressed by the PWM. The controller must generate
motor commands that subsequently produce a code similar to C(t+T). The planner must find a code C(t+T) to
generate a desirable trajectory of the body. Importantly, the planner imposes a cost function on the controller
without itself knowing how to optimize it.

II-17. Structure of stimulus induced correlations in random networks with dis-
tance dependent connectivity
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Correlations among neural spike trains are believed to play an important role in information processing and learn-
ing [Averbeck et al. 2006]. The origin of correlations could be attributed to common inputs, which may arise
due to stimulus properties and/or the structure of the recurrent connectivity. Recently, it has become possible to
calculate the structure of correlation in the ongoing activity of a network from its recurrent connectivity [Pernice et
al. 2011]. However, it is not clear how the structure of input correlations interacts with the network connectivity to
shape the stimulus-induced correlation. We addressed this question using numerical simulations of random and
spatially structured networks of spiking neurons. Specifically we considered ring networks with nearest-neighbor
connectivity, which could be transformed in to random network by rewiring a fraction of neurons to make distance
independent connections. Surprisingly, we found that input correlation can both correlate and de-correlated the
network response. In random networks the input correlations always resulted in a net increase in the output cor-
relations. However, in networks with nearest-neighbor couplings input correlations either increased or decreased
the output correlations depending on the ratio of local versus random connections. For a given network, below a threshold $\rho_{\text{tran}}$ input correlations were either ineffective or de-correlated the output. Importantly the parameter $\rho_{\text{tran}}$ increased with the ratio of distance-dependent and random connections in the network. Network correlations are tightly linked to the coding capacity of a network. Our works suggests that networks with some degree of distance dependent connectivity are capable of altering their coding capacity according to the stimulus properties.

II-18. Perturbative memory encoding in recurrent networks

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Various mechanisms for encoding memories in recurrent networks have been studied in the past few decades, most notably since the 1980s (Hopfield 1982, 1984). Given a prescribed list of memory patterns, however, it is still an unsolved problem how to arrange the connections between neurons in a recurrent network such that these – and only these – memories are encoded via stable fixed points of the network dynamics. The difficulty with standard attractor neural network approaches lies in the emergence of “spurious” states, corresponding to unintended memories outside the prescribed list. This phenomenon is especially apparent when the list contains overlapping (or non-orthogonal) memory patterns, although this case is prevalent in experimentally observed patterns of neural activity. Here we take a novel approach to memory encoding, where memories are encoded as perturbations of a “background” synaptic weight organization. In this framework, the connectivity matrix $W$ can be understood as the sum of two components, $W=J+A$, where $J$ corresponds to a fixed background of synaptic weights, and $A$ is a matrix of perturbations of these weights in the service of memory encoding. Whereas the matrix $J$ is generated by a simple neural field-type connectivity rule, with connection strengths depending only on the arrangement of neurons in a “feature space,” the matrix $A$ allows memories to be encoded from a prescribed list. Perhaps surprisingly, we find that addressing the problem of encoding overlapping memory patterns in the presence of certain backgrounds helps, rather than hinders, finding appropriate connectivity matrices. These backgrounds are special in that they allow great flexibility to encode, or unencode, new memories. Interestingly, we find unexpected connections to discrete geometry that enable greater control in designing networks with desired sets of stable fixed points.

II-19. Efficient horizontal and vertical information processing in neural networks

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Neural networks are characterized by their ability of processing large amount of input in parallel. Typical analyses of the network architecture focus on the cluster coefficient (local communication) and shortest path length (long-range signal propagation). The approach treats every nodes (neurons) equally and do not consider any particular direction of functional information flow in the networks. However, the approach may not fully characterize the architecture of neural networks as they are distinct from other types of networks in at least two ways: 1) a neural network has a specific direction of information flow: signals enter the network from a specific set of input neurons, processed by local neurons and leave the network from output neurons. 2) The neural pathways via
multiple synaptic connections may be functionally more important than the direct synaptic connections (shortest pathways). To address the issues, we propose a novel analysis which characterizes information flows in a neural network. Specifically, we measure two quantities: 1) processing speed: how quickly all vertical information pathways are established between input and output nodes and 2) information sharing: how far information entering a given input node travels horizontally to different output nodes. We analyzed C. Elegans neural networks, protocerebral bridge network in Drosophila, and, as comparison, artificially generated small-world and random networks. We found that while the small-world networks are faster in the processing speed and the random networks are superior in the information sharing, C. Elegans network and the protocerebral bridge network perform well in both measures. The result suggests that neural networks are very efficient in vertical (from input neurons to output neurons) as well as in horizontal (between input-output channels) information processing.

**II-20. Scale-invariant effective connectivity in spontaneously active monkey V1 cortical networks**

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Spontaneous activity in cortical areas is structured, potentially revealing neuronal connectivity. A major problem is that correlated activity between neurons might indicate connectivity between them, presence of common inputs, or both. Statistical models that try to disentangle the effects of these two correlation sources are typically intractable, and yet developing tractable ones is crucial to our understanding of how microcircuits are connected. We study the correlations generated in monkey V1 networks measured by multielectrode arrays (100 electrodes) during spontaneous activity. The spike train cross-correlograms (CCG) show a range of timescales up to a few hundred milliseconds and have asymmetric exponential tails. These long timescales are induced by bursts of activity whose rate and duration increase slowly with trial number. We show that stochastic linear rate (SLR) models fit with surprising level of accuracy the CCGs of the V1 data. The estimates of the connectivity matrix can be efficiently obtained from these fits. Crucially, SLR models are robust to the presence of common inputs and provide very reliable estimates of connectivity even in the presence of unobserved common inputs in networks of integrate-and-fire neurons. We show analytically that in SLR models the problems of estimating connectivity among units and their common inputs decouple, and therefore it allows solving for the connectivity matrix without knowledge of the common inputs in the network. We find that, unlike retina, the effective connectivity strength in V1 is roughly constant as a function of distance in the range 0.4-3mm, despite the fact that the correlations show a marked variation with distance in the same range. Therefore, we provide evidence for distance-invariant effective interactions between cortical neurons, suggesting that the dynamics of neurons and their connectivity interact in such a way that the effective connectivity lies close to a critical point with scale-invariant properties.
II-21. Synaptic consolidation: from synapses to behavioral modeling

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Hippocampal plasticity is widely believed to underlie episodic memory formation. In this area, synaptic plasticity consists of several phases spanning different time scales, from milliseconds to hours. Experiments have shown that long-term potentiation or depression (LTP/D) of synaptic weights is complemented by a maintenance mechanism which depends on several intrinsic factors but also on an external novelty signal (Frey & Morris, 98). This maintenance signal is non local and leads to associative effects between different plastic events occurring within one single neuron. A behavioral analogue has been developed, in which fear Long-Term Memory (LTM) of rodents is shown to obey similar rules (Moncada & Viola, 07). We propose a model network bridging the two concepts, LTP/D and LTM. The model consists of three layers of integrate-and-fire units representing hippocampal place cells, lateral amygdala neurons coding for emotional memory and a decision unit inspired from (Wang, 02). Initial storage and longer temporal evolution of spatial or emotional memory is implement via an updated version of the Tag-Trigger-Consolidation (TagTriC) model by (Ziegler, Clopath et al, 08), developed to reproduce induction and maintenance of LTP/D in CA1. Simulation results show that the functional properties of TagTriC transpose to this behavioral paradigm. Moreover, the model was able to explain a lack of associative effects observed when two events occurred within a certain time window. Responsible for this interference is a resetting of the plastic modifications induced within the hippocampal layer when active consecutively in different contexts. This interaction unfolds naturally from our modified TagTriC consistent with tag resetting in vitro (Sajikumar & Frey, 04). This work proposes a first step towards integration of different levels, functional plasticity and behavior, of a general theory of memory. It supports the tagging and capture hypothesis as a basic building block for episodic memory.

II-22. An adaptive spiking neural network for decision making in partially observable environments

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Predicting future events is essential for deciding between alternative courses of action, some of which may lead to rewarding outcomes, others which may result in loss of resources. Reinforcement Learning (RL) offers a theoretical framework for formalizing the problem of predicting the result of interactions with the environment and adapting behavior so as to choose an optimal course of action. RL’s popularity in neuroscience is at least partly due to its success in modeling neural data as exemplified by the well-known interpretation of dopamine neurons activity as a temporal-difference reward-prediction error. Considerable effort has recently been devoted to extending the RL formalism to the case of only partially observable environments, a situation which is commonly abstractly formalized as a Partially Observable Markov Decision Process (POMDP). In an attempt to bridge the abstract algorithmic RL formalism with a biophysically plausible neural network implementation, we study a spiking network model endowed with representations of internal states and their values, in addition to observable features of the external environment. Our model defines a probabilistic policy which corresponds to a set of transition probabilities between internal states conditional on an observed external stimulus. We show how this architecture is formally equivalent to a finite-state controller (FSC), a finite policy parametrization which has been shown to efficiently approximate an optimal POMDP policy under many circumstances. This structure has several advantages. FSCs induce finite-state Markov chains in a POMDP, and thus simplify the problem of computing policy values. FSCs deal with a finite set of discrete states, as opposed to the high-dimensional belief-space of
exact POMDP methods. From an implementational point of view, the discrete nature of FSC states allow us to represent them as attractors of the neural dynamics of a spiking network. Fundings: DARPA SyNAPSE; Gatsby, Kavli, Sloan-Swartz and Swiss National Science Foundations

II-23. Learning precisely timed spiking responses

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Experiments have revealed precisely timed patterns of spikes in several neuronal systems, raising the possibility that these temporal signals are used by the brain to encode and transmit sensory information. It is thus important to understand the capability of neural circuits to learn to produce stimulus specific temporally precise spikes. Learning to spike at given times is challenging since the spike threshold and the ensuing reset introduce strongly nonlinear dependence of the voltage on the value of the synaptic weights. We develop error-based supervised learning paradigms that force the neuron to spike only near the desired times, during learning, allowing the learning of precise spike times using Perceptron-like rules. For feed-forward networks, our model enables leaky integrate-and-fire neurons to learn any set of spike patterns that is realizable by a LIF neuron, with arbitrarily high precision in finite time. For the first time the capacity of generating multiple desired spiking patterns by a LIF neuron is calculated. Importantly, we show that this capacity obeys a scaling relation between the maximum total output spike count and the number of spikes in a single neuronal integration time. Our novel learning paradigms can be used for training recurrent networks to generate multiple stimulus specific periodic and aperiodic spike sequences. Interestingly, when the trained patterns consist of multiple spike pattern cycles, learning leads to the creation of stable periodic spike patterns, without enforcing stability constraints. The learning paradigms can be directly employed for learning timed responses to stimuli, such as in classical conditioning, as well as for learning to detect the occurrence of precisely timed stimulus features. In recurrent networks, our learning can be applied for temporal sequence generation, for associative recall of temporal sequences, and for transferring spike sequences between networks, e.g. from a short-term to a long-term memory storage.

II-24. Synaptic scaling generically stabilizes circuit connectivity

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Conventional plasticity (e.g. Hebbian [Hebb, 1949] or Spike-Timing Dependent Plasticity [STDP; Bi and Poo, 1998]) does in general not stabilize synaptic connection strength (or weights). Most of the existing plasticity rules use stability mechanisms that rely on biologically unrealistic assumptions (e.g. Oja rule [Oja, 1982], weight normalization [Gerstner and Kistler, 2002], sliding threshold [Bienenstock et al., 1982] or simply hard boundaries [Song et al., 2000]). This led us to systematically analyze the stability properties of synaptic scaling [Turrigiano et al, 1998; Turrigiano and Nelson, 2004] in combination with plasticity rules. Synaptic scaling uses the difference between a neuron's output activity and a desired target activity to scale its weight and this takes place on a larger time scale compared to conventional plasticity. We developed an analytical method [Tetzlaff et al., 2011] to understand the weight dynamics resulting from synaptic scaling and conventional synaptic plasticity, independent
of the exact form of the plasticity rule (e.g. Hebbian or STDP). This method reveals that synaptic scaling offers robust weight stabilization if the scaling depends also on the weight itself. Then synaptic scaling suffices to stabilize weights and no additional (presumably non-biological) stabilization mechanism (see above) is needed. Furthermore, weights converge towards a diverse set of stable values that are determined (proportional) by their presynaptic activity. Thus, synaptic scaling in combination with, for example, Hebbian plasticity can build up memory traces and lead to cell assembly formation [Hebb, 1949] even in random recurrent networks [Tetzlaff et al., 2011]. Our analytical method enables us to estimate the size and the duration of such assemblies depending on input strength and plasticity parameters. Weight dependent synaptic scaling is, thus, a biologically realistic candidate for both stabilizing circuit connectivity and generating memory traces in neuronal networks.

II-25. Regularisation reveals smooth dynamics of shared variability in neural population activity

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Experimental advances have made it possible to simultaneously record the spiking activity of dozens or even hundreds of cortical neurons, and have thus crystallised the importance of understanding the statistical structure of population activity. Latent factor models, including Gaussian-process factor analysis and hidden linear dynamical system (LDS) models, are particularly well suited to capture shared variance in some cortical recordings (Macke et al., NIPS 2011). How important is the dynamical structure of such models? Parametric statistical models may be evaluated on their ability to generalise. If the model’s structure accords well with the true structure of the data, then parameter values estimated from one set of data should provide respectable predictions for another set. Generalisation is often helped by a regulariser - a term that biases parameters towards values favoured a priori. A common approach to regularisation penalises large parameter values: applied to the LDS dynamics matrix this favours short correlation timescales in the latent space and hence also in the observation space. We propose an alternative regularisation scheme for LDSs which penalises deviations from constancy. This corresponds to a prior on dynamics favouring longer timescales. We show that this approach yields a better statistical model for neural data from primate motor cortex using likelihood on test data, as well as a previously established cross-prediction measure. This finding, that holds for a wide range of training set sizes and latent dimensions, suggests that shared variability in the neural population is indeed best described by a smooth process in time. Furthermore, our fitting method is guaranteed to yield stable systems, ruling out biologically-implausible high firing rates and variances when predicting neural activity with LDSs. Appropriate regularisation of this sort may help overcome the difficulties posed by limited data to both scientific and prosthetic applications.

II-26. Identifying endogenous rhythmic spatio-temporal patterns in micro-electrode array recordings

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Microelectrode arrays are a privileged recording modality to study neural processes with a very fine spatial and temporal resolution. They capture the activity of small populations and permit assessment of synergistic interactions between cells. Patterns of rhythmic ongoing activity are of particular interest because they reflect the intrinsic dynamics of neural populations and the way such dynamics may optimize the processing of incoming information. In this study, we identify the various coherent spatio-temporal patterns of rhythmic activity occurring across time using a two steps approach. First, signals were bandpass filtered in a relevant frequency band and subsequently Hilbert-transformed. Second, the complex patterns of activity occurring across time were clustered using a graph cut algorithm based on a phase shift invariant similarity measure. This invariance is a key-property of our approach to isolate wave propagation phenomena. We apply our method to Local Field Potentials recorded in the inferior convexity of the Prefrontal Cortex (icPFC) in two anesthetized macaques using a multi electrode array. We found a dominant travelling wave pattern in the beta band (15-25Hz), propagating along the ventral-dorsal plane, emerging and vanishing across time both in the absence of visual stimulation (spontaneous activity) and during binocular stimulation with movie clips. By computing mutual information, we showed that the amplitude of this wave actually carries sensory information during the presentation of several movies. Altogether, our analysis provides evidence for travelling wave phenomena reflecting the distributed computation in icPFC, which is known to be involved in higher order sensory processing. More generally, our approach enables the unsupervised analysis of the complex spatio-temporal neural dynamics in ongoing signals, providing key information to understand cooperative mechanisms in spatially distributed neural populations.

II-27. Embracing disorder: making sense of complex population codes

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Cognitive tasks require the joint activity of a large population of neurons. Hence there is no a priori reason to find single neurons with easily interpretable activity profiles. Yet when we record from single neurons, we look for and bias our models by precisely these neurons. Here, we use data from the delayed vibrotactile discrimination task from the Romo laboratory to highlight the “not easily interpretable” neurons[1,2]. We then train a randomly connected recurrent neural network to perform the same task [3]. Even though this network has an inherent disorder in its design, we are able to tease apart the underlying dynamical principles that enable the model to perform the task. Finally, we discuss potential caveats of this framework such as generalization and reset—and propose ways to overcome them. Our work stresses the need to consider all recorded neurons when forming models of network dynamics. Research supported by the Swartz, Gatsby, Mathers and Kavli Foundations. [1] Barak O, Tsodyks M, Romo R. Neuronal population coding of parametric working memory. Journal of Neuroscience 2010;30(28):9424. [2] Brody CD, Hernandez A, Zainos A, Romo R. Timing and neural encoding of somatosensory parametric working memory in macaque prefrontal cortex. Cerebral cortex 2003;13(11):1196-1207 [3] Sussillo D, Abbott LF. Generating coherent patterns of activity from chaotic neural networks. Neuron 2009 Aug;63(4):544-557.
II-28. The Coherence of Brain and Environment, not Input Statistics, Determines Neural Correlations

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Coherent behavior arises from the dynamic interaction of the brain with the environment across multiple timescales. Sensory/motor feedback via the environment has been show to be crucial to sensory perception. For example, new born infants can sense the disengagement of feedback with their mothers from a very early age (Murray et al., Social perception in infants, 1985), and sensory responses are significantly different in the actively and passively sensing conditions (Neil and Stryker, 2010; Harris and Theile, 2011). Here, we conduct a theoretical investigation into the implications of this feedback loop for the characterization of neural dynamics. We construct a minimal stochastic dynamical model that is consistent with the observed phenomenology of the rat barrel cortex, where sensitivity and intra-neural correlations is greater in the quiet attentive state than the whisking state (Poulet and Petersen, 2008). We hypothesize that the quiet attentive state corresponds to an open loop condition (without environmental feedback) and the whisking state corresponds to a closed loop condition (with the environmental feedback). We demonstrate that the reduction of neural correlations from the quiet attentive to whisking states can robustly arise from the stabilization of a system, originally close to a dynamical instability, by environmental feedback. Importantly, even if the input stimuli in the open loop condition is identical to the input in the closed loop condition this is insufficient to elicit a change in brain state and the coherence of the system to the input also remains small. This suggests that the feedback interaction, but not the input statistics, is critical for the reduction of neural correlation. We discuss the implications of this result for active perception and more broadly for experimental work attempting to characterize the operation of neuronal populations in an open loop condition.

II-29. Sparse gamma rhythms arising via clustering in adapting neuronal networks

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Gamma rhythms (30-100 Hz) are an extensively studied synchronous brain state responsible for a number of sensory, memory, and motor processes. Experimental evidence suggests that fast-spiking interneurons are responsible for carrying the high frequency components of the rhythm, while regular-spiking pyramidal neurons fire sparsely. We propose that a combination of spike frequency adaptation and global inhibition may be responsible for this behavior. Excitatory neurons form several clusters that fire every few cycles of the fast oscillation. Irregularity in their interspike intervals results from the combination of minor heterogeneities in network architecture and external noise that triggers cycle skipping. This is first shown in a detailed biophysical network model and then analyzed thoroughly in an idealized model. We exploit the fact that the timescale of adaptation is much slower than that of the other variables. Using both singular perturbation theory and a weak coupling analysis, we predict the relationship between the number of clusters arising spontaneously in the network as it relates to the adaptation time constant. Both approaches identify the same power law scaling of cluster number to adaptation time constant, which is corroborated in numerical simulations of the full system. Thus, we develop several testable predictions regarding the formation and characteristics of gamma rhythms with sparsely firing excitatory neurons.
II-30. Spatial properties of the hippocampal theta rhythm in the hippocampus

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The theta rhythm is a prominent hippocampal oscillation that may serve as a reference for decoding the activity of neurons known as place cells. One salient property of this rhythm is that it is spatially inhomogeneous in phase and amplitude. However, current models of hippocampal physiology and function are largely based on the idea of a single, global theta oscillation. By characterizing the spatial variations, we may better understand the generative process underlying the theta rhythm(s), as well as the functional consequences of spatial variation upon the neural code. We conduct our study using multi-electrode array (MEA) recordings of activity in a cross-section of region CA1 in freely-moving rats. The spatial variations in the LFP are found largely within a two-dimensional, complex subspace; the 1st component captures a phase gradient across space (i.e. a traveling wave), while the 2nd component represents the magnitude of this gradient (i.e. wave velocity). These two components evolve in an interdependent manner: their relative phase drifts over time, and their amplitudes are anti-correlated over several seconds. Furthermore, they correlate with neural activity: during ripples, which are characterized by a transient increase in spiking activity across many neurons, the 2nd component exhibits a brief increase in power. These ripple events account for only some of the variation in the 2nd component. We study the additional variation by examining the joint evolution of the spatial LFP with behavioral variables (velocity and acceleration) as well as population spiking activity. Finally, we assess the functional utility of spatial structure by comparing a phase precession model based on the classical, single-site LFP, to one that incorporates fluctuations in the phase gradient.

II-31. Human cortical neurons form functionally isolated networks during propofol-induced unconsciousness

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General anesthesia is associated with striking patterns in the electroencephalogram (EEG), such as a large
amplitude slow (<1 Hz) oscillation and an increase in gamma (25-40 Hz) power. The neurophysiology underlying these effects is poorly understood. Although the molecular-level effects of many general anesthetic drugs are well studied, how these effects in single cells modulate electrical activity in larger-scale networks to produce unconsciousness is unclear. To address this question, we recorded single units, local field potentials (LFP), and intracranial EEG from three patients throughout a clinical induction of general anesthesia with the drug propofol. We found that propofol-induced unconsciousness is not due to widespread neuronal silencing, but instead is associated with specific changes in the structure of neuronal spiking. Although propofol enhances inhibitory signaling via GABA-A synaptic connections, a large subset of units (54%) continue to spike at high rates after loss of consciousness (LOC). However, within seconds of LOC, action potentials become entrained to the phase of a local slow oscillation in the LFP. Spikes occur in short bursts of activity locked to the trough of the slow oscillation, during which significant local network structure is preserved. At the peaks of the slow oscillation, activity is periodically silenced, interrupting local processing. In addition, we find that the slow oscillation is asynchronous across distant cortical regions, potentially impairing long-range communication. We conclude that propofol-induced loss of consciousness is associated with slow neuronal rhythms that isolate cortical networks both temporally and spatially, preventing sustained local information processing as well as coordinated global network interactions.

II-32. Information theoretic limits on performance in short-term memory tasks

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Short-term memory is limited. Early notions, that only a fixed number of items can be stored in memory, have been amended by recent experiments showing that memory systems can flexibly allocate memory resources across fewer or more items with a corresponding trade-off in recall accuracy. However, it remains unclear what factors limit working memory, and how it is best modeled to include parameters like item number, storage interval duration, and item complexity. Here, we build a normative, or information-theoretically ideal, model for the short-term memory of a set of analog variables. We treat all inputs presented to the memory system on an equal footing, as information. Noisy neural dynamics, that degrade memory over the storage interval, are interpreted as passing the information through a noisy channel. We first show why this mapping is appropriate. Next, we derive fundamental limitations on short-term memory performance using information theoretic results on optimal communication over noisy channels. We show how the resulting performance – which depends on optimal encoding and decoding of the stored information for the given channel noise – scales with item number, storage time, and the dynamic range of the inputs. We apply these results to a visual working memory task, and compare predictions for memory performance with psychophysical findings. The functional dependence of recall on the parameters listed above is well-predicted by the normative model, suggesting that the brain performs very good information encoding before the storage period, and decoding after. As we show, these results stand in clear contrast to the predictions made if the brain were directly storing the uncoded variables in continuous attractor networks matched to the dimension and coding range of the variables.
II-33. Information processing changes during development in primary auditory cortex

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Sensory neurons encode information about environmental stimuli. Recent work in information theory has developed novel measures for quantifying exactly how much information neurons carry about a particular stimulus – in particular, the specific information (SI) and stimulus specific information (SSI). Although these tools have previously been used to analyze responses from adult auditory cortex (Montgomery & Wehr, 2010), how the developing brain encodes information about the sensory environment remains largely unknown. To address this question, we apply several information theoretic approaches to sound-evoked multiunit spiking responses from the developing rat primary auditory cortex. We find that 1) both the mutual information and SSI peak from postnatal days 16 to 18 coincident with an increase in receptive field bandwidth tuning, 2) the maximal SSI corresponds to the characteristic frequency (frequency with the highest firing rate), and 3) that this correspondence degrades with age. These findings provide insight into the information processing capabilities of the developing auditory cortex.

II-34. The neural mechanisms involved in finding specific objects and switching between targets

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Finding a specific object requires neural mechanisms that can integrate visual information (i.e. what you are looking “at”) with task-specific information (i.e. what you are looking “for”). To investigate the neural mechanisms by which the brain determines whether a currently viewed scene contains a sought target, we recorded the responses of neurons in inferotemporal cortex (IT) and perirhinal cortex (PRH) while monkeys performed an object search task. Each trial began with the presentation of a cued target object, followed by the sequential presentation of a random number of distractor objects, and then a target match; monkeys were rewarded for indicating the presentation of the target. We found that PRH neurons had higher average target/distractor discriminability (d') than neurons in IT. However, the specific response properties underlying this difference were difficult to discern because neurons in both IT and PRH were heterogeneously modulated by mixtures of visual, working memory, and target/distractor information. We thus developed a procedure to deconstruct each neuron’s responses into a weighted sum of intuitive basis functions. A neuron’s target/distractor discriminability could then be determined by a function that is: 1) proportional to the projection of a neuron’s responses along a dimension that captures the average target/distractor modulation, 2) inversely proportional to the combined projection of a neuron’s responses along dimensions that capture all other types of modulation (i.e. visual, working memory and residual), and 3) inversely proportional to a neuron’s variability across trials. This analysis revealed that increased PRH target/distractor discriminability resulted from increased target/distractor modulation rather than more trivial differences between the two populations. These results suggest the existence of PRH computations that are designed to detect the presence of a target, invariant of target identity.
II-35. Second order dimensionality reduction using minimum and maximum mutual information models

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Conventional methods used to characterize multidimensional neural feature selectivity, such as spike-triggered covariance (STC) or maximally informative dimensions (MID), are limited to Gaussian stimuli or are only able to identify a small number of features due to the curse of dimensionality. To overcome these issues, we propose two new dimensionality reduction methods that use minimum and maximum information models. These methods are information theoretic extensions of STC that can be used with non-Gaussian stimulus distributions to find relevant linear subspaces of arbitrary dimensionality. We compare these new methods to the conventional methods in two ways: with biologically-inspired simulated neurons responding to natural images and with recordings from macaque retinal and thalamic cells responding to naturalistic time-varying stimuli. With non-Gaussian stimuli, the minimum and maximum information methods significantly outperform STC in all cases, whereas MID performs best in the regime of low dimensional feature spaces. These new techniques should improve the characterization of neural features in higher areas of the brain where the application of currently available approaches is restricted.

II-36. Optimal neural tuning for arbitrary stimulus priors

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What controls and determines the characteristic shape of a neuron’s tuning curve? Previous work has suggested that neural tuning curves are the result of an optimal representation of stimulus information, and thus e.g. should change with varying stimulus presentation times (Bethge, et al 2002). Here, we address the question how such optimal neural tuning should depend on the stimulus distribution. We first consider the case in which a neuron’s firing rates are Poisson distributed with mean firing rate determined by its tuning curve h(s), with max/min constraints. The expected squared reconstruction error of the stimulus magnitude s is bounded by Fisher Information, via the Cramer-Rao bound. For any arbitrary stimulus distribution, this error is minimal when the Euler-Lagrange equation is satisfied, leading to the analytical solution for the neuron’s optimal tuning curve. The result reduces to the well-known quadratic form of the optimal tuning curve in the special case of a uniform prior distribution (Brunel & Nadal 1998). We have generalized our analytic derivation to account for other types of noise, such as e.g. stimulus dependent, additive Gaussian noise. Furthermore, our analysis can be extended to optimize other information theoretic quantities such as mutual information. Numerical simulations successfully validated our theoretical results. In addition, we analyzed electro-physiological recordings of the spiking activity of the blowfly H1 neurons, with visual motion stimulus (de Ruyter, et al 1997). By fitting the the observed spiking activity to optimal tuning curve according to our model, we were able to derive the stimulus distribution for which the blowfly neuron is optimally tuned. Our results suggest that stimulus speed is approximately Gaussian distributed with mean 0 deg/sec and standard deviation 8 deg/sec. This prediction is in agreement with previous studies that have found a prior for slow stimulus speed (Stocker & Simoncelli 2006).
II-37. A generative Model for Adaptation in Primary Visual Cortex Neurons derived from Movie Statistics

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Adaptation is a phenomenon found in many neural systems whereby the response of a neuron is affected (e.g., reduced) by stimulus history. We focus on primary visual cortex (V1), for which there is considerable experimental data, yet the computational principles underlying adaptation effects are incompletely understood. We hypothesize that the brain is “adapted” to the statistical properties of natural movies over time. Based on the Gaussian Scale Mixture (GSM; Wainwright and Simoncelli, 1999) generative model, we developed a computational model that captures temporal statistical dependencies between oriented filters. Analogous to our previous work on spatial context (Coen-Cagli, Dayan, Schwartz, 2009), we considered a mixture model that combines two extreme cases: one where the input stimuli seen in the recent past are statistically coordinated with the current input, and one where they are independent. The parameters of the model, including the prior probability over the mixture components, are learned from an ensemble of natural movies. Using Bayesian inference we computed model responses to novel stimuli. Akin to divisive normalization (e.g., Heeger 1996), in response to a relatively constant visual stimulus, the current (test) input is suppressed, in a divisive fashion, by the past (adapter) inputs; conversely, with a rapidly changing signal, the model deems the inputs independent and no suppression results. Our model replicated response suppression of the test stimuli to an optimally oriented adapter, which has previously been ascribed to divisive normalization. Additionally, when we assumed that the probability of the adapter normalizing the test depended on the orientation difference between the two conditions, rather than on their absolute orientations, we accounted for repulsion of tuning curves, an effect not explained by standard divisive normalization. The model can be used to make predictions about adaptation to more natural (slow and fast varying) visual input.

II-38. Identifying dendritic processing in Drosophila OSNs

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In sensory neurophysiology, both the input and the output of neural circuits are typically available for reverse-engineering a sensory system. Since parameters of the underlying biophysical circuits are usually unknown, algorithms are devised for identifying parameters of input/output-equivalent models. The widely used identification algorithms (i) assume that spikes are generated according to an inhomogeneous Poisson process; (ii) rely on stimuli having a particular distribution and/or being white; and (iii) require the evaluation of the PSTH through a time-consuming repetition of complex experiments [1]. In [2] and [3] we investigated the identification of parameters in a wide class of neural circuits consisting of linear dendritic processing filters in cascade with spiking neuron models, including conductance-based models such as the Hodgkin-Huxley neuron. The novel methodology assumes that input stimuli are bandlimited, or smooth. In many sensory modalities, including olfaction, this is a natural assumption since in practice it is very difficult to deliver stimuli that are purely white and/or have a particular distribution. Furthermore, since the model parameters are computed directly from spike times, the proposed methodology circumvents the burden of repeating the same experiment. Finally, this methodology bridges the gap between identification using artificial and naturalistic stimuli and provides key insights into the relationship between the identified kernel and the space of input stimuli. Here we tested our identification methodology on the input/output data that we recorded from olfactory sensory neurons of Drosophila melanogaster. We modeled the transduction of an odor-ant concentration into an ionic current using a linear filter. Spike generation was described by an integrate-and-fire neuron with random thresholds. Upon cross-validation, the identified [Filter]-[Ideal IAF/RT] model consistently outperformed the LNP model derived from the same data set using STA. Furthermore,
the model was constructed from a single experimental trial.

II-39. Support Vector Machines in Spiking Neurons with Non-Linear Dendrites

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The nonlinearities of synaptic integration in the dendritic trees of many neuron types are well established experimentally. However, their role in neural information processing is still an open challenge. According to one proposal (Poirazi and Mel, 2001; Polsky et al., 2004) the thin dendritic branches endow pyramidal cells with a functional ‘two-layer’ Perceptron architecture. However, it is unclear if this architecture can be utilized for nonlinear computation in the temporal domain. Here we propose that dendritic nonlinearity allows neurons to emulate Temporal Support Vector Machines (T-SVM) with nonlinear kernels. The T-SVM is a system that generates desired precisely timed output spikes in response to input spike trains. Many interesting tasks involve complex, nonlinear relations between input and output spike times, which cannot be emulated by linear summation of inputs. In the T-SVM, the postsynaptic voltage is a weighted sum of contributions, each of which (analogous to a support vector) sums nonlinearly a subset of synaptic inputs. The weighted contributions of the SVs to the total voltage represent the SV coefficients. We develop a learning algorithm that yields the maximum-margin solution, in which the postsynaptic voltage has maximal deflection from the threshold. Such a solution enjoys robustness to noise and enhanced generalization abilities. Importantly, despite the fact that each time point in the example patterns can contribute a SV, we show that in the optimal solution only a small set of discrete time points contribute. We apply the T-SVM to several nonlinear problems, such as the spatio-temporal XOR problem and interval estimation tasks. We show that T-SVM systems can be realized by a leaky integrate-and-fire neuron in which inputs arriving on the same dendritic branch are summed nonlinearly. Thus, dendritic nonlinearities may allow neurons to implement complex mappings between input spike trains and precisely timed responses.

II-40. Combinatorial neural codes from a mathematical coding theory perspective

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Shannon’s seminal work in the 1940s gave rise to two distinct, though interrelated, areas of research: information theory and mathematical coding theory. While information theory has had a strong influence on theoretical neuroscience, ideas from mathematical coding theory have received considerably less attention. In particular, the idea of a code functioning primarily to enable accurate and efficient error correction is often overlooked in neural coding theory, though there have been some recent exceptions (Hopfield 2008, Sreenivasan & Fiete, 2011). We take a new look at neural coding from the mathematical coding theory perspective, focusing on combinatorial codes derived from neurons with idealized receptive fields. These codes can be easily thought of as binary codes, with 1s and 0s denoting neurons that are “on” or “off” in response to a given stimulus. Although it has been recently argued that the entorhinal grid cell code may be quite good for error correction (Sreenivasan & Fiete, 2011), we show that more typical receptive field codes (RF codes) perform quite poorly as compared to random codes.
with matching size, length, and sparsity. The error-correcting performance of RF codes “catches up,” however, when a small tolerance to error, in terms of a metric inherited from the stimulus space, is introduced. The error tolerance reflects the fact that perception of parametric stimuli is often inexact. We suggest that a decrease in error-correcting capability may be a necessary compromise for neural codes that reflect relationships between stimuli via relationships between codewords.

II-41. A concurrent brain-machine interface for enhanced motor function

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Brain-machine interfaces (BMIs) largely focus on restoring original motor function. However, a more compelling aim of such research is the development of BMIs that can surpass original motor function by also considering the higher-level goal of the task. Since typical tasks consist of sequential movements, a BMI that can concurrently decode the complete sequence before execution may be able to reformulate and perform such motor plans more effectively. Here, we demonstrate that such concurrent decoding is possible as a result of a neural partitioning mechanism during working memory. Using population-wide modeling, we discover two functionally distinct neural subpopulations in the primate premotor cortex that allow two planned targets of a sequential movement to be concurrently held in working memory without degradation. Such surprising stability occurs because one subpopulation always encodes only currently held target information and the other always encodes only newly added target information, irrespective of target locations. We also find that surprisingly small subpopulations are sufficient for reliable decoding. Based on these findings, we develop a BMI that can simultaneously decode the full motor sequence in advance and then accurately execute it as desired.

II-42. Global Synchronous Spontaneous Activity in Xenopus Optic Tectum

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Patterned spontaneous activity is often critical to the development of neural circuits underlying topographic organization. Thus, studying spontaneous activity patterns and their source can elucidate how the functional features of neural circuits emerge. Although the optic tectum of Xenopus tadpoles is a model system for studying developmental plasticity of topographic organization, its spontaneous activity has been relatively overlooked in studies of circuit development. We studied spatio-temporal patterns of spontaneous activity in the tectum using in vivo two-photon calcium imaging technique combined with a bulk loading cell-permeate tracer, Oregon Green BAPTA1-AM. Our goals in the study are to define the developmental characteristics of spontaneous activity patterns in the tectum and to determine their source. Using a long imaging time window (6-8 min) with a slow frame speed (0.6 frames/s), we found globally synchronized spontaneous activity, which was confirmed by the additional imaging sessions with faster frame speeds (10-100 frames/s) in a subset of the preparations. We also found that spontaneous activity patterns depended on developmental stage and not visual experience. To understand the source of the patterned activity, tectal input was systematically removed by enucleating a contralateral eye (visual
system) and/or cutting the connection with the hindbrain (e.g., auditory, somatosensory, and lateral-line systems). Whereas removing visual or mechanosensory input alone had little effect on the patterned spontaneous activity, removing both of them drastically decreased event frequency and magnitude. The result is novel because it not only suggests that both visual and mechanosensory inputs are necessary, but also that a non-linear combination of visual and mechanosensory inputs generates the patterned spontaneous activity. This study is, to our knowledge, the first to show globally synchronized spontaneous activity by non-linear input combination in the developing brain.

II-43. The Distinct Behavior of Membrane Potential and Spike Train Statistics

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Understanding information processing in neuronal networks, requires a precise description of population responses. Theoretical approaches typically focus on spiking activity. However, spikes provide a sparse representation of a cell’s activity. Membrane potentials are continuously modulated by a cell’s input, and cells connected by gap junctions respond to changes in each other’s membrane potentials. Popular recording techniques, such as those of voltage sensitive dyes and local field potentials, capture a mixture of subthreshold and spiking activity. Theoretical approaches to describe the statistical structure of membrane potential responses have not been fully developed. We present theoretical tools to examine how the statistics of inputs to neurons determine the marginal and joint statistics of their membrane potentials. This allows us to study how membrane potential and spiking statistics are related. Counter to intuition, current coded signals are reliably reflected by membrane potentials and firing rates in distinct regimes: Firing rates are sensitive to modulations of a cell’s input current when excitation is strong and firing rates are high. In contrast, the mean membrane potential is most sensitive to such modulations when excitation is weak and firing rates low. We find that when two uncoupled cells receive correlated inputs, their spiking correlations and membrane potential correlations are reflect their inputs in distinct regimes. Hence, models that capture the spiking output of cells in a network may provide an incomplete picture of population activity. These findings illuminate some of the fundamental filtering properties of neurons and have significant implications for the interpretation of experimental recordings. We illustrate their impact by considering the correlation between signals representing the pooled activity of cell populations, such as those obtained using voltage sensitive dyes. We show that pooled signals can exhibit a decrease in correlations while spiking correlations between pairs of cells increase.

II-44. The spatiotemporal structure of learned and recalled information in whole frontal cortical networks

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A central tenet of memory processing suggests that information is likely stored by neocortical networks through the precise pattern of their neural activations. What these patterns are and how they stably represent associations between learning and recall remains poorly understood. Specifically, are associations encoded by the patterns of firing rates across neurons, the patterns of interactions (cross-correlations) between neurons, or some com-
II-45. Inhibition of return in natural vision revealed by non-parametric analysis of gaze

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Active exploration of the visual world depends on sequential shifts of gaze that bring prioritized regions of a scene into central vision. The efficiency of this system is commonly attributed to a mechanism of “inhibition of return” (IOR) that discourages re-examination of previously-visited locations. Such a process is fundamental to computational models of attentional selection and paralleled by neurophysiological observations of inhibition of target-related activity in visuomotor areas. However, studies examining eye movements in naturalistic visual scenes appear to contradict the hypothesis that IOR promotes exploration. Instead, these reports reveal a surprisingly strong tendency to shift gaze back to the previously fixated location—suggesting that refixations might even be facilitated under natural conditions. Here we resolve this apparent contradiction, based on a nonparametric conditional density analysis of gaze patterns recorded during both free-viewing and search of naturalistic scenes. We show that the observed frequency of return saccades is in fact substantially less than predicted for a memoryless system—demonstrating that refixation is actively inhibited under natural viewing conditions. This study has important implications for computational models of selection based on a salience or priority map, which have until now lacked quantitative estimates of the strength and specificity of return inhibition in natural vision. Furthermore, our analysis reveals that memory for gaze history significantly influences the way in which natural scenes are explored, contrary to accounts that suggest visual search has no memory.

II-46. Evidence for Attention-dependent inactivation of Sodium Channels

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The shape of the action potentials emitted by a neuron can vary, depending on the gating of the neuron’s Na+ and K+ channels, which become inactivated by depolarization. These changes are more pronounced among broad spiking neurons, by virtue of the slower kinetics of the K+ and Na+ channels expressed by these neurons. Consistent with this, we find that broad spiking neurons Area V4 of the awake macaque exhibit reductions in
action potential height following spiking activity. These changes in action potential height provide a moment-to-moment “window” into a neuron’s internal state, allowing us to see how it changes when attention is directed into the neuron’s receptive field. We hypothesized that if attentional feedback signals depolarize neurons, this would result in changes in action potential height. Consistent with this, we find significant reductions in action potential height with attention, which are more pronounced among broad- than narrow-spiking neurons. A portion of this reduction in height results from attention-dependent increases in firing rate, but after controlling for this, we find an additional significant reduction in action potential height with attention. In addition to reducing action potential height, depolarizing currents have also been found to reduce burst firing among pyramidal neurons. We reasoned that if attention leads to an increase in the depolarization of V4 neurons, this might reduce their tendency to fire action potentials in bursts. Consistent with this, we find a significant reduction in burstiness with attention among broad spiking neurons. Together, these results provide evidence for attention-dependent depolarization of cortical neurons, and provide constraints on conductance-based models of attentional state.

II-47. Cognitive efficiency explains intelligence effects on risk sensitivity and temporal discounting

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Qualitative and quantitative similarities between risk sensitivity and temporal discounting have led researchers (Hayden, 2007) to suggest a common underlying mechanism. (Burks, 2009) have recently showed that both risk sensitivity and intertemporal discounting appear to be correlated with general intelligence of human subjects. In particular, subjects with greater intelligence demonstrate lower discount rates and greater risk neutrality than subjects with lower measures of general intelligence. This observation has led them to postulate a high-level model for the emergence of these biases as a process of detecting a true utility signal that must be separated from noise via perceptual processes, with greater intelligence being associated with lesser noise. Instead of assuming that intelligence somehow improves perceptual signal quality, we show that a choice model that attempts to elicit subject preferences by minimizing the cost of memory recall provides a mechanistic explanation for the observations recorded in (Burks, 2009) and (Platt, 2007) while making additional testable predictions. Our choice model considers preference construction to be a process of recalling past beliefs about the goodness of options into working memory from long-term memory with minimal possible cognitive effort. Cognitive effort, in turn, is defined in terms of information-theoretic surprise of past experiences with respect to expectations such that highly surprising and highly unsurprising experiences become easier to recall. Our model replicates the positive correlation between general intelligence and lower risk-seeking for low probability high gain options observed in Burks et al. and further predicts that this behavior can be understood as resulting from a flattening of the sigmoidal probability weighting curve defined in prospect theory. Consequently, we further predict that greater intelligence should be positively correlated with lower risk aversion to options with low probability of high loss. Lastly, we also show a correlation between intelligence and intertemporal preference consistency.

II-48. Modeling maladaptive decision-making in a rat version of the Iowa Gambling Task

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Deficits in decision-making have been repeatedly observed in various psychiatric disorders (e.g., ADHD, Mania, OCD) and are often assessed using the Iowa Gambling Task (IGT). The IGT represents a realistic decision-making task where subjects have to choose between targets associated with rewards and penalties of varying likelihood and amplitude. Previous studies have shown that a third of healthy subjects perform poorly in the IGT, as observed in psychiatric patients [1]. Recently, the IGT was adapted for rodents (the Rat Gambling Task, RGT). As in human studies, a third of healthy rats were found to exhibit poor decision-making [2]. These rats were then run on a battery of tests to extract measures of impulsivity, reward sensitivity, behavioral inflexibility and risk-seeking. Poor decision-makers were always characterized by high scores for a combination of these behavioral traits. We modified the TD-learning algorithm to model learning and decision-making in the RGT and include reward sensitivity, inflexibility and risk-seeking. This novel model was then used to assess: (1) how the behavioral traits influence learning (2) whether they can explain different performances in healthy subjects. The model was able to account for the performances of good and poor decision-makers. The model was fitted to individual rat performances to describe their levels of reward sensitivity, inflexibility and risk-seeking. The parameters correlated significantly with the scores obtained from experiments assessing these behavioral traits. This suggests that the mathematical description of the traits is valid. This work supports the hypothesis that a combination of high scores for reward sensitivity, inflexibility and risk-seeking affects the rats’ learning by altering reward prediction and their ability to reverse their initial estimations. Biased perception and representation of the environment lead to aberrant decisions according to the real outcome of the task but optimal according to the rat’s internal model.

II-49. A mechanism for value-guided choice based on the excitation-inhibition balance in prefrontal cortex

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There have been few mechanistic explanations of fMRI signals observed during cognitive tasks. Here we use a mechanistic biophysical model to predict both behavioural performance and the dynamics of an fMRI value comparison signal in ventromedial prefrontal cortex (vmPFC). The predictions depend on the levels of excitation relative to inhibition in the vmPFC, which we estimate using MR spectroscopy. These data provide evidence for a neural competition mechanism in vmPFC supporting value-guided choice.

II-50. An optimal control perspective of the competition hypothesis

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A soccer player moves the ball down the field, looking for an open teammate or a chance at the goal. To be effective, the player should maintain this set of possible goals, waiting to see which will become the best option. The soccer player faces an example of a common control problem, where we must initiate an action plan, even when the final goal is partially or completely unknown. To handle both goal ambiguity and changes in goals while acting, the sensorimotor system must be able to generate flexible and partially prepared plans. Recent experimental findings support this hypothesis, suggesting the brain generates several concurrent policies associated with alternative goals. These policies compete against each other, while perceptual information is used to bias
this competition, until a single policy is followed. Despite the experimental evidence, little is known about
the optimality of such policy competition. In the current study, we propose an extended optimal control framework
to model human/animal behavior in the presence of multiple potential goals and show that goal competition is a
natural by-product of handling goal uncertainty. We show that the optimal strategy in the presence of goal ambi-
guity can be expressed as a weighted mixture of multiple control policies, each of which produces a sequence of
actions associated with particular goals. One of the novelties of this framework is that the weight factor includes
both the effort cost and the benefits to achieve each goal, as well as the prior knowledge associated with the
goals, producing near-optimal behavior.

II-51. Decision making and working memory in a parietal-prefrontal loop model

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Working memory and decision-making involve a distributed interacting network of brain areas, with the parietal
and prefrontal cortices (PPC and PFC) at the core. However, the differential roles of these areas and the na-
ture of their interactions are poorly understood. To examine these issues, we model both cognitive functions in
a loop circuit model of interacting modules PPC and PFC. Within each module, excitatory populations selective
for choice options compete through mutual inhibition. Populations send long-range projections between modules
onto excitatory and inhibitory cells. Stimulus input enters into PPC, reflecting the dorsal visual pathway. We iden-
tify conditions where both areas display persistent activity during working memory, and intervening distractors are
represented in PPC but filtered in PFC. These dynamics are observed experimentally and functionally desirable:
PPC encodes saliency and PFC ensures robustness according to behavioral demands. Feedback from PFC to
PPC can flexibly gate whether each stimulus is filtered or maintained in working memory. We propose the con-
cept of pathway-specific excitation-inhibition balance for long-range projections. In this regime, only differences
in activity are propagated and integrated downstream, after the local computation is completed. Balance thereby
enables gating and serial computation within the distributed network. The same circuit model is applicable to
interactions between functionally distinct cell types, ‘target selection’ cells in PPC and ‘response’ cells in PFC. It
provides a mechanistic explanation of the experimental observation that reaction time correlates with the separa-
tion time of target selection cells and the onset time of response cells. We explore when the two modules receive
different, potentially conflicting, inputs, relevant to multisensory and reward-biased decision-making. Integration
of these inputs depends on the relative strengths of local and long-range connections. With strong local and
weak long-range connections, the network can generate ‘conflict states’. We examine conflict dynamics and how
conflict may be resolved.

II-52. Control allows confidence learning

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Risky decisions invariably involve prediction—given a set of current data, make an estimate of a future state. In
such cases, it is important to know not only the estimate, but also whether that estimate is reliable. Are we likely
to succeed right now? Should we defer the decision and if so, what will be the reliability of a future estimate?
How do you learn these quantities from data? Here we investigated the hypothesis that the ability to evaluate
performance reliability depends on the ability to do credit assignment on errors (motor error, trajectory prediction,
etc.). Observers were divided into two groups. Both groups watched a “swarm” of dots moving via a particular dynamics model toward a target. The “no control” group had to determine which half of the target the swarm would impact. The “control” group had to ensure target impact and was allowed to adjust the swarm’s position during flight to do so, providing additional information useful for credit assignment. At any point in the trajectory they could “lock in” the path. For both groups, the earlier a response was locked in, the more points would be earned if it was correct. Observers’ actual extrapolation uncertainty was measured in interleaved blocks of trials where they extrapolated the swarm’s target location from a set trajectory. This allowed direct calculation of the “optimal” response time given observers’ actual extrapolation ability and uncertainty. Observers in the “control” group improved their decision-making behavior by tracking their performance reliability. By contrast, the “no control” group appeared unable to utilize this information. Instead, they heavily relied upon previous trial outcomes and current trial conditions, rather than their individual abilities more generally. These results demonstrate the importance of control in learning and appropriate confidence in risky decision-making.

II-53. A rodent model for studying mechanisms of behavioral response variability

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Behavioral variability is essential for exploration and successful competition in social settings. How and to what degree animals are able to generate variable behavior remains a central question in neuroscience. To examine this question we determined if rats were able to successfully compete against a series of artificial agents designed to punish progressively smaller deviations from the optimal strategy of selecting an action according to a memory-less coin toss. On each trial, the rat and the competitor selected one of two reward ports and the reward was delivered if both made the same selection. Three competitive agents were used. Competitor 1 implemented an algorithm that based its prediction on the detection of biases in animals’ choice patterns using the data from the entire session (Lee et al, 2004). Competitor 2 also used an extended history but adapted more rapidly. Competitor 3 used a large set of more local features to make its prediction (Freund and Schapire, 1997). We find that in the absence of a strongly adaptive environment, rodents generate highly structured behavioral sequences. When faced with progressively tougher competitors, however, they rapidly generate more variable behavioral sequences. To examine strategies that rats used to successfully compete against each agent, we assessed their ability to detect and learn a specific rewarding sequence while competing against each of the algorithms. Limited exposure to the adaptive environment that only punished more global patterns (Competitor 2) left rats sensitive to the local statistics of the environment and more able to detect and generate preferentially rewarded sequential choices. Having competed against the more robust Competitor 3, however, rats appeared to abandon a memory-based strategy and were unable to find rewarded patterns efficiently. Their flexibility in adapting memory-based and memory-less behavioral strategies makes rodents an ideal model to study neural mechanisms of response variability.

II-54. Adaptive reinforcement learning in dynamic environments

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In reinforcement learning (RL), the learning rate is a fundamental parameter that determines how past prediction errors affect future predictions. While in modelling the learning rate is often kept constant, it has been shown that organisms adapt their learning rate to the statistics of the environment. We have previously proposed an RL algorithm that adapts the learning rate by minimizing the overall prediction risk through Q-learning (i.e., by maximizing the prediction precision). This implicitly incorporates additional information about underlying processes and thus accelerates learning. Here, we test and further develop this model by studying how the learning rate in humans adapts in a changing environment using functional magnetic resonance imaging (fMRI). Twenty healthy subjects participated in an fMRI study. Each participant viewed a series of samples drawn from a normal distribution and was asked to make a series of predictions about the statistics of the distribution. Known to the participants, the statistics of the distribution were subject to change throughout the experiment, resulting in stable and volatile periods. Reinforcement learning models (with and without adaptive learning rates) were fitted to the behavioral data. The resulting parameter estimates reflect the subjects’ beliefs about the true state of the world and were entered as regressors in the imaging analysis. We find regions involved in processing uncertainty such as the anterior cingulate cortex (ACC), anterior insula and caudate to reflect the (objective and subjective) statistics of the environment as well as individual learning rates. (This study was funded by NCCR Affective Sciences and the Neurochoice project of SystemsX. We also gratefully acknowledge support from the research priority program at the University of Zurich “Foundations of Human Social Behavior” and NCCR FINRISK.)

II-55. Scientists are suboptimal in judging scientific data

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It is well-established that the human brain is close to optimal in solving relatively simple tasks, such as combining two perceptual cues (Knill and Richards, 1996), but uses suboptimal heuristics when dealing with probabilities at a more cognitive level (Tversky & Kahneman, 1974). It has been argued that deviations from optimality tend to be smaller when the statistics of the task are familiar (Griffiths and Tenenbaum, 2006) or when probabilities are communicated in implicit rather than explicit form (Trommershauser, Maloney, Landy, 2008). We tested scientists on a task that satisfies both criteria, yet we found suboptimal behavior. Subjects were presented with noisy data points generated by one of two possible linear models. The points were presented in a single scatter plot (1-plot displays) or distributed across two scatter plots (2-plot displays). Subjects reported which of the two models was most likely to have generated the data points and rated their confidence. The optimal observer would base his model choice on the sign of the log posterior ratio for both options (which we call the decision variable, d) and his confidence on its magnitude. When conditioned on d, we found that human performance was largely independent of the number of scatter plots, but the confidence ratings were significantly lower in the 2-plot condition. This suggests that subjects were unable to optimally combine evidence across two scatter plots. Human responses are accurately described by a model in which the points in the scatter plots are represented in a noisy manner and d is logistically mapped to confidence rating. When faced with relatively abstract probabilistic information, the brain is apparently unable to utilize the circuitry that serves it so well in cue combination.
II-56. A hippocampal-cortical network underlies model-based planning in humans

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How do we deliberate about the best action to take, without direct experience of the possible outcomes? The instrumental decisions of humans and animals can be broadly classified into two types: habitual responses and goal-directed plans. These are distinguished by the representations they develop: action-reward contingencies estimated via direct experience in the former, and incidentally acquired stimulus-stimulus associations, used to develop flexible plans, in the latter. Computational models of reinforcement learning (RL) describe the development of these two types of representations, termed “model-free” or “model-based”, respectively. Model-free algorithms have been applied to extraordinary success in describing the neural architecture of habitual decisions, in large part because the action-reward representation offers a strong match to biological signals. However, the search for similar correlates of goal-directed decisions have been frustrated by the wide range of possible representations that might be learned by model-based algorithms. We approach this problem by engaging human subjects in a task in which the available associative information is restricted to a specific form, and comparing the fit of models that describe response behavior driven by this information. We successfully describe goal-directed response and choice behavior using predictions of a model-based algorithm, and, using fMRI, identify hippocampus and category-selective visual cortical regions as key loci of learned associative representations that support this behavior. Building on this observation, we explore neural activity during the course of decision making. In particular, we examine how human subjects deliberate about goal-directed plans, and provide support for a model architecture where these plans are constructed by sampling from available stimulus-stimulus associations, reinstating them from a cache of hippocampally-mediated episodic memories.

II-57. Push-pull neural architecture naturally arises from optimal sensory stimulus detection

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Push-pull neural architecture is a recurring property of sensory processing organization across modalities and species. Examples include V1 simple cells (Hubel and Wiesel, J. Physiol., 1962), retinal ganglion cells (Meister et al, J. Neurosci., 2008), LGN neurons (Hirsch et al, Nat. Neurosci., 2005), vestibular neurons (Jones et al, J. Neurophys., 1984), and motion-detecting H1 neuron in flies (Ögmen and Gagné, Neural Networks, 1990). In this work, we attempt to answer the question of why the push-pull architecture prevails in the brain by considering a normative model of sensory decision-making. Sensory systems are often tasked with detecting discrete changes in sensory states based on a noisy stream of inputs. Efficient detection of these state changes requires negotiating a trade-off between detection speed and accuracy. Previously, we showed that the Bayes-optimal control policy for detecting a change in a single stream of noisy inputs requires accumulating Bayesian evidence up to a fixed threshold, and that the optimal procedure naturally gives rise to integrate-and-fire neuronal dynamics, with the gain and firing threshold parameters determined by stimulus statistics and task constraints (Yu, NIPS, 2007). Here, we extend the framework to show that when the task is to detect the onset of one of multiple possible stimulus states, the optimal policy can be realized with a push-pull feed-forward neural architecture. For example, in order to detect a change from a no-motion state to a state with motion in one of two possible directions, the theoretically optimal neural detector must positively integrate the evidence in the preferred direction, and negatively integrate the evidence in the anti-preferred direction, until the cumulative evidence for the preferred direction exceeds a threshold. We also examine how the optimal detection policy and the implicated push-pull neural dynamics
should change as a function of task goals and constraints.

II-58. Concurrent integration and gating of sensory information with orthogonal mixed representations

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Computations in neural circuits are inherently flexible, allowing humans and animals to respond to sensory stimuli with actions that are appropriate in a given context. Fundamental to this flexibility is the ability to integrate only context-relevant sensory information while ignoring irrelevant, distracting information. We studied the neural mechanisms underlying such context-dependent gating in monkeys performing two different sensory discriminations on the same set of visual stimuli. A contextual cue instructed the monkeys to report either the direction of motion or the color of a noisy visual stimulus with a saccade to one of two targets. During this task, we recorded neural responses from the frontal eye fields (FEF). We found that the gating of relevant sensory signals, and their integration towards a choice, can be understood as two aspects of a single dynamical process reflected in FEF population responses. Using linear regression, we identified a multitude of task-related signals represented simultaneously in the responses of FEF neurons, including the direction of motion and the color of the stimulus, the context, and the developing choice. While these different signals are mixed at the level of single neurons, they can be separated at the level of the population by projecting the neuronal activity onto the corresponding regression vectors. To understand better the nature of the mixed signals in FEF, we trained a recurrent network model to integrate only one of two noisy input streams. We found that the network created two context-dependent, approximate line attractors to integrate the relevant sensory inputs. Surprisingly, both the relevant and irrelevant inputs drive the network activity along directions in state space that are almost orthogonal to the direction of integration. This model reproduces the observed dynamic representation of the task-related signals in FEF and reveals a previously unknown mechanism of gating and integration.

II-59. Object completion along the ventral visual stream: neural signatures and computational mechanisms

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Object recognition in natural environments is characterized by significant variability and ambiguity due to object overlap and occlusion. Foreground clutter can obscure critical object features, yet recognition remains robust using only partial information. Here we combine intracranial neurophysiological recordings along the human ventral visual stream with computational models to study the neural circuits involved in recognizing occluded objects. We
evaluate the hypothesis that neural circuits involved in object recognition utilize top-down projections to enhance object representation by recovering occluded features from stored memories. To evaluate this hypothesis, we construct a computational model of object recognition consisting of a hierarchy of reciprocally connected feature processing layers. The model produces a representation in the highest levels capable of sustained recognition accuracy in spite of significant occlusion. Object completion emerges from the interplay of feedforward and feedback connections. Purely feedforward versions of the model do not produce such complete representations. The model constitutes a biologically plausible solution to the challenge of object occlusion and leads to testable predictions about psychophysical performance and neurophysiological responses under occluded conditions. We confirm previous psychophysical findings suggesting that recognition of occluded objects leads to longer reaction times. To examine the neural circuitry underlying object completion, we record field potentials from electrodes implanted in 12 epilepsy patients for clinical reasons. Subjects are presented with 100 ms flashes of 25 exemplar objects drawn from 5 categories and perform a forced choice categorization task. In a subset of these trials, objects are occluded by presenting them through random spatial arrangements of Gaussian “bubbles”. Consistent with the model predictions, occlusion attenuates the physiological responses and leads to delays in object selectivity. The computational, psychophysical and physiological results suggest that top-down projections may play a critical role in object completion.

II-60. Decoding semantic content from fMRI responses to natural movies

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Considerable interest has developed in decoding visual stimuli from brain responses measured using functional magnetic resonance imaging (fMRI). A recent study from our laboratory showed that we can recover a great deal of information about the visual structure of natural movies from evoked fMRI responses [Nishimoto et al, 2011]. Here we use a similar approach to decode the semantic content of natural movies. While the structural features of visual stimuli (e.g. Gabor wavelets) are reasonably well understood, considerable debate surrounds the representation of semantics in the brain. To address this problem we recorded brain activity while subjects viewed two hours of silent natural movie clips. Other individuals then annotated each movie, writing either a free prose description of each second of video or simply listing objects and actions that were present. These annotations were then transformed into several different semantic feature spaces, each embodying a different hypothesis about semantic representation in the brain. These included latent semantic analysis (LSA), latent Dirichlet allocation (LDA), and WordNet. Regularized linear regression was then used to predict the response of each voxel in the brain as a weighted sum of features in the candidate semantic space. Finally, direct and Bayesian decoding methods were used to recover the semantic content of novel visual stimuli not used to train the models. We found that all of these methods and models can recover significant semantic information from fMRI data. Analysis of the estimated models revealed that as much as 27% of the cortex is involved in representing visual semantic information, including inferior temporal, medial parietal, medial frontal and inferior frontal cortices. These results show that we can accurately model and decode the representation of dynamic semantic information in the brain.
II-61. Direction vs. category selectivity in LIP and MT neurons in delayed match-to-category task

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Freedman and colleagues have conducted a series of neurophysiological experiments to examine neural responses during delayed match-to-category (DMC) tasks in lateral intraparietal cortex (LIP), and medial temporal cortex (MT). Although much has been revealed about the information encoded in these areas, little is known about how different signals interact and evolve over the time course of a trial. Such knowledge is crucial in determining the neural mechanism of categorization. We took a fresh look at the work done by Freedman and Assad (2006) that used random-dot motion stimuli to train DMC task. Here we report two major insights from our preliminary analyses. A) In naïve monkeys, LIP neurons are tuned uniformly to directions of motion (Fanini and Assad, 2009) but after DMC training they robustly reflect the categories of stimuli (Freedman and Assad, 2006). We characterize the dynamics of motion direction and category signals and found that most LIP neurons is tuned to motion directions early in the sample period before category signal arises. We found that the tuning curves of LIP neurons are redistributed after learning, i.e. more LIP neurons are tuned to the directions near the center of the categories than the directions near the category boundary. Such a shift in stimulus representation facilitates the discriminatory decision that the task requires. B) We found that although MT activities straightforwardly represent motion directions of stimuli during sample period, their activity is modulated by test stimulus categories in the test period. This signal might be fed back from categorical decision area to guide synaptic learning. Accompanying this analysis, we construct a firing rate model to probe the mechanism and functional benefits associated with these two findings. Specifically, we investigate how reward-dependent synaptic plasticity and feedback from categorical decision area to MT may lead to the redistribution of LIP tuning curves.

II-62. Recovery of a shared spike-timing-dependent synaptic plasticity resource in natural spike trains

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Studies of spike-timing dependent plasticity (STDP) have revealed that long-term changes in the strength of a synapse may be substantially modulated by temporal relationships between multiple pre- and post-synaptic spikes. While long-term potentiation (LTP) and long-term depression (LTD) of synaptic strength have been modeled as distinct or separate functional mechanisms (Dan and Poo, Physiol Rev, 2006; Abbott and Nelson, Nature, 2000), here we present a new shared resource model. Motivation for this model originated from our analysis of unsupervised learning stability with STDP for multi-spike trains. Our model allows fast, stable and diverse learning of temporal spike patterns with a biologically-consistent spiking neural network. Surprisingly, the resource model also accurately predicts in vitro observations of STDP in natural multi-spike trains. We discuss the potential implications and candidate commonalities in natural short-term and long-term plasticity mechanisms.

We propose that LTP and LTD may be cooperative with closely-linked mechanisms, as opposed to competitive with separate functional mechanisms. Specifically, we propose a shared resource model for synaptic plasticity with three elements: 1) commitment to synaptic strength modification is modulated by availability of synaptic resources shared between potentiation and depression mechanisms; 2) resources are depleted by commitment to synaptic
potentiation or depression, depending on the magnitude of modification; and 3) the shared resources available for a synapse replenish over time. In a simple form, the resource model has only one parameter, the time constant of the resource recovery. This resource is phenomenological, but could represent any one or combination of biological factors (e.g., internal Ca2+, receptor expression, phosphorylation state, CaMKII activation, and/or gene transcription).

II-63. Pairwise analysis can account for network structures arising from spike-timing dependent plasticity

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Spike timing-dependent plasticity (STDP) modifies synaptic strengths on the basis of timing information available locally at each synapse. Despite this, STDP can give rise to global structures when it acts within a recurrently connected network. We analyze the types of structures that STDP can produce in a network of spiking neurons both by running network simulations and through a mathematical analysis of the effects of STDP on interactions between pairs of neurons. This provides an analytically tractable way of relating the structures arising in a network to properties of the STDP model being used to modify synapses. We show how conventional pair-based STDP acts as a loop-eliminating mechanism and organizes neurons into in- and out-hubs, depending on the external input: sub-populations of neurons that receive higher external input turn into out-hubs once the synaptic weights reach steady state, and subpopulations that receive lower external input turn into in-hubs. Loop-elimination increases when depression dominates and decreases when potentiation dominates. In addition, we find that STDP with dominant depression implements a buffering mechanism for network firing rates. STDP with a shifted temporal window can enhance recurrent connections in a network, and also functions as a homeostatic mechanism that maintains a roughly constant average value of the synaptic strengths. In general, studying pairwise interactions of neurons provides a number of important insights about the structures that STDP can produce in large networks.

II-64. Similarity of spontaneous and sensory-evoked activity in cortex does not imply learning

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Sensory cortex is spontaneously active, and this spontaneous activity has statistical properties that are remarkably similar to those of sensory-evoked activity. The significance of this similarity, however, is unclear. One interpretation comes from theories of learning in neural networks, such as Boltzmann machines. Through synaptic plasticity, such networks learn a model of the probability distribution of their inputs. When later presented with a partial or absent input, the network produces activity patterns sampled from the posterior or prior of the learned distribution, respectively. The success of this learning can then be observed in the similarity between spontaneous and evoked activity. In support of this idea, a recent study analyzed multiunit activity in ferret V1 and found that the Kullback-Leibler (KL) divergence between spontaneous and evoked firing patterns was substantially higher.
in juveniles than in adults (Berkes et al., Science, 2011). Here we provide a more parsimonious explanation of these findings. In population recordings of A1 and V1, we found that the joint structure of multiunit spike trains was largely determined by network dynamics, which we summarized by the mean firing rate on each electrode and the distribution (over time) of the population rate. Furthermore, even a randomly-connected recurrent spiking model exhibits a transition between a state of poor spontaneous-evoked match to a state of high match, after increasing a tonic conductance without any form of learning. Thus, in both cortical recordings and simulated networks, the KL divergence is dominated by changes in network dynamics, and changes in multiunit distributions can occur without synaptic plasticity. We conclude that the level of similarity between spontaneous and evoked activity must be interpreted with caution: its changes need not be a signature of learning-related modifications in synaptic strength; and high similarity does not imply that a network has learned a model of the environment.

II-65. Learning from positive and negative rewards in a spiking neural network model of basal ganglia

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Despite of vast amount of experimental findings collected on role of basal ganglia in reinforcement learning, there is still lack in spiking neural network models that use plausible plasticity mechanisms to demonstrate reward-based learning. In this work we extend a spiking actor-critic network model of basal ganglia introduced by Potjans et. al., aiming to create a minimal realistic model of learning from positive and negative rewards. We hypothesize that not only the actor part, dorsal striatum, but also the critics part, the ventral striatum are subdivided in distinct populations of medium spiny neurons (MSN), that carry either D1 or D2 dopamine (DA) receptor type. This segregation allows explicit representation of both positive and negative expected reward within respective population. In line with recent experiments, we further assume that D1 and D2 MSN populations have distinct, opposing DA-modulated bidirectional synaptic plasticity, where high DA release induce potentiation (LTP) in D1 and depression (LTD) in D2 MSN, and reversely, low DA release leads to LTD in D1 and LTP in D2 MSN. We implement the spiking network model in simulator NEST and conduct experiments involving application of delayed rewards in a grid world setting, where a moving agent has to reach a goal state while maximizing the total obtained reward. We demonstrate that the network can learn to reach the goal equally well from both positive and negative rewards distributed in the grid world environment. Specifically, it can be shown that the network is also able to cope with the learning task even if only negative rewards are available, as opposed to the original model. The spiking network model provides thus further hints on functional role of D1-D2 MSN segregation within striatum and explains necessity for reversed direction of DA-dependent plasticity found at synapses converging on distinct striatal MSN types.

II-66. On the “Site” and “Source” of Saccadic Countermanding: Reformulations of the Interactive Race Model

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Countermanding saccades toward a visual target can be modeled as a race between two processes: one that
produces a saccade (GO process) and the other that prevents the GO process from finishing (STOP process; Logan & Cowan, 1984, Psych Rev). An interactive race model was formulated to explore how the STOP process can prevent GO from finishing through lateral inhibition, motivated by the finding that firing rates in presaccadic movement cells in the saccadic generator network, including the frontal eye field (FEF), superior colliculus (SC), basal ganglia, etc., which may instantiate the GO process, decline markedly when saccades are successfully inhibited (Boucher et al. 2007, Psych Rev). However, the interactive race model did not take into account the full temporal dynamics of fixation cells in the network, which may instantiate the STOP process. We incorporated this aspect of physiological data in revised interactive race models and tested several reformulations to examine core assumptions of the original model. We found that models that assumed an external inhibitory control (e.g., blocking input to the GO unit, boosting input to the STOP unit, or strengthening the inhibitory connection from the STOP unit to the GO unit) after the presentation of a countermanding signal fit the behavioral data better than models that did not. The former models also exhibited the activation functions of the GO and STOP units that resembled the activities of the movement and fixation cells. We conclude that the source of inhibitory control exists outside of the site (i.e., FEF, SC) of saccadic countermanding.

II-67. Dimensionality in motor cortex: differences between models and experiment

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During movement, neurons in motor cortex exhibit complex, time-varying response patterns. Yet while it has been difficult to determine what movement variables are represented by these responses, it is relatively easier to ask how many variables are encoded. This can be done by assessing dimensionality using principal component analysis (PCA). We analyzed multi-electrode recordings from two monkeys performing a reaching task involving several different arm movements (e.g. right versus left, curved versus straight). We first assessed dimensionality across neurons—i.e., given the responses of k neurons, is the response of the k+1th neuron a linear combination of the first k? We then assessed dimensionality across movements—i.e. given the population responses for k movements, is the population response for the k+1th movement a linear combination of the first k? We first examined simulated data from a traditional model, where each neuron is tuned to reach end-point (during planning) and velocity (during movement). These simulated data had firing rates / noise properties matched to the real data. For both simulated data sets, the across-neuron and across-movement dimensionalities were low and nearly equal. This is expected; the model neurons represent a modest number of movement parameters. However, the results from the experimental data differed strikingly from those of the model. The experimental data shows high dimensionality across neurons, yet remarkably low dimensionality across movements. This asymmetry across dimensionality measures is dramatic in the data, yet absent in the traditional model. Thus, the data differ in both quantitative and qualitative ways from the predictions of a traditional model. Nevertheless, this result is compatible with what is expected of many classes of dynamical systems. For example, a high-dimensional dynamical system could show such an effect if its initial states (one per movement) lay on a low-dimensional manifold.
II-68. Infinite-horizon optimal feedback control models for biological systems: application to target jump

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Optimal feedback control models have been highly successful in explaining many aspects of goal-directed reaching movements. However, most such models use a finite-horizon formulation and thus have to pre-fix movement duration instead of predicting it. Consequently, to determine movement duration, these models have to be run multiple times with different pre-fixed durations until an appropriate duration, according to some criteria, is found via trial and error. The finite-horizon models are particularly inadequate to account for experiments in which the target jumps to a new location at various times during reaching because these models have to know the new movement duration, and compute a new solution for this duration, after the target jumps. To resolve this and other problems of finite-horizon models, we and others recently proposed that an infinite-horizon formulation provides a better framework for understanding biological motor control. Specifically, we implemented Phillis's (1985) steady-state solution to an infinite-horizon optimal feedback control model. We showed that the model predicts movement duration (Fitts’s law), and explains movement trajectories better than finite-horizon models. In the current study, we extended the model in two important ways to make it more biologically plausible. First, we introduced state-dependent noise into sensory feedback to incorporate Webber's law. Second, we included delay for sensory feedback. To our knowledge, these features are not properly incorporated into previous optimal feedback control models. We then analytically derived the solution to the extended model, and applied it to explain key observations of target-jump experiments, including uni- and bi-modal speed profiles under various conditions. Contrary to previous suggestions of multiple mechanisms, our model provides the first unified account for the target-jump experiments.

II-69. Theta-phase coding by grid cells in two-dimensional environments

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When a rat moves, grid cells in its entorhinal cortex become active in multiple regions of the external world that form a hexagonal lattice. As the animal traverses one such “firing field”, spikes tend to occur at successively earlier theta phases of the local field potential (“phase precession”). While phase precession when a rat runs along a one-dimensional path has been demonstrated, whether the same phenomenon occurs in the open field is less clear. Here, we analyze phase precession in both one- and two-dimensional environments. For rats running on a linear track, we show that spike phases provide 80\% more spatial information than spike counts, thereby improving the position estimate derived from a single neuron down to a few centimeters. To understand how spike phase variability limits the resolution, we analyze spike trains run by run. Phase precession on single runs is significantly stronger than the pooled-run data suggest. Furthermore, no correlations in the spike sequences exist across the multiple firing fields, suggesting that each field independently encodes physical space. In two-dimensional environments, a rat’s path can curve, go through the center of the grid field, or swerve and miss the center completely; additionally, running speed is highly variable—in contrast to the linear track. Despite these differences, the slope and the correlation of phase precession in one and two dimensions are quite similar.
Interestingly, runs that graze a grid field tangentially lead to steeper phase precession, as opposed to runs through the field center. If the run through one firing field is long and winding, however, phase precession decreases midway, and the grid cell’s spikes lock to a new preferred phase. Such observations pose constraints on the possible mechanisms of phase precession.

**II-70. Suppressing Actions in the Basal Ganglia**

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Action suppression is thought to be a core component of executive function. Impaired action suppression plays an important role in many pathologies such as Parkinson’s Disease, Tourette Syndrome, drug addiction or gambling. A common clinical tool to detect impaired action suppression is the stop-signal task, in which human subjects have to rapidly suppress imminent movements. To test previous proposals that parts of the basal ganglia act as a “brake” on behavior, we developed a rat variant of the stop-signal task and recorded neural activity from different basal ganglia subregions simultaneously (striatum, globus pallidus, substantia nigra, pars reticulata; SNr, and subthalamic nucleus; STN). We found that movement initiation was marked by firing-rate decreases in the output region SNr, in line with disinhibition of thalamocortical drive during action initiation. Importantly, during successful action suppression the SNr firing-rate decreases were interrupted by a brief short-latency response to the stop-signal. During failed action suppression there was no response to the stop-signal in SNr. In contrast, we found STN units that exhibited fast responses to the stop-signal in both successful and failed action suppression. This suggests that the STN-SNr transmission of sensory signals is crucial for reactive inhibition of behavior. We conclude that SNr performs sensorimotor integration by combining the STN sensory stop-signal response with action-related signals from the striatum.

**II-71. Phase coding of trajectories by grid cells in unconstrained environments**

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It is thought that EEG and LFP oscillations reflect large amounts of coherent activity in the brain and that neurons represent information via use of temporal and rate coding. In phase coding, the firing of a neuron relative to the phase of LFP rhythms also carries information. Hippocampal place cells fire at earlier phases (precess) in hippocampal theta as the animal moves through the place field on a linear track and in the open field. Grid cells in medial entorhinal cortex (MEC) fire in an array of positions falling on the vertices of a hexagonal grid, and precess against MEC theta on the linear track. However, an in-depth analysis of the phase-coding of grid cells in the open field has yet to be performed. We have developed a novel technique to aid in this analysis. We estimate how “in field” an animal is using the rate map, and from the rising and falling of the “in-fieldness” along the animal’s trajectory we extract phasic information using the Hilbert transform. This gives us a score for how much the animal has completed each pass, which we call the “pass-index.” Similar to place cells, the firing of grid cells precesses against theta as the animal moves through a field, irrespective of the direction or speed of the pass. In addition, grid cells precess as the animal moves through the field regardless of the entrance and exit angle of the pass or how close the pass comes to the center. This gives grid cells the capacity for finely coding their recent trajectories.
via phase coding, and may have implications for models that generate grid cells. The pass-index can be applied to any state space, and may provide insights into the mechanisms by which the brain uses phase coding in other systems.

II-72. Statistics of junctions in natural images

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Studies on image features like edges and contours have provided insights into how the visual system efficiently processes images from the natural world. Junctions are a loosely defined class of image features that has received comparatively little attention. Using the Berkeley Segmentation Database, we measured several properties across up to 10,000 junctions present in 500 natural images. These statistics shed light on what types of occlusions give rise to junctions and why a large percentage of junctions cannot be detected locally by human observers or automated methods. Junctions were defined as the points of intersection between three hand-segmented objects with high agreement across segmentations by multiple subjects. In order to investigate occlusions, we measured the most common angles found at Y-junctions. The most common angle was slightly less than 180 degrees; the most common angle triplet was roughly (88 deg, 108 deg, 164 deg). We measured the probabilities of occurrence of the Michelson contrast between the three wedges of Y-junctions. We found approximately 40% of Y-junctions have an edge with a Michelson contrast of less than 0.05, making them invisible locally. The most common triplet of contrasts has all three magnitudes below 0.15. Previous psychophysical work has found that 45-50% of junctions cannot be identified by the visual system using only local information, which is in line with our estimated fraction of junctions with one contour having near-zero contrast. These results will be discussed in the context of efficient coding of junctions by the visual system and a Bayesian approach for junction identification in natural images.

II-73. V1 and A1 maps: different topographies, a common organizing principle

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Contrary to the long-held idea that the sensory cortices exhibit similar topography, recent physiology has indicated a difference between the primary visual cortex (V1) and the primary auditory cortex (A1). On a single-cell scale, the V1 retinotopic map is smooth (Ohki et al., 2006; Smith & Hausser, 2010), whereas the A1 tonotopic map is disordered (Bandyopadhyay et al., 2010). This discrepancy suggests that V1 and A1 use fundamentally different information processing strategies; however, we hypothesize that the discrepancy emerges not from the difference of organizing principles, but from that of environmental statistics. A V1 model study (Hyvarinen & Hoyer, 2001) showed that a smooth retinotopic and orientation map can emerge from visual scene statistics; in addition, our previous study on A1 (Terashima & Hosoya, 2009) suggested that one of the statistical characteristics of auditory stimuli, compared to visual ones, is correlations between distant frequencies. In this study, to model the disordered A1 map, we investigated how the V1 map model behaves when the input is “auditory”. First, to vary the input “auditoriness”, i.e., the degree of correlations between distant coordinates, we used one-dimensional artificial
inputs. When the inputs were vision-like (simply locally correlated), the model produced smooth maps; however, as the input “auditoriness” increased, maps were more disordered. Second, we used natural visual and auditory stimuli, and compared the maps’ smoothness. As previously reported, the natural images resulted in a map with smoothly changing retinotopy. In contrast, when the input was spectrograms of the human voice, the map was significantly disordered. Therefore, the single model can produce both V1-like and A1-like maps, depending on the input statistics, which are in fact different between vision and audition. The results suggest that the different topographies of V1 and A1 may be a natural consequence of adapting to natural stimulus statistics.

II-74. Task-dependent feature representations of complex sounds in human auditory cortex

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Real-world sounds vary in a plethora of different ways and it is unclear which features are encoded in auditory cortex. Electrophysiological evidence of rapid plasticity in non-human auditory cortex suggests that the information represented varies depending on task demands. However, limitations in methods for neural measurement have made it difficult to study auditory feature information coding in the human brain. Investigating how feature tuning differs between individuals and under varying task demands could not only foster understanding of how complex sounds are represented and how features are integrated to learn to categorize new and recognize familiar sounds, but also have implications for people suffering from abnormalities in auditory processing. In order to assess which acoustic and abstracted features of complex natural sounds are represented in human auditory regions during perception and two cognitive tasks (change detection and imagery), we used functional magnetic resonance imaging (fMRI) and multivariate pattern analysis (MVPA), which exploits information in distributed neural networks and is robust to individual differences in anatomy. Our results show that the information encoded in spatially distributed patterns of activity is task-dependent. Only during imagery but not during perception or short-term memory maintenance was semantic information represented in auditory regions. During perception and short-term memory maintenance, activity patterns in auditory regions contained stimulus-specific but not abstracted, categorical information. Additionally, differences in activation magnitude and pattern distinctiveness in auditory regions were related to individuals’ memory capacity and imagery vividness. This indicates that auditory cortex is recruited for processes beyond analyzing simple feature information, playing an important role in maintaining sustained representations of sounds in short-term memory and encoding abstracted information during imagery. The demonstrated suitability of multivariate methods for analyzing feature coding in human auditory cortex using fMRI provides exciting opportunities to investigate how neural representations vary within as well as between individuals.

II-75. Predictive Coding with linear threshold neurons

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Neurons must faithfully code natural signals that may vary by orders of magnitude over a short time scale, for example following a saccade, yet possess only a limited dynamic range. This dynamic range requirement may be reduced by subtracting components of the signal that can be predicted from the past; this is a predictive coding strategy (Srinivasan et al, 1982). Such compression of the dynamic range can be implemented by a
feedback inhibition circuit, where Neuron 2 (long time constant) computes the prediction, which is then subtracted from the full signal transmitted through Neuron 1 (short time constant). We studied the optimal parameters of a linear predictive coding network for input with a mixture of low (predictable) and high frequency (unpredictable) components. Minimizing transmission power, we find the predictor neuron’s time constant must be matched to the temporal correlation length of the input. However, when the ratio of low and high frequency components is varied, the optimal network was shown to require different feedback strengths, simultaneously varying the length of time over which the predictive cell sums, as well as the amplitude of the returning feedback. This need for a variable feedback immediately suggested that a nonlinearity applied to the output of the feedback cell would provide a response better than the optimal linear threshold cell, over a range of contrast intensities. We present a model that utilizes a linear-threshold function on the output of the predictive cell. We demonstrate that this model does indeed reduce the cost compared to the optimal linear network. Further, it is able to model many of the nonlinear effects measured with changing contrast, without having to adapt its properties at each contrast level (unlike alternative models) (Laughlin 1994; Victor 1987).

**II-76. Serotonergic modulation of sensory information processing**

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Involved in a wide range of cognitive functions, serotonin is an important neuromodulator. A common theme that emerges from many studies is that activation of the serotonergic system facilitates motor activity and suppresses sensory information processing. Specifically, in the rodent olfactory system serotonin modulates both sniffing and odor processing, and is therefore well positioned to control olfaction. In rats engaged in an olfactory discrimination task it was shown that neurons within the dorsal raphe nucleus, the major source of serotonin to the cerebral cortex, modulate their activity in response to specific sensory, motor and reward variables. In addition, it was shown that serotonin alters the response properties of olfactory bulb neurons. However the impact of this activity on behaviour and perception remains largely unknown. To address this issue we use optogenetic, electrophysiological and behavioral approaches. By viral delivery of the light-activated cation channel channelrhodopsin-2 into serotonergic neurons, we are able to specifically identify these neurons during extracellular recording, and to activate them with millisecond precision. We find that DRN illumination elicits a prominent response, which we term optical field potential (OFP). The OFP displays a number of characteristics similar to those of typical serotonergic neurons, such as waveform shape and frequency adaptation, suggesting that it represents the summed firing of synchronously active neurons. We are extending this method to study the effects of serotonin release on the response properties of olfactory cortex by activating serotonergic neurons during odor presentations or afferent stimulation in-vivo and in brain slices. By controlling serotonin release in mice as they discriminate between various odors, we hope to establish the relationship between serotonergic activity on the one hand and perception and behavior on the other. We believe that the results of this study will provide new insight into the functioning of this little-understood system.
II-77. Temporal aspect of odor stimuli and odor identity and intensity coding by Olfactory Receptor Neurons

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Odor stimuli elicit spatio-temporal patterns of activity in the brain. Spatial patterns arise from the specificity of the interaction between odorants and odorant receptors expressed in different olfactory receptor neurons (ORNs). But which features of odor stimuli are represented in temporal patterns and their role in odor coding remains unknown. We performed single sensillum recordings from the Drosophila antenna simultaneously with measurements of the odorant concentration reaching the fly. We found that stimulus dynamics depend on odor type before any interaction with the olfactory system occurs. Individual ORNs follow these differences in stimulus dynamics with such precision that a linear-nonlinear model can predict the response of one ORN to different odorants solely from measurements of the stimulus. This finding suggests that odorant structure might not always be the sole source of information regarding odor identity and that stimulus dynamics also carries information about the identity of an odorant. Importantly we found that within the sensitivity range of a single ORN the degree and time-scale of adaptation are independent of stimulus intensity and background. As a consequence, ORN response dynamics are remarkably similar across a large range of stimulus intensities. Hence, an individual ORN can independently capture odor identity and intensity in the dynamics and magnitude of its response. The decomposition of odor identity and intensity has been attributed to chemical structure recognition by a repertoire of ORNs and circuit processing downstream from the ORNs. Our results suggest a mechanism by which temporal patterns of activity in ORNs may also contribute to this decomposition by capturing odor-specific stimulus dynamics independently of the intensity of the signal. Odor discrimination and tracking therefore may rely on features of odorant dynamics in addition to features of odorant structure.

II-78. Adaptive sharpening of tuning in the auditory system of the cricket

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Natural environments barrage the animal with complex stimuli. This constitutes a special challenge for sensory systems, as interference between stimulus components can lead to information loss. To maximize information transfer interference has to be minimized. In a linear encoder this can be achieved by suppressing the gain or decorrelating the filters for individual components. The interference problem also pertains to crickets, whose auditory world is divided into a low-frequency channel associated with mating calls and a high-frequency channel linked to predator signals. This clear behavioral partition is reflected in the simple layout of the auditory system: in the prothoracic ganglion exist two ascending neurons (AN1, AN2) that are most excited at different carrier frequencies and receive inhibition from a broadly-tuned local neuron (ON1). However, both AN respond to predator and mate signals at high intensities, leading to potential interference. We recorded responses from all three neurons in the network while presenting amplitude-modulated stimuli with either single carrier frequencies or with a mixture of mate and predator carriers. Temporal and spectral tuning was quantified by estimating linear-nonlinear models consisting of a filter and a nonlinearity. Coding properties changed adaptively to minimize interference: while tuning for carrier frequency was relatively broad for single-carrier stimuli, the system’s tuning was much sharper when confronted with multiple carriers due to “side-band” suppression. Additionally, changes in filter shape led...
to a decorrelation of the temporal selectivity for song- and predator-specific sounds. An abstract network model reveals that this adaptive coding can arise through the logarithmic nonlinearity inherent in the dB transformation of the auditory system. Untuned feed-forward inhibition further sharpens tuning through an “iceberg effect” and decorrelates the filters. Logarithmic encoding of intensities and broadly-tuned inhibition are mechanisms also at work in cortex and constitute thus general mechanisms underlying the efficient representation of complex stimuli.

II-79. Performing noise reduction using realistic spectro-temporal receptive fields as modulation filters

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Natural auditory scenes are often composed of a multitude of competing sounds from distinct sound sources that the brain must parse in order to extract relevant information. Despite decades of research into the so-called cocktail party problem, it remains unclear how the brain isolates sounds from individual sound sources. Drawing on recent work in the avian auditory cortex, we have devised a model to perform noise reduction in such complex auditory scenes. Studies characterizing the spectro-temporal receptive fields (STRFs) of neurons in primary and secondary avian auditory cortex have discovered tuning to an array of spectro-temporal modulations. Consequently, it has been shown that the ensemble modulation tuning of these neurons reflects the spectro-temporal modulations present in bird song. Our model exploits this ensemble tuning by using model neurons, described by their STRFs, as modulation filters, selectively responding to the presence of modulations corresponding to bird song within a complex noisy stimulus. The STRFs used by the model can be taken from actual neurons, or they can be learned using an iterative sparse coding algorithm. By projecting the noisy stimulus onto a population of STRFs we can obtain a “neural response”. The set of responses provides a time-varying readout of the presence of song in the noisy stimulus, and since we know the frequency response properties of each STRF, the responses can be used to isolate song in time-frequency space. We thus utilize these filters to generate time-frequency gains that are then applied to the noisy stimulus to produce an estimated reconstruction of the clean song. This model performs at least as well as other state-of-the-art methods for noise reduction. This model also performs well on speech stimuli, successfully separating a target speech stimulus from competing background noise, even when the background noise is composed of competing speech or crowd noise.

II-80. Encoding of ultra-sonic vocalizations in the rodent primary auditory cortex

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Rats produce complex vocalizations in communicating with each other. Over 10 types of distinct ultra-sonic calls can be distinguished in their repertoire. Neurons in the primary auditory cortex respond selectively to con-specific vocalizations. However, the precise mechanisms of how complex vocalizations are encoded in the auditory pathway are not well understood. To learn how the auditory cortex encoded information about rat vocalizations, we presented a library of recorded and purified vocalizations to awake rodents, recorded neural activity in the auditory cortex and constructed a mathematical model that allowed to predict A1 responses to novel vocalizations. To generate a library of acoustic stimuli, we first constructed a sparse representation of the recorded vocalizations. Each vocalization was modeled as an amplitude- and frequency- modulated tone (akin to a whistle). A1
responses were selective for a small fraction of vocalizations. To examine temporal invariance in responses of A1 neurons, these vocalizations were slowed down (two-fold) and accelerated (two-fold). A1 neurons exhibited limited temporal invariance in their responses. To measure the temporal parameters of neuronal responses, we next presented a long USV-based stimulus, consisting of 350 purified vocalizations, concatenated into a long stimulus sequence. A1 neurons exhibited reliable and specific responses to this sequence. We used the responses of populations of neurons to cluster the vocalizations into 10 categories. Furthermore, we used a generalized linear-non-linear model to predict A1 responses. The GLNM was modified from standard methods, as the stimulus was represented in a sparse fashion, through amplitude and frequency modulation variables, rather than a spectrogram. The GLNM, trained on the first 200 vocalizations, gave accurate predictions for neuronal responses to the remaining 150 vocalizations (correlation coefficients up to .78). Our study shows that neurons in the primary auditory cortex exhibit high temporal precision and selectivity in encoding ultra-sonic vocalizations.

II-81. Symmetry in the neural representation of visual motion

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The distribution of angular motion in natural scenes has an overrepresentation of horizontal and, to a lesser extent, vertical movement. The mirror symmetries in natural optic flow distributions constrain the class of direction selective (DS) functions which can maximize the information between the direction of motion and the neural response. In this work, we develop a theory of optimal DS response for single neurons and for pairs of neurons, and compare predictions with responses observed in DS neurons in the mouse LGN. Natural scene optic flow statistics are compared with the responses of DS neurons in the mouse LGN as revealed by in vivo two photon calcium imaging to determine whether those neurons are optimal for encoding information alone or as pairs of neurons.

II-82. The omitted stimulus response originates in ON bipolar cells

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Previous work showed that retinal ganglion cells respond robustly to violations of periodic stimulus patterns with an extra burst of action potentials (Schwartz et al., Nat Neurosci. 2007). The latency of this burst increases as the period of the flash sequence is increased, such that the peak firing rate coincides with the time of the next expected flash. This phenomenon is called the omitted stimulus response (OSR), and is one example of complex pattern detection in the retina (Schwartz et al., J. Neurophysiol. 2008). Several models have been proposed to explain the origin of the OSR. One class of biophysical models proposes a resonant element in the inner retinal circuit that continues to oscillate after the stimulus ends (Gao et al., Network 2009). A second hypothesis is that the OSR is caused by the changes in mean light level that interact with the standard biphasic temporal tuning of ganglion cells (Werner et al., J. Neurophysiol. 2008). To distinguish among these and other possibilities, voltage-clamp recording of retinal ganglion cells were performed while presenting full-field flash sequences with periods...
ranging from 8-20 Hz. The latency of the input currents to ganglion cells shifted linearly with the period of the flash sequences, suggesting that the OSR originates upstream of ganglion cells. Whole-cell voltage clamp recordings of bipolar cells from retinal slices show that ON bipolar cells, but not OFF bipolar cells, have an OSR in their input currents. Additionally, the OSR is not present in suction electrode recordings of currents in cone outer segments. Finally, the OSR is abolished by the bath application of APB, which specifically blocks the mGluR6 receptor found in ON bipolar cells. These results suggest that the OSR originates in the dendrites of ON bipolar cells, possibly due to the dynamics of the mGluR6 second messenger cascade.

II-83. Saccade-confounded image statistics explain visual crowding

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Processing of shape information in human peripheral visual fields is impeded beyond what can be expected by poorer spatial resolution. Visual crowding—the inability to identify objects in clutter—has been shown to be the primary factor limiting shape perception in peripheral vision. Despite the well documented effects of crowding, its underlying causes are poorly understood. Since spatial attention both facilitates learning of image statistics and directs saccadic eye movements, we propose that the acquisition of image statistics in peripheral visual fields is confounded by eye-movement artifacts. Specifically, the image statistics acquired under a peripherally deployed spotlight of attention is systematically biased by saccade-induced image displacements. These erroneously represented image statistics lead to inappropriate contextual interactions in the periphery and cause crowding. We simulated the acquisition of joint orientation statistics from attended image regions within a spatial extent defined by the lateral connections of a V1 neuron. The stimulations were conducted over a range of retinal eccentricities and allowed for a non-zero temporal overlap between the trailing edge of attention and the onset of saccades. We show that orientation statistics acquired under such conditions misrepresent the underlying image statistics in two major aspects: (a) whereas the true image statistics dictate a co-circular pattern of connectivity (Sigman et al., 2001), the connectivity pattern in the periphery would have a preference for iso-orientation; (b) the extent of the mispresented statistics have a strong radial bias reflecting the fact that saccades are radial eye movements connecting the fovea to the attended peripheral locations. With a single free parameter (temporal overlap between saccade and attention), our results provide a simple quantitative explanation for the characteristic shape of the spatial extent of crowding (Bouma, 1970; Toet & Levi, 1992) and suggest a root cause of form-vision deficits in peripheral vision.

II-84. Neurons in macaque area CIP respect the geometric topology of 3D object orientation

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Interacting with objects in 3D space, for instance grasping them, often requires determining their spatial orientation. Here we investigate the visual encoding of 3D object orientation. An object's spatial orientation generally has three degrees of freedom represented by the special orthogonal matrices. Within this space, neuronal tuning curves for 3D object orientation are constrained by symmetries and perceptual singularities that depend on the
physical structure of the viewed object. For instance, the 3D orientation of a plane can be represented by its unit normal, which lies on an antipodally symmetric sphere. Planar orientation therefore has two degrees of freedom, which we parameterize as tilt (rotations about the line-of-sight) and slant (rotations in depth). When the plane’s normal is perpendicular to the line-of-sight, the plane self-occludes, creating visibility constraints that eliminate the sphere’s equator. This geometric topology introduces theoretical constraints on neuronal tuning curves and suggests a metric for measuring perceptual distance between planes of different tilt-slants. To investigate if neuronal responses conform to these constraints, tuning curves were measured extracellularly from single neurons in the caudal intraparietal area (CIP) of macaque monkeys. The stimuli consisted of checkerboard planes rendered with monocular texture and binocular disparity cues. Many neurons were tuned for 3D surface orientation and, as expected from the modeling, an antipodally symmetric spherical function fit the data well. Tilt and slant were uniformly represented over the population. We also investigated the multiplicative separability of joint tilt-slant tuning curves (i.e., whether they are defined by the outer-product of independent tilt and slant tuning curves). Even though the geometry imposes strong constraints on this property, tilt-slant tuning was separable for most neurons. Our results suggest that the representation of 3D object orientation in area CIP respects the topological structure inherent in describing the visible configurations of objects.

II-85. Reconstruction of the connectome of the fruit fly visual system

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In 1950s, Hassenstein and Reichardt proposed an elementary motion detector (EMD) that computes correlations between visual signals offset in time and space (Figure 1A). Although most following experimental results (Borst, 2010) were largely consistent with the original proposal, there has never been a “smoking gun” that identifies particular neurons with the specific computations within the EMD. In fruit fly (Figure 1B), the EMD circuit is thought to be in the medulla (Figure 1C) because the upstream lamina does not contain directionally selective cells while the downstream lobula plate contains cells, such as H1, which integrate motion over visual field. The medulla was previously called an “impenetrable jungle” because of its complicated structure. To help uncover the neuronal EMD we pursued a reconstruction of the medulla using electron microscopy. Such reconstruction is made easier by the small size of the fly, stereotypic brain geometry from fly to fly, and the repeating columnar structure of the medulla. We imaged 90x90x90um³ volume and obtained a dataset of ~10¹² 3x3x40nm³ voxels. Next, we developed a semi-automated pipeline to assign synapses to individual neurons by tracing neuronal processes through this volume. The reconstructed circuit of 48 columnar neurons contains thousands of synapses. We identified individual neurons by matching their shape (Figure 1D) to previously reported light microscopy images of Golgi impregnations (Fischbach and Dittrich, 1989) and newly obtained GAL4-UAS lines (Pfeiffer et al. 2008, Nern & Rubin, 2011). These lines will allow genetic access to neurons of specific classes to determine their repertoire of neurotransmitters and synaptic receptors, manipulate their physiological properties, and monitor their activity. The emerging connectome (Figure 2), along with future physiological investigations, should be sufficient to conclusively resolve the nature of EMD mechanism in fruit fly, as well as provide insight into the other computations of the visual system.
II-86. Developmental regulation of sensory processing by spontaneous cortical activity

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Spontaneous activity generated intrinsically in thalamocortex utilizes the vast majority of the brain’s energy, but its function is poorly understood. Here we present evidence that the developmental initiation of spontaneous activity regulates sensory processing and plasticity. During development, sensory cortex transitions from an early period of relative sensory isolation, when the primary input is spontaneous bursting at the periphery, to a later period of continuous sensory input and active exploration. In humans this transition occurs at birth; in altricial mammals it occurs post-natally, for example at eye-opening in the visual system. In all sensory systems this transition is associated with a profound and rapid increase in spontaneous activity that matures sensory responses by eliminating immature bursts of thalamocortical network oscillations and replacing them with graded sensory responses. We are investigating the network mechanisms and function of this switch in pre-term infants and rodent models. Whole-cell patch clamp recordings in head fixed, but unanesthetized, rats show that the increased spontaneous activity is driven by changes in sub-threshold membrane dynamics consistent with the initiation of active states in the cortical network. This hypothesis is supported by a dependence on ascending mid or hind brain connections and norepinephrine, but not the presence of the eye. Surprisingly, degraded sensory experience (eye-closure) that induces regressive effects on receptive field formation, also modulates the nascent active states causing hyperexcitability and neuronal synchrony in the form of aberrant alpha-beta oscillations that modify spike-timing dynamics. We suggest that the regulation of cortical network dynamics contributes to circuit development and plasticity by dividing early development into two periods: an early period concurrent with spontaneous activity at the periphery that guides initial circuit formation in the absence of spontaneous cortical activity, and a late period when spontaneous intra-cortical activity permits sensory exploration and the onset of experience-dependent plasticity.

II-87. The combined micro-organization of orientation and spatial frequency tuning in primate V1

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Spatial frequency tuning is a highly salient property of neurons in primate V1 and has been well-characterized. However, the organization of spatial frequency across the V1 surface is far less understood than that of other properties, such as pinwheels of orientation preference. Discrepancy among previous attempts at characterizing spatial frequency organization may be due to insufficient imaging resolution (review: Purushothaman et al 2009). In this study, we use two-photon imaging to provide the first data demonstrating the cell-by-cell layout of spatial frequency maps in primate V1. We first show that similar to orientation, spatial frequency is organized continuously. Next, we used these data to ask how spatial frequency and orientation are jointly represented in V1. In general, the manner in which different functional maps are overlayed has important implications for the efficiency of local populations in representing visual scenery. The combined organization of orientation and spatial frequency tuning is of particularly interest, as any image can be represented by the combination of these two parameters. For efficient coding of both orientation and spatial frequency, we expect that a given region of retinotopic space should represent all combinations (within range) of the two parameters. Our results show that orientation and spatial frequency maps are indeed systematically organized at the fine spatial scale observed with two-photon imaging. We find that not only does spatial frequency change more rapidly when orientation is more constant, but also that the map gradients tend to be orthogonal within a 200 um region of interest. This organization may allow local
II-88. Effects of local orientation on large-scale representations in V1 bias perceived global shape

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Population responses to visual stimuli in the primate primary visual cortex are topographically organized at multiple spatial scales, each of which may be useful for a subset of visual judgments. At a fine scale, these responses are organized into orientation columns; signals at this scale might be useful for discriminating between different textures. At a larger (retinotopic) scale, the population responses seem to encode the contrast envelope of visual stimuli; signals at this scale might be useful for computing global shape. Are responses at this larger scale independent of the local orientation structure of the stimulus? To answer this question, we used voltage-sensitive dye imaging in fixating monkeys to measure V1 population responses to small isolated Gabor patches with a fixed contrast envelope and varying carrier orientations. We found that V1 response at the retinotopic scale is significantly elongated along the direction corresponding to the orientation of the carrier. Moreover, increasing the carrier frequency reduces this effect. Both of these results can be explained by an elongation of the V1 population receptive field along the preferred orientation, similar to findings in single V1 neurons. If we rely on these retinotopic-scale V1 population responses when making judgments about global shape, the results above suggest that local orientation might bias these judgments. We tested this prediction in a psychophysical task by having human subjects determine which of two small patches was more circular. Consistent with the physiological results, we found that human subjects perceive Gabor patches to be elongated along the orientation of the sinusoidal carrier, and that increasing the carrier frequency reduces this effect. Taken together, these results suggest that we make use of information from the retinotopic scale of V1 population responses when determining shape, and that for small stimuli, local orientation information can bias our perception of global shape.

II-89. Position-specific heterogeneity of orientation pooling in curvature-tuned neurons of macaque area V4

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Previous studies (Pasupathy & Connor, 1999; 2001) have shown that neurons in monkey visual area V4 are involved in the processing of shapes of intermediate complexity and are sensitive to curvature. These studies also suggest that curvature tuned neurons are position-invariant. We sought to examine the detailed mechanisms that endow V4 neurons with their shape-selective properties. We recorded responses of area V4 neurons in two male macaques to bars or curves. Bars were presented at 8 orientations. Curves were composed of 3 bars, linked together to yield varying degrees of curvature. Stimuli were presented in a fast reverse correlation sequence (30 per second) at various locations within the receptive field (RF) of peripheral V4 neurons, while the animals maintained fixation for 4s. The curved stimuli were presented on a 5x5 location grid centered on the RF, while the single oriented bars were presented on a finer 15x15 location grid. Consistent with previous studies, we found that response rank-order to the most- and least-preferred stimuli were preserved throughout the
RF. However, a fine-grained analysis of curvature tuning revealed a surprising result: curvature-tuned V4 neurons exhibit considerable spatial variation in their curvature preference. At a finer scale, such neurons exhibited local variation in orientation tuning. In contrast, neurons that preferred straight, rather than curved contours, exhibited spatially invariant orientation tuning, and correspondingly homogenous fine-scale orientation tuning maps. Both these patterns are consistent with a simple model in which orientation tuning is pooled, with tuning for straight or curved contours resulting, depending on the heterogeneity of patterns of orientation tuning inherited from V1.

II-90. Inhibition controls the spatiotemporal spread of responses in awake visual cortex

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The role of inhibition in shaping cortical activity is a topic of considerable debate. Numerous studies indicate that excitation and inhibition are balanced in magnitude and time-course during both spontaneous and sensory evoked activity. However, these studies have been performed in anesthetized animals; it is unknown how sensory responses are shaped by inhibition during wakefulness. We measured excitation and inhibition with whole-cell recordings in layer 2/3 of visual cortex in awake and urethane anesthetized mice. We recorded membrane potential responses in current clamp, and measured synaptic conductances in voltage clamp while pharmacologically blocking intrinsic conductances. An additional electrode measured population activity via the local field potential (LFP). Visual stimuli probed selectivity for spatial position (white and black bars, flashed for 100 ms in random positions). Awake and anesthetized responses differed dramatically. During anesthesia, LFP responses were evoked from large portions of visual space, and lasted hundreds of milliseconds after the stimulus. During wakefulness, in contrast, LFP responses to these same stimuli were localized in space and time. Current clamp recordings showed equally short-lasting membrane potential responses in awake versus anesthetized animals. Voltage clamp recordings revealed that inhibition during wakefulness is much larger than excitation and substantially less tuned for spatial position. It makes responses more transient by truncating the effects of excitation. Accordingly, fewer spikes were produced by stimuli during wakefulness, even though the membrane potential was ~3 mV more depolarized than during anesthesia. We conclude that during wakefulness, excitation and inhibition are not strictly balanced in visual cortex. Rather, inhibition exerts a more dominant influence that constrains the patterns of activity elicited in visual cortex during wakefulness.

II-91. Selectivity and invariance are greater in macaque V2 than V1

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As visual information passes through the visual hierarchy, neuronal responses are thought to become more selective to complex image features, and more invariant to identity-preserving image transformations. This transition has been observed for neural populations in areas V4 and IT (Rust and DiCarlo, 2010), although the precise nature of representations in these areas remains elusive. We examined this hypothesis in areas V1 and V2, using stimuli generated with a model of naturalistic image structure that has been linked to visual representation in V2 (Freeman and Simoncelli, 2011). We generated novel stimuli with model responses matched to those of an
original natural texture image. These images are perceptually similar, despite differences in their local features. We assessed how accurately the identity of such images can be estimated from neural populations by recording sequential single-unit responses in anesthetized macaque and training linear decoders on the combined population. To test for selectivity, we asked whether neural populations discriminated better among images generated from the model than among spectrally-matched images which lack the complex features captured by the model. Identification accuracy in V1 was indistinguishable for the two types of image, whereas V2 accuracy was 20% better for the model-generated images. Thus the V2 population is more selective for the features captured by the model than the V1 population. To test for invariance, we measured discrimination performance when the linear decoder was forced to generalize across multiple distinct images matched according to the model. The performance decrement was 50% larger for V1 than V2, indicating that the representation in V2 is more invariant to those features discarded by the model than the representation in V1. Our results demonstrate increases in both selectivity and invariance from V1 to V2, and explicitly link the features of our model to population responses in area V2.

II-92. Understanding V1 surround modulation with natural stimuli using a principled statistical model

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The response properties of neurons in primary visual cortex (V1) are usually measured with simple stimuli such as gratings, but this characterization has limited explanatory power under natural stimulation. Here we address the properties of V1 surround modulation recruited by naturalistic input. We show that a principled model of scenes that captures statistical dependencies between oriented filters explains neuronal responses better than energy models and canonical divisive normalization. Our model is a Mixture of Gaussian Scale Mixtures (MGSM; Coen-Cagli, Dayan, Schwartz, NIPS 2009) that characterizes linear and nonlinear dependencies between V1-like filters in natural images. Bayesian inference in the model generalizes divisive normalization: given an input, the model infers whether filter activations in center and surround locations are statistically coordinated (homogeneous) and therefore to be jointly divisively normalized. While most scene statistics models have been compared against neural responses to gratings, a stronger test is to assess how well they explain responses to natural inputs. We therefore measured surround modulation in macaque V1 with static natural images. The majority of cells were more strongly suppressed by images that the model classified as statistically homogeneous, than heterogeneous. This was not due to differences in the firing rates evoked by the stimuli confined to the receptive field, nor to the amount of energy in the surround, between the two classes of images. To compare to previous models, we then fit the MGSM and several descriptive models to the neuronal responses. Both the MGSM and divisive normalization with independent center and surround gains explained 50% of the variance, but the observed surround modulation correlated with the MGSM twice as well as with any other model. Our results support the idea that surround effects can be viewed as sensitivity in V1 to the inferred statistical homogeneity of visual input. Supported by the NIH (CRCNS-EY021371).
II-93. Thalamic Synchrony and Visual Orientation Information Transmission To Cortex

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Thalamic synchrony is highly effective at driving cortical spiking (Alonso et al., 1996; Usrey et al., 2000), and is an important part of the neural code that facilitates information transmission from the visual thalamus to cortex (Wang et al., 2010). Given that thalamic neurons with overlapping receptive fields are likely to converge at common cortical targets (Alonso et al., 1996; Reid and Alonso, 1995), a potential role for the synchronous activity of thalamic input in the establishment of cortical response properties emerges. We have found previously that synchronous activity computed across pairs of neurons in the LGN can contain surprisingly sharp orientation tuning, but precisely how this relationship is modulated across the larger population and regulates cortical firing is unknown. Here, we investigated this phenomenon using a leaky integrate and fire model driven by thalamic population activity whose synchrony we systematically controlled. At all levels of input synchrony the cortical response showed well-tuned responses of both membrane potential and firing rate, and exhibited similar sharpening of the orientation tuning in the cortical firing rate relative to the cortical membrane potential. We further found that the orientation tuning for cortical firing rate sharpened with increasing levels of input synchrony while orientation tuning for the cortical membrane potential was relatively invariant. Also, thalamic synchrony had a complex effect on cortical firing statistics. Using a Fisher Information metric to estimate decoder performance, we found that information in the cortical membrane potential about stimulus orientation was relatively invariant to the thalamic synchrony. Information in the cortical firing rate, however, increased with increasing synchrony until reaching a plateau at a thalamic synchrony level of approximately 12 ms, consistent with levels of timing precision observed in LGN activity in the natural environment (Butts et al., 2007; Desbordes et al., 2010).

II-94. Differences in sensitivity to neural timing among cortical areas

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The basic circuitry of auditory, visual, somatosensory and other cortical areas is highly stereotyped. However, it remains unclear whether this anatomical stereotypy implies functional homogeneity, or whether instead different cortical areas are specialized to process the diverse sensory inputs they receive. Here we have used a two alternative choice task to assess modality-specific differences in the ability of rats to exploit cortical spike timing. To isolate differences due to cortical circuitry rather than to sensory transduction and subcortical processing, we used electrical stimulation to drive activity in the cortex. We previously showed (Cosyne 2010) that the minimum detectable interstimulus interval varied over more than an order of magnitude, ranging from 1ms in barrel cortex and 3 ms in auditory cortex to 15 ms in visual cortex. Here we extend these results by asking how these differences arise. The temporal statistics of auditory, visual and somatosensory stimuli may be quite different, raising the possibility that the differential processing might arise as an experience-dependent adaptation to the different
stimulus ensembles. We therefore tested whether these differences are innate, or whether disruption of sensory stimulus statistics during development could affect the ability to exploit fine timing. We focused on the barrel cortex, reasoning that because the barrel cortex-implanted subjects achieved the best performance, this area might be the most sensitive to disruption. We did complete unilateral whisker trimming from birth to adulthood to disrupt barrel cortex development. We found that animals subjected to whisker clipping initially showed impairment in exploiting fine timing in barrel cortex. Surprisingly, behavioral training partially rescued this deficit. Our results suggest that different cortical areas are adapted to the specific structure of the input signals they process, and that precise spike timing may play a more important role for some cortical areas than for others.

II-95. Artificial synchronization across sensory cortical area is sufficient for behavioral discrimination

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Direct electrical microstimulation has been used to explore functional anatomy and to determine the participation of a particular cortical locus in sensory and motor coding. In these experiments, microstimulation has been typically delivered to one electrode at a time, producing a local increase in neuronal rate as well as in neuronal synchrony. Here we used electrical microstimulation of the visual and somatosensory cortices of the rat in both hemispheres, to test whether distributed patterns of artificial synchrony evoke a coherent brain activation that animals can signal by pressing different levers. To disambiguate synchrony from other related parameters, our experiments independently manipulated the rate and intensity of stimulation, the spatial locations of stimulation, the exact temporal sequence of stimulation patterns, and the degree of synchrony across stimulation sites. We found that rats reliably distinguished between two microstimulation patterns, differing only in the topography of synchrony among the electrodes. Also, their performance was proportional to the level of synchrony in the microstimulation patterns. We demonstrated that rats can recognize artificial current patterns containing precise synchronization features, thus providing the first direct evidence that artificial synchronous activity can guide behavior. These precise temporal information that the animals were able to discriminate can be used as feedback signals in machine interface arrangements.

II-96. Transient activation of distinct striatal pathways mimics changes in the value of actions

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In constantly changing environments, animals must adaptively select actions to achieve their goals. Recently, the striatum has been implicated in goal-directed action selection and striatal neural activity has been shown to represent the value of competing actions. This activity could generate a response bias toward an action of higher value. While this model is consistent with numerous studies, no study to date has demonstrated the direct impact of distinct striatal pathways on choice behavior in the context of a reward-based decision. Here we show that
unilateral transient optogenetic stimulation (500ms, 5∼20Hz) of the striatal direct or indirect pathway introduces opposing biases in the distribution of choices during a probabilistic switching task. Stimulation of dopamine D1- or D2-receptor expressing neurons biased choice but the effect of stimulation was dependent on recent choice and reward history. The behavioral bias introduced by stimulation is consistent with theoretical predictions of an additive change in the value for a given action and suggests the presence of a “winner-take-all” system within or downstream of the basal ganglia for action selection. Together this data supports a model in which striatal neurons pool a wide variety of cortical and thalamic inputs and convert them into a common currency of action value to bias choice.

II-97. Short-axon Cells Provide Both Excitatory and Inhibitory Drive to the Mitral/Tufted Cells

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Lateral interactions are thought to shape the olfactory bulb output (mitral/tufted—M/T cell firing rate), yet their roles and extent remain largely unknown. Short-axon (SA) cells in the glomerular layer, receive inputs from olfactory sensory neurons and/or external tufted (ET) cells and release both GABA and Dopamine, synapsing onto juxtaglomerular cells as far as tens of glomeruli away (Kiyokage et al., 2010). Computational models (Cleland et al., 2007) have suggested that SA cells may be involved in long-range normalization of bulb outputs, but to date their function in the intact brain has not been investigated. We used a Cre-loxP viral approach to express neuronal activity reporters (GCAMP3) or light gated switches (Channelrhodopsin2 and Halorhodopsin) in SA cells. We imaged GCAMP3 responses to a wide range of odor concentrations via wide-field microscopy. Odors induced transient, yet global SA responses, in contrast to focal glomerular patterns observed via intrinsic optical imaging (6 odors, 5 concentrations, 4 mice). To understand the effect of the SA network activity on the bulb output, we recorded from M/T cells in anaesthetized mice using extracellular tetrodes. In conjunction, we selectively activated/inactivated SA cells by shining blue/yellow light either throughout the dorsal bulb surface or in specific spatial patterns using a digital micro-mirror device (DMD). Pairing light with odor presentation at various concentrations indicated that SA cells provide both excitatory and inhibitory drive to the M/T cells (n=11). At low odorant concentrations excitatory input dominates, whereas in response to stronger stimuli, both excitatory and inhibitory drives are present. We are currently performing pharmacological manipulations to dissect these dual effects of SA cells. We propose that the SA network regulates the dynamic range of M/T cell firing by amplifying the weak inputs and downscaling the stronger ones.

II-98. A cell-type-specific population analysis of optogenetically evoked response in primary visual cortex

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Precisely timed coordination between excitatory and inhibitory neurons within and between layers of the cerebral cortex is a major element of brain function. Stimulus dynamics are believed to engage this E-I coordination in a different regime. In this study, we combined optogenetics tools with tetrode recording to correlate the dynamics of
network state transition in response to precisely controlled dynamics of the artificial light stimulus. By expressing ChR2 in fast spiking interneurons of layer II/III primary visual cortex in PV-Cre mice, we could selectively excite Fast Spiking (FS) interneurons in this layer by superficial illumination using very short pulses (<1ms) of light (~470 nm wavelength). Extracellular electrical activity was recorded using tetrode arrays in three mice under different frequencies of light stimulation. We used Dynamic Bayesian Networks—previously demonstrated to be more effective in capturing causal influence between simultaneously recorded neurons - to infer the functional connectivity across sorted units. To examine the consistency of these connectivity patterns, we computed adjacency matrices for each network graph and examined a reduced dimension feature space representation of these matrices. The results showed 76%±16% similarity between connectivity patterns across multiple repeated trials, compared to only 21%±14% similarity across different stimuli. We also examined Local Field Potentials (LFPs) dynamics as a proxy to assess distinct levels of population excitability, if any, under different stimulus conditions. We found distinct patterns of LFP time-locked to light pulse onset at different frequencies. These results suggest that inhibitory drive has a substantial influence on local network dynamics across multiple time scales. Taken together, our data and our dynamic Bayesian inference analysis suggest a novel framework to characterize the dynamics of computations in sensory cortical circuits.

II-99. A Model of I-Wave Generation during Transcranial Magnetic Stimulation (TMS)

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Transcranial magnetic stimulation (TMS) allows to manipulate neural activity non-invasively and much research is currently dedicated to exploiting this ability in clinical settings. But the details of how TMS induces neural activity patterns in cortical circuits remain poorly understood, which hampers targeted clinical application. In a standard TMS paradigm, single-pulse stimulation over the left motor cortex produces high-frequency repetitive responses of around 600Hz in descending motor pathways called I-waves. Although this paradigm is well-established experimentally and has been studied quite extensively, the detailed mechanisms of I-wave generation have remained unclear. Here we present a model that reproduces I-waves similar to those observed in epidural responses during in vivo recordings of conscious humans. The model consists of a detailed layer 5 (L5) pyramidal cell and a population of layer 2 and 3 (L2/3) neurons projecting to it. The model parsimoniously explains the mechanisms underlying I-wave generation together with some of their basic properties such as frequency, timing, and size. We argue that I-waves are a product of both extrinsic and intrinsic factors. By depolarizing large populations of L2/3 cells, magnetic stimulation causes a synchronized volley of EPSPs and IPSPs to impinge onto the dendritic trees of L5 cells. The intrinsic membrane properties of the L5 cells are then responsible for generating trains of action potentials at the characteristic I-wave frequency. Our model is shown to reproduce the effects of pharmacological interventions with drugs affecting GABA-ergic transmission on I-waves. By incorporating short-term synaptic depression of synapses from L2/3 onto L5 cells, our model also accounts for facilitation and depression effects observed in different paired-pulse stimulation protocols. Overall, our model reproduces findings from a range of experiments and brings us one step closer to designing stimulation protocols for specific clinical purposes.
III-1. A model of the effect of visual saliency on ethologically relevant, value-based decisions

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Recent studies have shown that race models accurately describe value-based decisions and that fixation durations at each alternative are directly related to the alternative’s relative value and are predictive of choices. However, bottom-up visual saliency also has a large effect on where people look. One recent study has shown that during two-alternative, value-based decisions, subjects’ decisions are biased towards more salient items. It’s unclear whether this occurs during multiple-alternative decisions and how information about saliency and value are combined. Here, we develop a model of how saliency and value combine to drive eye-movements and decisions in a multiple-alternative, forced-choice task. We hypothesize that each fixation location is the outcome of a decision about the next fixation location. We model this decision process using the drift diffusion model (DDM) assuming that each alternative has a DDM unit driven by a linear combination of saliency and value. By solving for the first passage times, we calculate the probability that gaze will transition from one alternative to another and the probability of the transition time. These probabilities define the transition matrix for a Markov chain that determines the probability of every gaze trajectory. Based on psychophysical data from ten human subjects performing a multiple-alternative, forced-choice task involving snack food items we show that this provides an accurate model of the choice probabilities. We also present a side-by-side comparison of both the predicted fixation locations and durations and those generated by human observers during this task. We show that combining the DDM with the traditional saliency model provides an accurate model of fixation durations, fixation locations and value-based choices.

III-2. Optimal placement of dynamic range by coordinated populations of retinal ganglion cells

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Neurons have a limited dynamic range, and as such must change their sensitivity to encode their current sensory environment. Previous work has derived the optimal placement of a cell’s dynamic range given an input, and certain neurons in the early stages of the visual system conform well to that prediction. However, much of the theoretical effort for understanding the encoding of time varying inputs considers a single neuron. Recent work has shown that distinct populations of retinal ganglion cells encode similar spatiotemporal features of the visual input, but have different thresholds—with one population encoding weaker inputs and the other stronger inputs. We sought to derive theoretically whether this coordinated behavior conforms to an optimal solution to the problem of representing a sensory input using two distinct neural populations. By modeling neurons with binary outputs, either spiking or not, placing a constraint on the overall firing rate of the model neurons, and accounting for noise in the responses, we show that experimentally measured response curves of ganglion cells together optimize the amount of information the two populations can provide about the distribution of light intensities in the input. This solution holds across a tenfold range of contrast distributions. Additionally, we show that the coordination that
we see within the retina is the optimal solution only if noise is considered, shedding light on the importance of accounting for variability in neural responses.

**III-3. Sparse codes for speech predict spectrotemporal receptive fields in the Inferior Colliculus**

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We have developed a sparse representation of speech that minimizes the number of active model neurons needed to represent typical speech sounds. Motivated by the fact that the number of neurons increases with each stage in the ascending auditory pathway, we explore overcompleteness in our model to see if it can better capture properties of spectrotemporal receptive fields (STRFs) compared with previous models. When trained on spectrograms of speech, our overcomplete, sparse coding model learns several well-known acoustic features of speech such as harmonic stacks, formants, onsets and terminations. However, we also find more exotic structures in the spectrogram representation of sound such as localized checkerboard patterns and frequency-modulated excitatory subregions flanked by suppressive sidebands. These localized checkerboard patterns are a hallmark of receptive fields found in the Inferior Colliculus (IC). We also compare additional model STRFs such as broadband and localized ON and OFF cells and Gabor-like patterns to experimental receptive fields found in IC as well as auditory thalamus and cortex. Additionally, our model neurons exhibit the same tradeoff in spectrotemporal resolution as has been observed in IC. To our knowledge, this is the first demonstration that receptive fields of neurons in the ascending mammalian auditory pathway beyond the auditory nerve can be predicted based on coding principles and the statistical properties of recorded sounds.

**III-4. Computing sparse representations using a network of integrate-and-fire neurons**

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As most neurons in our brain communicate using action potentials, realistic models of neural computation must contain spiking neurons. For many existing models, however, spikes represent a nuisance: it is difficult for a spiking model to achieve the same performance as a corresponding graded potential or firing rate model (Vogels et al., 2005, Deneve and Boerlin, 2011, Shapero et al., 2011). We address this issue in the context of the sparse representation problem, in which an arbitrary vector must be represented as a linear combination of a few feature vectors chosen from an over-complete dictionary (Olshausen and Field, 1996, Chen et al., 1998, Baraniuk, 2007). The sparse representation problem can serve as an example of neural computation because many natural signals can be sparsely represented (Gallant and Vinje, 2000) and because neuronal representations are sparse (DeWeese et al., 2003, Attwell and Laughlin, 2001, Lennie, 2003). Sparse representations can be computed by the Local Competitive Algorithm (Rozell et al 2008) on a network of graded potential neurons. Here, we propose a hybrid distributed algorithm (HDA), which computes sparse representations on the same network architecture as (Rozell et al., 2008) but using biologically inspired integrate-and-fire neurons instead. We call our algorithm hybrid because its neurons perform both gradient-descent-like steps on analog internal variables (membrane potentials)
and coordinate-descent-like steps via quantized external variables (spikes) communicated to each other. We prove the convergence of HDA analytically and show that HDA is stable against time-varying noise, specifically, the representation error decays as $1/\sqrt{t}$ for Poisson noise. We show numerically that the performance of HDA is on par with a corresponding network of graded potential neurons. Therefore, we demonstrate for the first time that, in addition to being energetically efficient (Laughlin et al., 1998), spiking neurons may be as computationally powerful as graded potential neurons are.

**III-5. On the role of cortical feedback on invariant odor perception in the mammalian olfactory system**

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Natural odor scenes are composed of odor plumes originating from multiple sources and traveling at fluctuating intensities that span several orders of magnitude. Despite this turbulence rodents readily identify odors of interest against varying, odor-rich backgrounds. This invariant identification poses in fact a challenging computational problem that appears in many sensory modalities and has been described as the ‘cocktail party problem’. Olfactory bulb models (Koulakov & Rinberg, 2011; Hopfield, 1991) have been proposed that solve this problem in the absence of strong cortical feedback, a prominent feature of bulb connectivity. We propose that cortical feedback is essential for invariant representation. We applied a model that relies on cortical feedback, Corrected Projections Algorithm (CPA) (Otazu & Leibold, 2011) into the olfactory domain. The model identifies odors in complex scenes by querying the incoming inputs against a large dictionary of learned odor representations and finds the sparsest combination of odorants that matches best the observed olfactory scene. CPA is unique in that a sparse representation is found by minimizing the difference between the observed odor signal and the signal estimate, without explicitly minimizing the number of active dictionary elements. The CPA architecture consists of a two layer neuronal network with large feedback. This feedback impinges on a separate class of neurons that form reciprocal inhibitory synapses with the principal neurons in the input layer. Interestingly, this bears striking resemblance to the mammalian olfactory system anatomy. The model predicts that the cortico-bulbar feedback onto granule cells represents binary variables encoding the presence or absence of a given odorant, invariant of concentration, temporal fluctuations or presence of background odors. We are currently testing this prediction by pairing simultaneous monitoring and optogenetic manipulation of cortical feedback and its bulbar targets in mice engaged in invariant odor perception tasks.

**III-6. Fast estimation of non-smooth non-stationary receptive fields**

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State space models have been established as a fundamental tool for statistical analysis of time series, e.g. the Kalman filter in the linear-Gaussian setting, with many neuroscience applications. However, their applicability is limited in practice to low-dimensional state spaces, since the computational complexity of the inference algorithms scales cubically with the state vector dimensionality $d$. Moreover, although non-Gaussian generalizations are available, these in general pertain to smooth signals and ignore several important aspects that may be present, e.g., sparsity. Here we present a general algorithm that addresses these issues to perform tractable inference in penalized state-space models. Our algorithm is applicable when the state-space dynamics obey log-concave distributions and the state vector is further penalized by appropriate convex norms. It computes the maximum-a-posteriori estimate using Newton’s method. We show that if the number of measurements per timestep is small,
then Newton’s direction can be computed with $O(d)$ complexity, using an efficient forward-backward scheme based on a series of low rank updates. This leads to substantial computational gains and makes the algorithm applicable to arbitrarily high-dimensional settings. A similar approach has been presented before in the Gaussian setting for voltage filtering in dendritic trees and smooth dynamic receptive field estimation. Here we extend it to a general non-smooth setting that can also model sparsity. Sparse penalties can act as regularizers for high-dimensional inference from a limited number of observations. Moreover, they can lead to interpretable model selection methods by promoting the inference of rare events. We apply our algorithm for the estimation of piecewise smooth functions from generalized linear model observations. As one specific example, we derive an effective method for correcting ocular motion artifacts during visual neuroscience experiments. In this case, the artifacts can be inferred by imposing sparse variations penalties on the state transitions.

III-7. Improving individual classification learning using a predictive maximum entropy model

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Learning to classify new complex stimuli into categories is a common cognitive task, which we seem to be doing regularly and almost effortlessly. Yet, the number of potential classification “rules” is exponential in the number of possible stimuli, which means that when we learn to classify from examples, we must be using priors and simplifying assumptions. Models of how people learn such tasks have often focused on finding measures of rule difficulty, and analysis of learning dynamics of first-order rules, such as “weather prediction” task. We conducted psychophysical experiments in which subjects had to learn to classify binary patterns, $x$, according to rules of different complexity. We found that in most cases people did not use single, simple stimulus features when learning to classify but instead combined them dynamically. We used a maximum entropy based approach to identify how subjects learned to combine stimulus features and a gradient ascent algorithm to model individual learning. Specifically, for every subject we find a probabilistic classifier that uses an exponential probability distribution over a weighted sum of stimulus features $f_i(x)$: the initial weights for each $f_i$ give the subject’s prior, and a learning rate, $h$, determines how they are changed after each example, using gradient ascent. This modeling framework reproduced with very high accuracy the individual learning curves of diverse population of subjects and rules, even when subjects failed to learn the task. Furthermore, fitting a model to the first part of the learning session enabled us to predict the future learning curve and single answers remarkably well. Finally, we used the model learned for a subject in the beginning of their session to infer which examples would benefit them the most. We then found that we can significantly improve subjects’ learning by such model-based teaching.

III-8. Internal representations of temporal statistics and feedback calibrate sensorimotor interval timing

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Recent results have shown that bias and variance trade-offs in time perception can be accounted for by ‘optimal’ probabilistic inference. However, specific temporal statistics of the stimuli seem to induce sub-optimal behaviours; for instance adaptor distributions, in which one inter-stimulus duration appears overwhelmingly often, typically cause a temporal recalibration effect that defies a simple account based on prior expectations. The Bayesian
ideal observer responses depend crucially on both the internal representation of the temporal context (subjective prior and likelihoods) and on the loss function; observed ‘sub-optimal’ behaviours could be caused by a systematic mismatch between the objective statistics of the experiment and their subjective counterparts. When, how and the degree to which people can learn a correct internal representation of the temporal context can be revealing of the underlying mechanisms. In this work, we studied how internal representations of temporal statistics are affected by uniform and adaptor distributions of action-stimulus intervals in a time interval reproduction paradigm. By providing different shapes of performance feedback (i.e. loss functions) to the subjects, we also investigated how the participants integrated external error signals with the temporal context. Our results show that temporal context calibrates sensorimotor timing according to the ‘scalar property’ of sensorimotor error on short/long intervals in the subsecond range. The subjects typically learnt smoothed approximations of the experimental distributions of stimuli, with a good estimate of their mean and variance but also took into account higher-order statistics. The responses were sensitive to the nature of the feedback provided, in general agreement with the behaviour predicted by the related loss function. Interestingly, the above results also held in the adaptor condition, implying that there are no significant limitations in learning complex temporal distributions of stimuli with the help of corrective feedback.

III-9. Generalization of uncertainty

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Many studies have demonstrated that the nervous system takes into account the uncertainty associated with state and feedback, in line with the predictions of Bayesian statistics. How populations of neurons represent the associated probability distributions is consequently a central topic in computational neuroscience. Generalization studies are a standard tool in movement neuroscience used to characterize underlying neural representations. Subjects adapt to perturbations for one type of movement and we then examine how this affects other movements. The resulting generalization curves are traditionally interpreted as a reflection of the tuning-curves for the underlying neural representations. Here we extended movement generalization experiments to ask how uncertainty is generalized. We vary uncertainty by changing the variance of the stochastic visuomotor perturbation. We assess uncertainty by introducing noisy visual information and measuring its influence on subjects’ reaches. In three experiments we ask how uncertainty affects the generalization of the mean, how uncertainty itself generalizes, and how mean and uncertainty interact. We then compare well-studied generalization-curves for the perturbation means with our measured variance/uncertainty generalization-curves. We find that standard linear generalization models in either the moments (Model M1) or probability space (M2) well describe the generalization of mean and variance (Experiments E1 and E2). However, we find truly surprising effects on the generalization of uncertainty when we perturb both the mean and the variance (E3): those directions where, during early training, subjects made errors had high uncertainty, far higher than predicted by regular generalization models. However, the effects can be readily understood in terms of a supervised learning model (M3): in those directions with large errors a high gain on the noisy feedback would have been optimal. We thus provide evidence of the involvement of supervised learning mechanisms in the acquisition of Bayes-like behavior.
III-10. Exact inference for time series data on nonstandard state spaces

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A variety of methods are available for smoothing time series data in unconstrained vector spaces (e.g., splines, Kalman filter approaches, or frequency domain methods). However, in many neuroscience settings we must perform inference and smoothing of time series in less-standard, non-vector state spaces. A prototypical example involves the estimation of firing rates (which are constrained to be positive) given spike train data. Other examples include smoothing of angular variables (e.g., orientations of visual stimuli, or joint angle data in a motor task) or oscillatory signals (e.g., local field potentials): in these cases, the relevant state space is a circle (or higher-dimensional sphere or torus), instead of the real line. A final example involves decoding the position of a rodent moving through a maze of some arbitrary topology. In each of these cases, standard vector-space smoothing methods can be adapted to form approximations to the quantities of interest, via Monte Carlo methods or deterministic approximation approaches (e.g., Laplace approximation or Expectation Propagation). However, exact optimal Bayesian inference methods have the potential to be faster, more reliable, and more accurate. Here we identify a broad model class in which exact inference can be performed efficiently by efficient dynamic programming methods. Our approach is based on a graphical (hidden Markov) model formulation in which the potential functions connecting nearby time bins have a certain “low-rank” structure that enables fast exact computation: we can draw exact samples and compute exact posterior distributions in time which scales linearly in the length of the observed time series, and quadratically with a measure of the complexity (the “rank”) of the examples discussed above.

III-11. Adaptive estimation of nonlinear response functions in V1 with Gaussian processes

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A common goal in neurophysiology experiments is to estimate a neuron's tuning across multiple stimulus dimensions from a minimal amount of data. Here we describe a method for adaptive stimulus selection in closed-loop experiments using a flexible model of the neural nonlinearity. Specifically, we model the nonlinearity $f$ in a linear-nonlinear-Poisson (LNP) neuron with a Gaussian process (GP). This provides a non-parametric description of the mapping from feature space to spike rate, and offers a nice tradeoff between flexibility and computational tractability relative to standard methods (e.g., parametric forms, histograms, cubic splines). We provide a simple algorithm for updating the posterior distribution over $f$ after each trial, and select the stimulus that maximizes the expected information gain about $f$ for the next trial. Our approach relies on a method for rapidly updating hyperparameters governing the GP prior using the Laplace approximation to the posterior over $f$. We demonstrate the efficacy of our method using data from color-tuned neurons in macaque V1. Single neurons were stimulated with spectrally modulated gabor patches, each of which defined a location in the three-dimensional space of cone contrasts. The integration of cone contrasts in V1 neurons can be highly nonlinear, and the shape of this nonlinearity varies considerably across neurons. We show that adaptive stimulus selection under the GP-LNP model substantially reduces the amount of data required to estimate these nonlinear functions. Finally, we extend the model to incorporate spike-history dependence, allowing the effects of spike-rate adaptation (which may arise when exploring high-response regions of the stimulus space) to be taken into account when estimating neural nonlinearities.
III-12. On the interaction of excitatory and inhibitory synaptic plasticity

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Cortical neurons receive a balance of excitatory and inhibitory synaptic currents. This balance has attracted significant interest because it is thought to be a central mechanism by which cortical networks maintain stable activity with the observed high degree of irregularity and little correlation across neurons and because it shapes cortical responses to sensory stimuli. An open question, however, is by which mechanism this balance arises and how it is maintained in the presence of excitatory plasticity. Recently, we suggested that inhibitory synaptic plasticity could serve as a self-organization mechanism by which networks can robustly self-tune into a balanced state. Because inhibition shapes neuronal responses to excitatory input, any form of excitatory synaptic plasticity that depends on pre- and postsynaptic activity will in turn be influenced by a rebalancing form of inhibitory plasticity. Here, we present a mathematical and computational analysis of this interaction. We study the dynamics of synaptic weights onto a single postsynaptic cell receiving both excitatory and inhibitory inputs. While inhibitory plasticity follows a rebalancing rule [3], we consider a variety of excitatory learning rules: simple Hebbian learning, BCM rules and spike timing dependent plasticity (STDP). Our analysis reveals that the learning dynamics can be non-trivial, depending on (i) the relative speed of learning of excitation and inhibition, (ii) the weight-limiting mechanism for the excitatory synapses and (iii) the degree of correlation between the excitatory and the inhibitory inputs. In particular, (i) homogeneous excitatory weights or transient, unstable input selectivity are common results of the interaction so that (ii) input selectivity forms only when the two forms of plasticity act synergistically. Moreover, (iii) inhibitory plasticity changes the temporal feature selectivity of STDP. These insights will help to understand how excitatory and inhibitory plasticity interact to form functional neural circuits.

III-13. Dynamics of Gap Junctions Inspired Networks

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We are interested in whether gap junction connected networks can support complex dynamics. To this end, we consider a network of neurons with gap junction connections, enhanced by additional intrinsic excitatory and global inhibitory currents. This system turns out to be equivalent to a nonlinear network with a synaptic weight matrix that has random off-diagonal elements with variance of order 1/N, and diagonal elements with variance of order 1. Such large diagonal terms make the network behave differently from the more commonly studied case where the diagonal terms make a negligible contribution. These networks have a trivial fixed point, which does not support interesting dynamics, so we began by examining its stability. We examine the eigenvalues of the stability matrix for this trivial fixed point, which are the same as the eigenvalues of the weight matrix. These do not fall into the typical circular region of the eigenvalues of random matrices, and we discuss methods for determining the shape of this region. For appropriate coupling strength, the trivial fixed point becomes unstable. When this happens, the network exhibits long-lasting chaotic “exploratory” activity that eventually leads to a stable, nontrivial fixed point. At the fixed point, the activity or voltage value of the neurons are predominantly determined by the diagonal elements of the connectivity matrix, with the off-diagonal elements serving as a source of noise. Simulations show that the lifetime of the transient chaotic stage grows exponentially with network size. Thus, a reasonably sized network can sustain complex activity and signal generation over large time intervals. This in turn
suggests that these networks can serve as a source of internal activity for motor, learning and memory process.

**III-14. Slow dynamics and high variability in balanced networks with clustered connections**

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Anatomical studies demonstrate that excitatory connections in cortex are not uniformly distributed but instead exhibit clustering into groups of highly connected neurons (Song et al., 2005, Perin et al. 2011). However, the implications of clustering for cortical activity are unclear. We study the effect of clustered excitatory connections on the dynamics of neuronal networks that exhibit high spike time variability due to a balance between excitation and inhibition (van Vreeswijk and Sompolinsky, 1996). Even modest clustering substantially changes the behavior of these networks, introducing slow dynamics where clusters of neurons transiently increase or decrease their firing rate. These fluctuations over long timescales or across trials are not captured by networks with simple uniform connection structures, which instead produce irregular firing with a fixed rate. Neurons in clustered networks exhibit both short timescale spiking variability and long timescale firing rate variability. A simplified model shows how stimuli bias networks toward particular attractor states in which certain clusters fire at high rates and others at low rates. In this way, stimuli reduce firing rate variability compared to the spontaneous state, as observed experimentally in many cortical systems (Churchland et al., 2010). Our model thus relates cortical architecture to the reported variability in spontaneous and evoked spiking activity.

**III-15. Phase precession through intrinsic neural resonance in continuous attractor models of grid cells**

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With one notable exception, the features of grid cells are remarkably well-modeled by recurrent network models (called continuous attractor or CA models) whose weights stabilize a restricted set of patterns in the neural population. The exception is a feature ubiquitous in layer II entorhinal grid cells: phase precession. As an animal moves through a grid cell's activity field, the neuron's spikes precess, or are emitted at progressively earlier phases of the oscillating local field potential (LFP). The presence of phase precession in competing temporal-interference models has been cited as a primary advantage. We show here that if a simple model of the resonant properties of layer II entorhinal neurons is included in CA network neurons, with appropriate phase coupling, the resulting grid cells will phase precess. We consider a 1-dimensional CA grid cell model network, in which neurons interact through local excitation and local surround inhibition. The neurons are intrinsic oscillators, with frequency f0 Hz. Neural spiking leads to perturbations in the phase of synaptic target neurons based on the phase difference between neurons and the sign of their interaction (excitatory or inhibitory). As the animal moves through a chain of grid fields, the phases of cells along this chain are progressively retarded, resulting in an LFP with lower frequency, f0-d. Spikes emitted by each cell at a fixed phase of its internal oscillation (e.g. at its peak), will precess forward relative to the lower-frequency LFP. The model predicts that phase precession depends on location rather than time spent in the response field, unlike models based on cellular processes with fixed time-constants. Further, the model makes testable predictions about how the precession rate varies with peak neural firing rates and animal velocity.
III-16. Error-driven learning within the Hippocampus; theta rhythm, and novelty based learning signals

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Previous evidence has shown that the theta rhythm within the hippocampus is crucial for encoding and recall, but its functional mechanism has yet to fully understood. Mathematical modeling work has suggested that different phases of this oscillatory signal facilitate hippocampal encoding or retrieval (Hasselmo, Bodelon & Wyble 2002). Similarly, neuroanatomical modeling has proposed the role of the subiculum, within a larger striatal circuit, as providing a dopamine facilitated novelty signal within area CA1 (Lisman & Grace 2005). The current work expands upon these ideas by implementing and testing them within an existing, biologically plausible, neural network model of the hippocampus (Norman & O’Reilly 2003). Representations are first encoded during the theta trough in the auto-encoder like Entorhinal Cortex (EC) to CA1 connections. However, during the subsequent peak of the theta wave, retrieval occurs such that the CA3 drives a completed pattern of activation in CA1 where it is compared against the pattern encoded during the theta trough, providing an error-driven learning signal. Similarly, the subiculum provides a novelty signal based on the mismatch of incoming stimuli and the completed pattern of activation within EC, which in turn drives a dynamic learning rate in the CA3 to CA1 connections. Simulations of this augmented model show enhanced performance through the error-driven learning signal, as well as the dynamic learning rate. Performance is assessed in the AB-AC cued recall task, as well as a raw learning capacity test, where the augmented hippocampal model is compared with a purely Hebbian based hippocampal model. Results, explored across various network sizes, show a decrease in interference between studied items, as well as an increase in raw capacity for the augmented model compared to the Hebbian model. The current work is presented in the development of a mechanistic account of pre-frontal interactions with hippocampal encoding and retrieval.

III-17. Intrinsic gradient networks: Highly recurrent neural networks with biologically plausible training

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Artificial neural networks are computationally powerful and exhibit brain-like dynamics. However, it is generally believed that the backpropagation algorithm, commonly used to train neural networks, is not biologically plausible; backpropagation messages must not directly affect the original feedforward messages, in contradiction to the pervasively recurrent architecture of the cortex. The recurrence of the cortex, together with the requirement that training signals project directly to the trained structures in the brain, implies that the cortex uses a single interdependent set of messages for both computation and learning. Moreover, when faced with complicated or ambiguous input, the cortex can withhold a motor response until processing is complete. We further assume that learning requires the approximate calculation of the gradient of a loss function, and restrict our attention to networks in which this gradient can be calculated completely at a single network state. From this modest set of constraints, we derive a novel class of recurrent neural networks, intrinsic gradient networks, for which the gradient of the loss function with respect to the parameters is a simple function of the network state when a self-identified output has been produced. Intrinsic gradient networks do not generally segregate “feedforward” computation signals from “feedback” training signals, and so are potentially consistent with the pervasive recurrence observed in the cortex. Within the class of intrinsic gradient networks, it is easy to identify highly recurrent instances for...
III-18. Plasticity in chaotic random recurrent networks leads to complex but non-chaotic neural trajectories

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It's clear that much of the computational power of the brain derives from the complex dynamics generated by recurrent neural networks. Ongoing activity in the absence of input is hallmark of the brain and recurrent neural networks operating in “high-gain” regimes. Analytical and numerical simulation results, however, show that the dynamics in random recurrent networks capable of generating ongoing activity tend to be chaotic and difficult to control (1,2,3). While synaptic plasticity within recurrent networks may provide a manner to control neural dynamics, incorporating plasticity in recurrent networks has proven to be challenging. Learning rules in recurrent networks have been heavily influenced by those in feedforward networks where weights are changed in order to minimize the error between the actual output and the desired target. One successful approach has been to use carefully controlled feedback from a readout (output) to partially drive the dynamics within the recurrent network (4,5). Although recent studies have incorporated plasticity in the recurrent weights, e.g. (5), these approaches have not dramatically enhanced the computational power of neural networks. Here we propose an alternate strategy where the weights in an initially random, chaotic recurrent network of firing rate units are trained to reproduce their natural or “innate” trajectory during a long time window—in essence making the network do more robustly what it already does. After this initial phase the trained neural trajectory can then be used to drive the desired output patterns as with previous state-dependent or reservoir computing approaches (6,7). We show that the innate trajectory, originally a portion of the chaotic attractor, becomes a locally stable attracting trajectory (“stable transient channel”) while maintaining its original complexity.

III-19. Reliable and unreliable spike times in sparsely connected networks

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If the same sensory stimulus is presented multiple times to a neuronal network, how similar are the spike trains that it evokes? This question of the reproducibility, or reliability, of stimulus-induced spike times has a long history in neuroscience. Here, we contribute new results on how features of spiking network dynamics constrain this reliability. We focus on networks with sparse, random connectivity and balanced excitation and inhibition. Such networks have attracted great interest, as they reproduce the irregular firing that typifies cortical activity. For several models of neural dynamics, this activity is known to be chaotic, with extremely strong sensitivity of spike outputs on tiny changes in a network’s initial conditions [VanVreeswijk and Sompolinsky, 1996, Monteforte and Wolf, 2010, London et al., 2010]. These chaotic networks are by definition unreliable. Here, our goal is to understand whether this is essentially always the case, or whether there are non-chaotic—and hence reliable—varieties of balanced networks as well. We consider sparse networks of inhibitory and excitatory neurons, modeled as phase variables, randomly coupled and driven by independent temporally structured inputs. We explore the impact of two key parameters. The first is the amplitude of a signal impinging on the network. The second is the superthreshold vs. subthreshold state of the individual cells—that is, whether they are in mean-driven vs. fluctuation-driven regimes.
We show that both parameters strongly impact network reliability. In particular, a range of networks with moderate signal amplitudes and excitable single-cell dynamics exhibit sustained irregular activity that is not chaotic. Such networks reliably respond to a given input, with high spike timing accuracy on several trials with distinct initial conditions. These same networks become unreliable when individual cells come closer to superthreshold states, connecting with results for sparse recurrent networks in the literature.

**III-20. Response of a Hodgkin-Huxley model VCN octopus cell to sounds with pitch**

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Pitch, a fundamental attribute of complex sounds, is vital for both music and vocal communication. Fundamental frequency (F0) is the defining characteristic of any periodic sound; however, it is not known how the auditory system determines F0. A prevailing hypothesis is that temporal fine structure (TFS) of the waveform is crucial for proper pitch perception. Auditory-nerve (AN) fibers preserve both TFS and envelope by phase locking to the dominant periodicities present in sounds. The temporal representation of periodicity is enhanced by octopus cells in the ventral cochlear nucleus, but is not maintained in more central auditory nuclei such as the inferior colliculus or auditory cortex. It is hypothesized that coincidence detection, a property of octopus cells, is a physiologically feasible mechanism for re-encoding temporal information present in auditory-nerve fibers into a firing rate-based representation. Octopus cells receive input from many AN fibers with a broad range of characteristic frequencies, have a large low-threshold K+ conductance, and can entrain to click trains up to 1 kHz. In this study, it is shown that a Hodgkin-Huxley model of an octopus cell with model AN fiber input responds with high firing rates and strong synchrony to pitch stimuli. Stimuli tested include click trains, harmonic tone complexes (with cosine and positive/negative Schroeder phase), broadband noise, and iterated ripped noise. Firing rate and synchrony of a model octopus cell were positively correlated to pitch strength. These results support the hypothesis that octopus cells are responsible for converting temporal information present in AN fibers to an average firing rate representation of F0.

**III-21. Ion Channels Overcome the Biophysical Constraints of Neuron Morphology**

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Neurons have a vast variety of different morphological architectures [1]. It is likely that this difference in neuron morphology reflects a difference in function. However, it is unclear whether the purpose of this morphology diversity is to allow a neuron to make the necessary connections in the neural circuit or whether the structure itself is required to produce the appropriate input-output transfer function of a neuron. Here we show that in most cases a set of ion channels can be found that enables a neuron with a distinct morphology to replicate the spiking behavior of neurons of different morphologies. This suggests that the brain has substantial flexibility with regard to its structure and information processing strategies. We show that the brain could, with the correct selection of ion channels, vary neural morphology without changing the spiking activity of a neuron.
Ill-22. A Sequential Prediction Approach to Measure Time-Varying Causality in Ensemble Neural Recordings

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Tracking the dynamics of neural systems is crucial for understanding how they adapt their responses to relevant biological information. Rather than relying on correlation, recent neuroscientific endeavors have evolved towards developing statistical measures of causality based on Granger’s notion [1]. However, his detailed quantitative formulation, based on the multivariate autoregressive (MVAR) models, is problematic when observations are not continuous (for example, binary-valued neural spike trains). More recently, the log-likelihood ratio has been applied to embody Granger’s notion for arbitrary modalities [2,3]. Secondly, Granger’s original formulation assumes a time-invariant MVAR model; but dynamic, time-varying causal interactions arise naturally in the brain, and changes within different neural populations might arise at different times. Current attempts to provide a sequence of discrete snapshots of the dynamics using temporal windows do not track the evolution in a fine time scale, assume that all changes occur at the same time, and assume time-invariant dynamics within windows [3]. Here, we propose a time-varying causality measure in ensemble neural spike trains using a sequential prediction approach. Our approach measures the reduction in loss between two dynamic, provably good, sequential predictors—one with the past of candidate “effector” and the other without. When applied to neural activity recorded in the primary motor cortex of monkey, which was trained to perform a visuomotor task [3], the proposed method tracks time-varying causal interactions and observes more interactions after visual stimulus, which is consistent with our previous findings [3]. Additionally, it provides detailed temporal information causal dynamics, changes of which occur at different times and durations (Fig. 1).

Ill-23. Memory formation, recall and forgetting in neuronal networks

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Which processes are behind the ability of biological neuronal circuits for memory formation, recall, and forgetting (e.g., objects or facts) is still under heavy debate in neuroscience. Although several theoretical approaches exist (e.g. Hopfield networks [Hopfield, 1982], attractor networks [Mongillo et al., 2008], Liquid-state machines [Maass et al., 2002]), each approach has difficulties like, for instance, arbitrary non-biological constraints (e.g. Hopfield networks), predefined connectivity (e.g. attractor networks), or supervised recall (e.g. Liquid-state machines). In Tetzlaff et al., 2011 we analyzed a combination of conventional plasticity [e.g. Hebb, 1949] and synaptic scaling [Turrigiano et al., 1998] that builds up memory traces (cell assemblies) induced by external inputs. Here we show that the combination of this mechanism with inhibition can also form (“learn”), retrieve and delete clusters of highly connected neurons within recurrent neuronal networks. Synapses in such a cluster are significantly stronger than those between different clusters, thus similar connectivity patterns recently observed in the cortex [Perin et al., 2011]. In our model inter-cluster connection strength directly depends on duration and frequency of the presentation of an unknown entity. Thus, for complete recall of a well-learned (often presented) entity, a smaller fraction of cluster neurons have to be stimulated and recall is quick. Well-trained clusters are not only quantitatively but also qualitatively different from sporadically-trained clusters: The time scale for forgetting the former is significantly longer than for the latter so that it takes longer to forget a well-learned entity. Synaptic scaling in combination with conventional plasticity thus leads to 1) learning of new memory entities, 2) recalling of clusters while synaptic weights remain plastic which additionally supports memory formation through reconsolidation, and
3) forgetting, which depends on the state (well- or sporadically-learned) the cluster is in.

III-24. On the complementary strengths and weaknesses of spatial vs. hybrid map formation algorithms

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Map formation is a core process in visual development. Conventional algorithms that use neighborhood-based learning are well suited to learn retinotopic maps of one or two non-mutually-exclusive features—notably the combined orientation and ocular dominance map in V1. Cells in more ventral areas including V4 and IT respond to a wide range of more complex object features, potentially constituting hundreds or thousands of different feature types [1,2]. Given that object recognition is location-invariant, every point in the visual field should in principle be analyzed in parallel by all features, implying that every feature should form its own map tiling the visual field. The physical interdigitation of multiple feature maps presents a challenge for conventional self-organizing map (SOM) algorithms: within such a “multimap”, a neuron will be surrounded by neurons coding multiple different feature types, preventing neurons from co-training based only on their spatial proximity. We developed a hybrid algorithm in which co-training of neurons depends both on their spatial proximity and the correlation of their responses to incoming stimuli. We contrasted the behavior of this hybrid spatial-correlational learning rule with a conventional SOM algorithm, finding the following double dissociation: The conventional SOM was learned a good retinotopic maps of a single feature, but when multiple feature maps were trained simultaneously, the cortical space was partitioned into mutually exclusive single-feature islands with periodic gaps in retinotopic coverage. In contrast, the hybrid algorithm produced locally jumbled (salt-and-pepper) structure for a single feature, but when presented with multiple features, produced fully interdigitated maps, each with good coverage both in retinal and feature dimensions. Our results suggest that pure spatial map formation algorithms could be specialized for development of single-feature maps such as in V1, whereas hybrid spatial-correlation-based development allows for simultaneous mapping of multiple independent features as found in higher visual areas.

III-25. Active self-organization of disordered arrangements of orientation preference in cortical networks

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Response characteristics of orientation tuned neurons in the visual cortex appear to be similar in mammalian lineages widely separated in evolution. The spatial arrangements of tuning properties across the cortex, however, show fundamental differences. While in primates and carnivores orientation preference varies progressively forming orientation maps, in rodents it appears to be randomly distributed. Recently, it has been shown that orientation maps in different species realize a common design which can be explained by activity-dependent self-organization.
of large scale neuronal circuits (Kaschube et al., Science 2010). It remains unclear, however, whether a similar approach can also explain rodent functional organization. Here we present an analytically tractable symmetry-based model of the activity-dependent development of orientation selectivity that can describe both types of organization. In the model neurons interact in a distance dependent manner both with isotropically inhibition and excitation and with orientation selective excitation. By symmetry this model has a large set of exact map solutions. Analytically examining their stability, we find that, independent of the fraction of selective interactions, with strong short range inhibition all map solutions become unstable. We show numerically that in this regime, disordered arrangements of orientation preferences become the attractor state of the network. We examine generalizations of the model to binocular tuning and determined a parameter regime in which an initially independent tuning for each eye is matched only after the emergence of selectivity, as was recently reported (Wang et al., Neuron 2010). Even while the neurons independently organize their inputs to achieve binocular matching, the disordered structure in the network is actively generated. Our results demonstrate, that a disordered arrangement of orientation selectivity can be actively generated by a dynamical process of self-organization.

III-26. Nonnormal amplification in random balanced neuronal networks

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In dynamical models of cortical networks, noisy inputs can be amplified into structured activity fluctuations by the recurrent connectivity, essentially through a combination of two distinct mechanisms. First, those patterns that self-reproduce by passage through the connectivity matrix W display large but slow fluctuations (dynamical slowing). Second, if W is nonnormal in the mathematical sense, it may hide a functionally feedforward network of strongly coupled activity patterns, allowing for transient amplification on fast time scales. The latter mechanism of nonnormal amplification has recently emerged in the neuroscience literature, though only in the context of a network with specific structure [Murphy and Miller (2009)], or networks explicitly designed to exhibit the phenomenon [Ganguli et al. (2008); Goldman (2009); Benayoun et al. (2010)]. It is not clear to what extent nonnormality affects the dynamics of more generic models of cortex. Here we investigate the tradeoff between nonnormal amplification and dynamical slowing in large random neuronal networks composed of excitatory and inhibitory neurons. Assuming linear stochastic dynamics, we derive an exact expression for the expected amount of purely nonnormal amplification. We find that nonnormality primarily gives rise to macroscopic fluctuations of the global population firing rate, which explains the positive mean pairwise correlation among network neurons. Amplification along more detailed spatial patterns is microscopic, however, and its total amount is very restricted if dynamical slowing needs to be kept low. Thus, in order to achieve strong transient amplification with little slowing, the connectivity must be structured, so that the synaptic strengths can afford larger values – a region where amplification in fact explodes – while self-reproducing patterns are discouraged. We discuss why this could be a desirable feature for sensory cortices that need to track fast-changing signals, and we give a plausible example of structure that favors nonnormal amplification.

III-27. Non-linear predictive coding and dynamic decorrelation in early sensory systems

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Reacting to stimuli is crucial to animals—survival yet must be done accurately—a conflict known as the speed-
accuracy tradeoff. Correct reactions become challenging if functionally different stimuli elicit similar neural activation patterns. Discriminability can be improved by pattern decorrelation—processing stimuli that are functionally different, yet elicit similar activity, to make output activity more distinct (Wiechart et al. 2010). Such a process inherently involves amplifying differences between activity patterns. However, even repetitions of the same stimulus have differences in activity, i.e., noise, which does not contribute to discriminability and will degrade performance. Thus, amplifying differences between patterns is potentially risky. If signal always has given characteristics e.g., low spatial frequency, and noise different ones e.g., high spatial frequency, then noise can be filtered out. However, signals may be similar to what is noise in a different context e.g., high spatial frequency components induced by edges, making decorrelation difficult. This is similar to overfitting in statistics, for which a common solution is using powerful models that can in principle fit the noise, but enforcing regularization, making overfitting less likely. Here we show that a nonlinear recurrent network, a simplified model of early sensory processing, performing regularized predictive coding decorrelates activity. Solving the nonlinear dynamics, we demonstrate that interneurons initially subtracts highly regularized, i.e., less susceptible to noise, predictions but with time subtract progressively less regularized predictions, resulting in increased decorrelation, and improving discriminability. Consistent with experiments, decorrelation develops over time and is only partial (Gridhar et al. 2011). This is explained in our model by the temporal dynamics of regularization enforced by interneuron nonlinearity. Thus, our study provides insight into the fundamental question of speed-accuracy tradeoffs, and a theoretical framework explaining the mechanistic basis and dynamics of decorrelation in early sensory circuits.

III-28. Frequency analysis of short-term memory in nonlinear network models

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Recurrent neuronal networks have been proposed as generic models for storing temporal signals in their dynamic states. However, previous analysis of the short term memory capacity of recurrent networks has largely focused on linear networks with no intrinsic dynamics. Here we study short-term memory of randomly connected rate-based neural networks with strong, balanced connectivity and nonlinear firing rate functions. When these networks are driven by a strong input pulse, its effect resonates in the network 50–100 times longer than the time constant of individual network neurons. This memory is of limited computational use, however, because the strong input erases any traces of preceding input. To study memory capacity for continuous signals, networks were driven with zero-mean Gaussian white-noise input, and a linear readout of the network state was used to reconstruct the input history. Signal reconstruction error of this readout was computed as a function of input frequency and elapsed time. Network memory profiles fall into two regimes. When the input signal has a small amplitude, it fails to fully suppress the intrinsic chaotic dynamics of the network, most notably at lower frequencies. When input to the network is strong, new inputs overwrite the representation of preceding inputs. Between these two regimes we find an optimum input amplitude at which network memory is greatest. The interaction between memory and network architecture—including size, connection density and strength—was characterized through simulation. Spatial targeting of input populations was also explored as a means of exploiting network architecture to improve suppression of chaos and to increase memory duration. In conjunction, these findings provide guidelines by which network architecture may be tailored to achieve greater memory capacity in networks of neurons with limited dynamic range.
Ill-29. Local control of non-local information routing in spiking neuronal networks

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To delve with behaviorally relevant changes in context or to subserve top-down control of neural processing dynamic routing of information between neuronal assemblies is essential in a functional brain. Recent experimental and theoretical studies [1-3] show that coherent oscillations among local circuits may create such information channels. Here we show how network-wide information flow patterns in oscillatory networks can be controlled by local changes within a sub-region only. Thus local structural and dynamical changes, induced e.g. by local stimulation or synaptic plasticity are capable of controlling the information routing at distant locations. We first derive an analytical expression for the information flow in hierarchical networks of reduced phase-amplitude oscillators with strongly connected clusters and weaker inter-cluster couplings. Our analytics unravel that local changes can remotely control the information transmission between two other distant, physically unchanged groups. Moreover, by switching among local multi-stable dynamical states the global information flow pattern in the network can be changed in a dynamical way. We link our theoretical findings to more realistic clustered networks of spiking neurons exhibiting pyramidal interneuron gamma (PING) oscillations. We derive an semi-analytical expression for the information flow between the PING clusters and identify the same local information flow control mechanisms. Moreover, by introducing a coding scheme based on the spike ordering we show that these information channels act as “carrier channels” for complex representations encoded in precise patterns of neuronal firing. Collective dynamics of interacting brain rhythms thus equip a network with local control mechanisms for non-local routing of large amounts of information in a way akin to a “clocked” combinatorial circuit. [1] T. Womelsdorf et al., Science 316, 1609–1612 (2007). [2] A. Buehlmann, G. Deco, PLoS Comput. Biol. 6, e1000934 (2010). [3] D. Battaglia, A. Witt, F. Wolf, T. Geisel, in review (2011).

Ill-30. Between-pair spike-field coherence comparison

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Recent experiments in neuroscience have compared the strength of association between neural spike trains and oscillations present in local field potential (LFP) recordings. The measure employed in these comparisons, “spike-field coherence”, is a frequency dependent measure of linear association, and is shown to depend on overall neural activity. Dependence upon overall neural activity, that is, dependence upon the total number of spikes, renders comparison of spike-field coherence across experimental context difficult. In this presentation, an inferential procedure based upon a generalized linear model is shown to be capable of separating the effects of overall neural activity from spike train-LFP oscillatory coupling. This separation provides a means to compare the strength of oscillatory association between spike train-LFP pairs independent of differences in spiking rate. Following a review of the generalized linear modelling framework of point process neural activity a specific class
of generalized linear models are introduced. This model class, employing a piece-wise constant link function relating an LFP rhythm to neural response, is used to develop an hypothesis test capable of detecting changes in spike train-LFP oscillatory coupling. The performance of this hypothesis test is validated, both in simulation and on real data, and is compared to the method of spike thinning previously employed to facilitate across-context spike-field coherence comparison. By equalizing the overall neural activity through a spike removal process prior to spike-field coherence computation, this latter method seeks to equalize the dependence of spike-field coherence estimates upon neural activity prior to across-pair comparison. It is shown to be deleterious in at least one example, and is approximately equivalent to the proposed method when neural spiking rates are comparable. The proposed method of inference provides a principled statistical procedure by which across-context change in spike train-LFP rhythmic association can be directly inferred, independent of neural spiking rates.

III-31. Bayesian entropy estimation for infinite neural alphabets

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Shannon entropy quantifies the information that may be conveyed by a vector of neural responses, and has featured prominently in the analysis of neural codes. However, entropy is notoriously difficult to estimate from data, particularly in the “undersampled” regime, where the number of possible response patterns (or “words”) K is larger than the number of observed responses ("samples") N. Here we describe a Bayesian method for estimating entropy from datasets where the number of possible words (i.e., the size of the neural alphabet) is arbitrarily large or unknown. Our approach follows that of Nemenman et al, who formulated a Bayesian entropy estimator using a “mixture-of-Dirichlets” prior over the space of discrete distributions on K bins. Here we extend this approach in several directions. First, we formulate two priors over discrete, countably infinite distributions using mixtures of Dirichlet processes (DP) or Pitman-Yor (PY) processes. (These processes play a central role in nonparametric Bayesian statistics, and are useful when the number of parameters or “bins” is not known a priori.) We analytically derive a set of mixing weights over these processes so that the resulting improper prior over entropy is approximately flat across a semi-infinite range. Secondly, we consider the posterior over entropy given a dataset (which contains some observed number of words but an unknown number of unobserved words), and show that the posterior mean can be efficiently computed via a simple 1D or 2D numerical integral. Remarkably, for most datasets the expected entropy given data is finite, even though the distributions have positive probability on infinitely many bins and the prior is improper. We compare our approach to previous methods, including an approximate Bayesian entropy estimator and a frequentist “coverage-adjusted” estimator designed for unknown or infinite K.

III-32. Parallel pathways for information processing in the retina: the ON and OFF dichotomy

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Over twenty different ganglion cell types have been identified in the mammalian retina, believed to represent parallel channels of information transmission. In an effort to understand the origins and functional implications of this diversity, we examine the division into ON and OFF channels for the processing of light and dark increments
in a visual scene. The ON and OFF pathways have been hypothesized to emerge for the rapid and metabolically efficient signaling of changes in light intensity (Schiller 1992), however, this idea has never been formalized. We quantify the information gain in a system with two cell types of opposite light responses, ON and OFF, and compare it to a system with one cell type, ON-ON. In the regime of low firing rates (one spike per integration time) typical for retinal ganglion cells, the optimal mutual information between a stimulus and a cell's response is transmitted by Poisson neurons which use only two firing rates: zero and maximal (Stein 1967, Shamai, 1990, Nikitin et al. 2009). We extend the single cell analysis to a system of two cells with binary response functions, described by the response threshold. Constraining the maximum or the mean firing rate in both systems, ON-OFF and ON-ON, results in only a minor information gain for the ON-OFF system. This unexpectedly small difference between the two schemes, as measured by the mutual information, suggests the need to explore other criteria for optimality: (1) We examine natural images which may contain ecologically-relevant information not captured by the mutual information. (2) In addition to static images, we also compare the performance of the two schemes for their speed of encoding of temporally fluctuating light intensities.

**III-33. Fisher and Shannon information in finite neural populations**

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The precision of the neural code is commonly investigated using two different families of statistical measures: (i) Shannon mutual information and derived quantities when investigating very small populations of neurons and (ii) Fisher information when studying large populations. These statistical tools are no longer the preserve of theorists, and are being applied by experimental research groups in the analysis of empirical data. Although the relationship between information theoretic and Fisher-based measures in the limit of infinite neural populations is relatively well understood, how these measures compare in finite size populations has not yet been systematically explored. We aim to close this gap. We are particularly interested in understanding which stimuli are best encoded (in terms of discrimination) by a given neuron within a population and how this depends on the chosen measure. We use a novel Monte Carlo approach to compute a stimulus-specific decomposition of the mutual information (the stimulus-specific information) for model populations of up to 256 neurons and show that Fisher information can be used to accurately estimate both mutual information and stimulus-specific information (SSI) for populations of the order of 100 neurons, even in the presence of biologically realistic variability, noise correlations and experimentally relevant integration times. According to both measures, the stimuli that are best encoded are then those falling at the flanks of the neuron's tuning curve. In populations of less than around 50 neurons, however, Fisher information can be misleading.

**III-34. Maximally informative stimulus energies in the analysis of neural responses to natural signals**

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We have developed Maximally Informative Energies as a method for describing the responses of neurons to complex and potentially high-dimensional stimuli, in cases where the response has a quadratic dependence on the stimulus. This extends the maximally informative approach to neurons with receptive fields that are sensitive to the covariance structure of the stimulus preceding a spike rather than depending only on a linear projection. We illustrate the practical feasibility of this procedure in three model systems: 1) Non-phase-locked auditory neurons responding to complex, natural, acoustic stimuli. These neurons respond to sound energy in a selected bandwidth,
but do not discriminate among signals shifted by small times. 2) Complex cells in the visual cortex responding to natural scenes. These exhibit invariance to small spatial displacements of the relevant, oriented stimulus feature. 3) Motion-sensitive visual neurons that compute a velocity, independent of the absolute position of the objects that are moving. The invariance that is common to all three systems, means that the neurons are sensitive to multiple stimulus dimensions, although these different dimensions effectively correspond to the same stimulus feature occurring at different times relative to the spike. To capture this intuition concisely, our simplest starting point is a model in which a quadratic projection of the stimulus onto a receptive field is computed. To extract this quadratic dependence in the presence of a naturalistic stimulus distribution, we extend the earlier notion of maximizing mutual information to include quadratic stimulus dependence and demonstrate that this approach leads to consistent inference. Our approach yields unbiased receptive field estimates, but requires optimization in a possibly rugged information landscape. We expect that this approach will help elucidate systematically the prevalence of sensitivity to high-order statistical features in sensory cortices for naturalistic stimuli.

III-35. A principle of brain communication based on compressive sampling and sparse coding

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Axonal projections between brain regions may constitute wiring bottlenecks for communication. Thus, some form of compression may be necessary for communication within the brain. Here we explore whether projecting neurons could compress local patterns of activity by simple random subsampling. Although there are many different algorithms for compression, few of them are well suited to be implemented in a biologically plausible fashion. We consider different alternatives for communication across wiring bottlenecks in the brain and argue that a combination of compressive sampling and sparse coding is a compelling potential mechanism. Previous work on compressive sampling has shown that under the assumption of sparsity, compressed signals can be reconstructed even when they are sampled at a rate less than the Nyquist rate. Here we show that meaningful recovery is possible through the use of sparse coding even when the subsampling matrix is not known. This is of particular interest in the brain where presumably a downstream region cannot know the local pattern of the connectivity in the upstream region. In simulations, we demonstrate this approach to compressive communication. Although the downstream representations learned in our simulations are not identical to the patterns in the upstream region, we are able to show that they bear a precise correspondence to the original signals in a way that preserves their information content.

III-36. Fitting receptive fields in V1 and V2 as linear combinations of nonlinear subunits

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Responses of early visual neurons are commonly described with a linear sensory filter followed by a spiking nonlinearity. In many cases these linear-nonlinear (LN) models capture a substantial fraction of the response variance. However, many cell types are not well fit (e.g. V1 complex cells), and are described instead as a
linear combination of LN “subunits” (altogether, LNL). The stimulus subspace spanned by these subunits can be estimated by analyzing the covariance of the spike-triggered stimulus distribution (STC), but this requires large amounts of data and cannot uniquely determine the form of the subunits. To overcome these limitations we introduce a procedure that fits an LNL subunit model directly. The model assumes that a single linear subunit is applied convolutionally over space, and that the field of linear responses is then transformed with a single, replicated nonlinearity. We fit the model (linear subunit, nonlinearity, and linear weighting over subunits) with alternating gradient descent. The model performs well on three sets of neural data (two collected in V1 and one in V2); the fitted subunit models capture similar visual information as STC with many fewer parameters and produce unique well-localized subunit features. In V1, the model can fit 2D (x-t) subunits for both simple and complex cells. For simple cells, the linear weighting is small at all but one location, indicating a single subunit; complex cell subunits are spatially dispersed. Fitting 3D (x-y-t) subunits to another set of V1 data reveals the expected combinations of orientation and direction tuning. For V2 neurons, instead of computing subunits directly from the stimulus, the model pools a spatial array of model V1 neurons tuned to local orientation and phase, creating subunits that are selective for the conjunction of V1-afferent features.

III-37. Two-layer synaptic integration in pyramidal neurons

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The two-layer model of synaptic integration is an abstract spike rate model analogous to a 2-layer artificial neural network, where the dendrites and soma constitute the first and second layers, respectively. In specific terms, the first layer consists of a set of independent sigmoidally-thresholded dendritic subunits whose outputs are represented as currents. These currents are summed linearly at the soma and run through the axo-somatic f-I curve to determine the cell’s output firing rate. A key assumption of the 2-layer model is that nonlinear interactions between synapses within a dendritic subunit are “private”, that is, whatever output is supposed to be produced by a subunit for a given pattern of inputs is always produced, and delivered to the soma, regardless of the “goings on” inside other subunits. However, somatic action potentials, which represent the combined outputs of all subunits, back-propagate into the dendritic arbor sometimes 10’s or even 100’s of times per second. These large-amplitude voltage signals sweeping repeatedly into the dendrites act as a form of crosstalk between subunits, and seem likely to disrupt and/or homogenize the subunit-specific voltage-based “calculations” taking place in different dendrites at any given time. How could subunit independence be maintained under such conditions? We used simple (abstract) and complex (compartmental) models to address this question. We found that an abstract, rate-based, 2-layer model can predict the mean firing rate of a detailed compartmental model with remarkable accuracy (R2>0.999, NRMSE<1%). In an analysis of the conductance, voltage, and current waveforms at various locations inside the cell during stimulation, we discovered why BPAPs leave functional compartmentalization essentially intact (Figure 1). Our results suggest that compartmentalized 2-layer processing is a ‘natural’ feature of pyramidal neuron dendrites.

III-38. A Population Approach to Coding and Decoding with Adapting Neurons

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Theoretical explorations of adaptation in spiking neurons often fall flat due to a dependance on the infinitely many spiking histories possible. Basic observables such as the Peri-Stimulus Time-Histogram (PSTH) and linear filter could not be expressed as an explicit function of the model's parameters. In the present article, we use
an approximation of the full dynamics which becomes exact in the limit of small population activity and/or weak refractoriness. This approximation allows us to derive an expression for encoding and decoding time-dependent stimulus in the population activity. In like manner, we derive an expression for the linear filter which shows how high-pass and band-pass properties can arise from distinct shapes of the spike after-potential. In all cases the approximation matches very well with direct simulations of large neuronal populations. An analytical expression can shed light onto previously obscure processes. Here we discover that the decoding of a population of weakly active neurons only requires two quantities: i) the instantaneous population activity and ii) an accumulation of the past history weighted by a factor that relates to the effective spike after-potential. The results presented here can be used to make mean-field theory models of neuron networks closer to experimental observations.

III-39. Improving neural control of a simulated arm by decoding intended future movement

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A brain-machine interface (BMI) records neural signals in real time from a subject's brain, interprets them as motor commands, and reroutes them to a device (e.g., a computer cursor or prosthetic arm) in order to restore the subject's lost motor function. Typically, a BMI that enables the control of a prosthetic arm decodes an intended hand position or velocity from the subject and uses a controller to generate joint torques to drive the arm accordingly. Previous studies taking this approach have chosen to decode the subject's desired arm state in the present moment and to use it as the command signal. However, this approach causes the prosthetic arm to lag behind the state desired by the user, as the dynamics of the arm constrain how quickly the controller can bring the arm's state in accordance with the commanded state. If the command signal is smoothed, by filtering the neural data or the signal itself, the arm will lag further behind the user's intent. To compensate for delay introduced by the controller and/or smoothing, we used a regularized Weiner filter to decode a subject's intended hand position in the future at a time lead equal to the known system delay, and used this value as the command signal. In our experiment, a monkey (Macaca mulatta) used a BMI implementing this approach to control a simulated arm to hit targets on a screen. Results from experiments with two BMIs with different system delays (100 and 200 milliseconds) show that the monkey can make significantly straighter and faster movements when the decoder predictively compensates for the delay. By varying the time by which we decode into the future, we also show that performance peaks near the time of the known system delay and degrades otherwise.

III-40. Long-term Decoding Stability without Retraining for Intracortical Brain Computer Interface

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Most current intracortical brain computer interface (BCI) systems rely on daily retraining. While this is feasible in a lab, it is not clear the burden of daily retraining will be viable in the clinic. We therefore sought to investigate the long-term stability of an intracortical BCI system without retraining. We recorded neural activity using a 96-electrode array implanted in the motor cortex of a rhesus macaque performing center-out reaches in 7 directions over 41 sessions spanning 48 days. One simple way to avoid retraining is to hold the decoder static from day to day. As expected, we found that when decoding reach direction based on threshold crossings collected during arm movement, the performance of such a static decoder was diminished compared to one which was retrained daily. However, we found no significant decline in performance across time for this decoder, though variability (standard deviation) from day to day was large. We then considered a second static model which allowed for a greater dispersion of spike counts than the standard method. Mean decoding performance increased from 59.4% to 70.0% while the standard deviation of day-to-day performance decreased from 12.1% to 7.9%. While these results must be reproduced in a closed-loop setting, we believe such insights into the role of decoder training will be important for the clinical translation of BCI systems.

III-41. An objective approach to learning movement-related features from local field potentials

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Past studies have shown that local field potentials (LFP) in the primary motor cortex (M1) encode information related to movement, enabling the possibility of using LFP as a control signal for brain-machine interfaces (BMI). A recent approach to incorporating LFP for BMI focused on the power of specific low frequency bands (0-10Hz and 20-40Hz), which are known to be modulated during movement execution. Conversely, Rickert et al. found multiple other frequency bands (<4, 6-13, 63-200Hz) that contain direction related information. Given the wide range of frequencies that appear to contain movement information, it is unclear how to determine the features most relevant to movement from all these frequency bands. Here, we present a novel approach to extracting features from LFP that are well modulated by movement. Specifically, this method searches for an optimal projection of the LFP that maximizes the variance of the activity across different movement directions, while minimizing the variance of the activity during movements in the same direction. This method objectively determines features in the LFP that differentiate between movement directions, instead of relying on a priori assumptions about particular LFP frequency bands. The learned features capture the aspect of the LFP that changes with movement direction but is consistent during movements in the same direction. Our results obtained from LFP recordings in M1 of macaque monkeys performing center-out reaching indicate that these features reflect contributions from the 0-40Hz and 120-200Hz bands of the LFP. Lastly, we demonstrate that these features can provide high accuracy in predicting hand position during movement with a correlation coefficient of 0.7.

III-42. Synaptic input correlations and membrane potential decorrelation in spontaneous cortical activity

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Spiking correlations between neurons have been found in many regions of the cortex and under multiple ex-
experimental conditions. Despite their important consequences for neural population coding, the origin and the magnitude of such correlations remains a highly debated issue. A large body of extracellular data reports spiking correlations of various strengths, but how synaptic input correlations translate into membrane potential and spike-output correlations remains largely unexplored. Using an in vitro thalamocortical slice preparation, we perform simultaneous recordings from pairs of layer IV neurons in the auditory cortex and measure synaptic potentials/currents, membrane potentials and spiking outputs. We calculate cross-correlations between excitatory and inhibitory inputs to investigate correlations emerging from the network topology. We furthermore evaluate membrane potential correlations at depolarized potentials in order to study how excitation and inhibition combine and give potentially rise to spike-output correlations. Irregular, spontaneous activity is induced through high potassium and low magnesium and calcium concentrations in the artificial cerebrospinal fluid. The impact of space clamp and the number of presynaptic neurons projecting to the recorded cells is investigated using recurrent network simulations in combination with compartmental modeling. We find that nearby neurons receive correlated excitatory and inhibitory input. Excitatory correlations are broader than inhibitory correlations which hints to more presynaptic excitatory than inhibitory neurons projecting to the recorded cell pair, in agreement with cortical architecture. We measure directly that excitation is correlated with inhibition thereby partially canceling each other and resulting in weak membrane potential correlations between neurons. Inhibition follows excitation with a short delay of a couple of milliseconds. Our data suggests that cortical networks are set up to partially cancel correlations emerging from the coupling between neurons. That active decorrelation is achieved through close tracking of excitation and inhibition. Our results provide the cellular correlate possibly leading to low spiking correlations.

III-43. Correlations in Spatially Heterogeneous Neuronal Networks

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How does network architecture together with response properties of individual neurons shape the response of a population of cells? How are the properties of neuronal networks related to the computations they have evolved to perform? To address these fundamental questions of systems neuroscience we have recently generalized linear response methods previously used to analyze the population responses of specific neuronal networks. This technique allows us to explicitly describe the correlation structure in the output of a network of spiking neurons in terms of synaptic architecture and the response properties of the constituent cells. Our technique also allows us to address a question that has recently received much attention: What is the magnitude and distribution of correlations in cortex? In particular, Renart, de la Rocha et al. have shown that even in densely connected networks, balance between excitation and inhibition can lead to a cancellation of correlations and an asynchronous state. However, experimental evidence has so far not conclusively demonstrated whether cortical dynamics is asynchronous. The question is complicated by recent simulations of a realistic model of the visual area V1 that demonstrated that different layers can exhibit differing correlation patterns. We examined the impact of spatial structure in networks on the statistics of population activity. Although earlier theoretical studies have frequently considered spatially homogeneous networks, it is known that in cortex the probability that two cells have a synaptic contact is dependent on physical distance. We explore the impact of these connectivity patterns by imposing spatial profiles on the synaptic weights in recurrent networks of spiking neurons. We successfully apply linear response methods to predict the effects altering the spatial structure of the network. Our aim is to help describe how input and architecture determine population activity, a question central to understanding the neural code.
III-44. Filtering and recurrent connectivity shape higher-order correlations in retinal circuits

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Neural circuits can, in principle, produce an enormous number of distinct multi-cell outputs—a number so large that it could never be measured experimentally. Pairwise maximum entropy (PME) methods suggest a dramatic simplification: the distribution of outputs of many circuits are well captured by models that rely only on activity of single neurons and neuron pairs. Recent empirical studies find that the activity patterns of some circuits are well described by PME models (Shlens et al., J Neurosci, 2006; 2009; Schneidman, et al., Nature, 2006), while other circuits show significant departures (e.g. Ohiorhenuan et al., Nature, 2010). What circuit properties will lead to success or failure of this model? In particular, what factors contribute to the remarkable success of PME models in retinal ganglion cells (RGCs)? We study spike patterns in RGC circuits with different architectures and inputs. When circuit parameters are matched to observed values from primate ON parasol RGCs, spike outputs were well described by PME models across a broad range of light stimuli. Two mechanistic features contribute to this success; the largely feedforward structure of the circuit and the temporal filtering of synaptic inputs. By modulating filtering properties and recurrent connectivity, we find the conditions under which, all other factors being equal, the circuit generates the greatest higher-order interactions (HOIs). The first is when bimodal light stimuli are processed by an “integrating” temporal filter vs. a “differentiating” one. The second is when coupling interactions are present, and are of intermediate strength. As filters and coupling differ across retinal ganglion cell classes, this leads to a number of predictions. For example, networks of OFF-parasol cells could produce larger HOIs than their ON counterparts due to their coupling, and networks of primate midget cells could generate HOIs due to their distinct filtering properties.

III-45. Neuronal populations model of associative retrieval

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Voluntary memory retrieval is one of the underpinnings of human cognitive functions. ‘Free recall’ experiments, where subjects have to repeat as many words as possible after a quick exposure, have long been used as a simplified setting to investigate this fundamental process. Nevertheless, the mechanisms underlying voluntary retrieval of information from memory are yet to be clarified. Interestingly, the number of retrieved items slowly grows with the number of presented items, excluding from the candidate mechanisms short-term memory, which has a limited fixed capacity. We study cue-less retrieval within a general theoretical framework inspired by the hypothesis of population coding of information. Items in memory are represented by overlapping groups of neurons, whose activation is a proxy for retrieval. Once an item is retrieved, it triggers the retrieval of the next one in an associative manner. The model dynamics can be mapped to a graph search algorithm, allowing its complete analysis. Consistently with experimental results, we found a sub-linear scaling between the number of retrieved items and the number of presented items. Moreover, the model predicts a non-trivial scaling for the variance of
the number of items, which we tested on existing experimental data. Due to its general nature, the model can be readily implemented in associative neural networks. We suggest that the validity of our results extends beyond the classic free recall paradigm.

### III-46. The correlation structure induced by fluctuations in attention

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Attention has traditionally been associated with an increase in firing rates, reflecting a change in the gain of the population. More recent studies also report a change in noise correlations, which is thought to reflect changes in functional connectivity. However, since the degree of attention can vary substantially from trial to trial even within one experimental condition, the measured correlations could actually reflect fluctuations in the attention-related feedback signal (gain) rather than feed-forward noise, as often assumed. To gain insights into this issue we analytically analyzed the standard model of spatial attention, where directing attention to the receptive field of a neuron increases its response gain. We assumed conditionally independent neurons (no noise correlations) and asked how uncontrolled fluctuations in attention affect the correlation structure. First, we found that this simple model of spatial attention explains the empirically measured correlation structure quite well. In addition to a positive average level of correlations, it predicts both an increase in correlations with firing rates, as observed in many studies, and a decrease in correlations with the difference of two neurons’ tuning functions—a structure generally referred to as limited range correlations. Second, we asked how fluctuations in attention would affect the accuracy of a population code, if treated as noise by a downstream readout. Based on previous theoretical results, it would be expected that they negatively affect readout accuracy because of the limited range correlations they induce. Surprisingly, we found that this is not the case: correlations due to random gain fluctuations do not affect readout accuracy because their major axis is orthogonal to changes in the stimulus orientation. Our results can be readily generalized to include feature-based attention. The model has very few free parameters and can potentially account for a large fraction of the observed spike count (co-)variance.

### III-47. Attentional effects in V1 are related to spatial gating but not to allocation of limited resources

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Attention can modulate neural responses in sensory cortical areas and can improve behavioral performance in detection and discrimination tasks. However, the nature and purpose of these modulations in V1 remain under debate. To examine the precise spatiotemporal dynamics of attentional modulations at the level of neural populations in V1, and to determine their potential purpose, we used voltage-sensitive dye imaging to measure V1 responses while monkeys performed a difficult detection task under focal or distributed attention. We found that despite improved behavioral performance under focal attention, V1 population responses at a single attended location (under focal attention) or at one of four attended locations (under distributed attention), are indistinguishable. This finding is inconsistent with the hypothesis that an important goal of attention is to allocate limited representational resources in V1 based on task demands. However, we found that V1 responses at all attended
locations are significantly elevated relative to actively ignored or irrelevant locations. This elevation operates on a spatial scale larger than the stimulus evoked response, and is initiated \( \sim 80 \) ms before stimulus onset. This widespread baseline elevation is consistent with the hypothesis that an important goal of attention in V1 is to limit the behavioral effect of task-irrelevant visual stimuli. The elevated baseline at attended locations could contribute to this selective spatial gating by biasing competition in subsequent processing stages in favor of task-relevant stimuli.

**III-48. Probabilistic palimpsest memory: multiplicity, binding and coverage in visual short-term memory**

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According to a standard view of short term memory, there is a rather rigid set of fixed ‘slots’ that can be independently filled (Vogel 1997), with recall errors arising from items that did not fit. Recent results instead suggest a unified shared working memory resource, with the signal/noise ratio for one item being reduced by the storage of others (Ma 2004, Husain 2008). There are substantial experimental and theoretical results based on this latter view, including evident sequential effects. Considering this shared working memory as a distributed code leads to a rich set of computational problems that have not been well addressed in conventional accounts of population coding. In particular, it becomes necessary to consider multiplicity (Sahani 2003, Amari 2005), with multiple items coexisting simultaneously in memory, overlaid on top of one another like a palimpsest (Savin 2011), and multidimensional binding, with some dimensions of an item providing information about the others during recall. We built a probabilistic model of a finite capacity working memory network, capable of reproducing the form of experimental psychophysical human data, only assuming a simple palimpsest-like storage process and a normative Bayesian recall process where uncertainty is propagated. The precision of recall decayed smoothly as the number of items increased because of interference between stored objects. Our model provided a parsimonious account of recall precision, binding errors and temporal effects. Interestingly, it also showed a similar distribution of errors to those that were thought to support a ‘slots’ model. At the heart of our approach was a specific proposal for the distributed representation of objects in memory. We showed how simple representations based on single features failed when multiple objects have to be distinguished, and how the addition of conjunctive neurons and appropriately tiling and covering the object space could rescue them.

**III-49. What does information seeking tell us about reinforcement learning?**

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Conventional theories of reinforcement learning explain how we choose actions to gain rewards, but we also often choose actions to help us predict rewards. This behavior is known as information seeking (or ‘early resolution of uncertainty’) in economics and a form of “observing behavior” in psychology. We recently found that many neurons involved in conventional reward seeking also send signals appropriate for information seeking, suggesting that these behaviors share a common neural mechanism. Thus it is crucial to understand how theories of reinforcement learning can be revised to produce information seeking, and what this implies about the underlying neural computations. Two major proposals to produce information seeking are nonlinear reinforcement, in which reinforcement from a state is a nonlinear function of its expected value, and distributional reinforcement, in which reinforcement is influenced by additional statistics of the value distribution such as variance and entropy. It is
believed that nonlinear theories are promising, making only small changes to conventional theories and giving a good account of existing data; while distributional theories are believed to be dubious, making predictions that lack experimental support. Here, however, we make three theoretical advances which show that exactly the opposite is the case. We first derive methods to measure reinforcement nonlinearities, and show that nonlinear theories can only explain existing neural and behavioral data by invoking severe nonlinearities that deviate far from conventional theories. Furthermore, we show that nonlinear theories can only produce robust information seeking by using a very specific family of nonlinearities, a family that was not considered in previous proposals and which makes several unlikely predictions about behavior. Finally, we show that distributional theories escape these limitations, and that upon careful inspection distributional theories are fully compatible with the experiments that were previously believed to exclude them.

III-50. Corticostriatal projections mediate auditory decisions

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How does sensory information get out of the cortex to drive actions? Representations of the acoustic world are constructed in the auditory cortex (ACx), but how these representations are used to effect decisions is largely unknown. Here we report for the first time that the projection of the ACx to the striatum drives decisions in rats, and that changes in corticostriatal synaptic strength may underlie learning in this task. We first developed a novel auditory task—modeled after the random dot motion task used to study area MT—designed to exploit the tonotopic organization of the ACx. We trained rats to discriminate low- and high-frequency “cloud-of-tones” stimuli (overlapping 30msec pure tones distributed over three octaves) in a two-alternative choice task. Subjects were required to report whether low or high tones were overrepresented; performance varied smoothly with stimulus frequency. We hypothesized that the ACx drives subjects’ choices through its projection to the striatum. To test this, we used ChR2 to selectively activate corticostriatal neurons in rats performing the task. Activation of corticostriatal neurons biased the subjects’ choices as predicted by the neurons’ frequency tuning. These results suggest not only that the ACx is causally involved in this task, but also that information propagates beyond the ACx via the corticostriatal projection. To test the role of the corticostriatal synapse in encoding associations between sounds and motor responses, we are using ChR2-evoked corticostriatal local field potentials as a proxy for synaptic strength. Preliminary results indicate that acquisition of the task increases the strength of these connections. Although it would be naive to suggest that we have identified the “engram” for this task, our findings suggest a simple model in which learning the association between frequency and action occurs by strengthening of a subset of feedforward projections.

III-51. Task set switching: dissecting ideal observer models and their approximation

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Learning task sets and switching between them is ubiquitous in everyday behavior. Despite this, little is known about how efficient humans are in their use of information when performing either learning or switching. Previous task set switching models either contained heuristic components, or were unable to reproduce important features
in human behavior. Here, we address task set learning and switching from the ideal observer perspective, based on an episodic task in which—based on noisy feedback—humans had to learn stimulus/response associations (the task sets), and in which these associations changed over time. The ideal observer model resulting from this task structure is similar to inference in sticky Hidden Markov Models, in which both the feedback noise and the switching structure are inferred. When compared to a large dataset of performing humans, we found that these humans receive on average above 90% of the optimal reward, as determined by the ideal observer model. Furthermore, and in contrast to standard change point detection models, our model captured well important behavioral features, such as faster switching and reduced exploration when switching into previously learned task sets. Optimal behavior requires subjects to memorize all previous observations and actions, which is clearly intractable. By limiting the model's memory, we found that it is sufficient to remember the last 6 trials while still featuring human-like performance. Still, even the limited memory variant required extensive MCMC sampling to perform accurate inference. We alleviated the latter by the introduction of a variational Bayesian approximation that significantly simplified the inference with a negligible drop in performance, thus providing a tractable explanation for how humans are able to feature the observed behavior. The use of particle filters did not provide a good alternative explanation, as they struggled to handle the discontinuous nature of the task.

III-52. Evidence for incidental structured learning and abstraction in cognitive reinforcement learning

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Executive functions and learning share common neural substrates essential for their expression, notably in prefrontal cortex and basal ganglia. Understanding how they interact requires studying how cognitive control facilitates learning, but also how learning provides the (potentially hidden) structure, such as abstract rules or task-sets, needed for cognitive control. We investigate this question from four complementary angles. First, we present a new experimental paradigm to assess whether subjects spontaneously build structure into a learning problem when not cued to do so, as evidenced by patterns of errors and response times. Second, we develop a new computational model inspired by non-parametric Bayesian methods, specifying how the learner might infer hidden structure in the form of task-sets and decide whether to re-use that structure, or to create a new task set, in new contexts. Third, we develop a neurobiologically explicit model to assess potential mechanisms of such interactive structured learning in multiple circuits linking frontal cortex and basal ganglia. Last, we use electroencephalography to explore the neural correlates of these cognitive processes. Results showed that subjects have a strong predilection to build structure into learning, potentially allowing them to generalize this abstract structure in subsequent opportunities, in a way accounted for by the computational model. The neural network robustly exhibited the behavioral pattern of data predicted by the model and observed in human subjects, providing a biologically realistic implementation of the functional model and thus providing a firm grounding for predictions on the neural correlates implicated in the process, such as prefrontal, parietal cortex and basal ganglia. Thus, this work exemplifies how linking of two levels of computational modeling offers the means to relate behavioral and neural observation to further our understanding of the mechanisms of structure learning in humans.
III-53. Inactivation of rat frontal and parietal cortex during a temporal integration of evidence task

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Decision-making has been modeled as a process of noisy integration of evidence over time until reaching a decision-commitment bound. To study the neural mechanisms underlying this process in rats, we used a task previously developed in our lab, the Poisson Clicks Accumulation task. Rats were trained to hear two independent Poisson click trains, one from a left speaker and one from a right speaker, and at the end of the stimulus, orient towards the one that played the greater number of clicks. Trial difficulty was controlled by varying the difference between the two Poisson rates. Stimulus durations were controlled by the experimenter. Perfect decisions require counting clicks over time, to compare the two totals. We investigated the role of two cortical areas, the posterior parietal cortex (PPC) and the frontal orienting fields (FOF), both of which have been implicated in sensory integration and planning orienting movements. We reversibly inactivated these areas by applying the GABAA receptor agonist muscimol while animals performed the task. Unilateral inactivation of the FOF profoundly impaired orienting contralateral to the infusion site, in a manner independent of trial difficulty. Unilateral inactivation of the PPC also impaired contralateral orienting, but to a lesser degree than FOF inactivation, and the degree of impairment was greater for hard than for easy trials. These data show that both areas are involved in performance of the task, and are consistent with a feedforward model in which graded evidence integration is performed in the PPC while final motor planning is performed in the FOF. We are further testing and developing this model by performing bilateral inactivations, as well as simultaneous inactivation of both the FOF and the PPC. Our data will provide constraints on the functional relationship and differential roles of the PPC and the FOF in perceptual decision-making.

III-54. Coherent network-wide fluctuations of neural activity in the PFC during behavioral uncertainty

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When unpredictable changes occur in the environment, decisions based on outdated information can become unprofitable or even hazardous. During these moments of uncertainty, animals tend to rapidly adjust their behavioral strategy from one based on experience (exploitation) to one that re-evaluates the possible options (exploration) (Quilodran et al. 2008, Daw et al. 2006). It has been proposed that widespread ‘resets’ in information processing might be beneficial during such behavioral transitions, with new information taking precedence over older, potentially outdated representations (Gers et al. 2000, Bouret & Sara 2005, Dayan & Yu 2006, Nassar et al. 2010). Such resets would be most likely to occur in areas of the brain that monitor task performance and guide future decisions, such as the prefrontal cortex. It has been demonstrated that single-cell activity in the prefrontal cortex can fluctuate rapidly as shifts occur in the state of the environment (Durstewitz et al. 2010, Hayden et al. 2011) or the internal state of the animal (Critchley et al. 2001, Huettel et al. 2005, Kepecs et al. 2010, Kiani & Shadlen 2009) but neurophysiological evidence for widespread, coordinated dynamics indicative of possible network resets is missing. We present evidence that in the rodent anterior cingulate cortex, an area known to be important for flexible behavior, fluctuations in activity often happen in unison across a large fraction of simultaneously recorded
cells. Using a novel task that provides a behavioral readout for periods of uncertainty, we find that such network fluctuations preferentially occur as animals transition from a strategy of exploitation to less-certain or exploratory behavior. These observations suggest that neurons in the prefrontal cortex can modulate task representations in unison when it is computationally advantageous.

III-55. Dissecting the Contributions of Sensory and Category Uncertainty in Perceptual Decision-Making

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It is commonly assumed that perceptual decisions are difficult because of sensory uncertainty, i.e. noise in the stimulus or stimulus transduction process. This phenomenon can be captured using drift-diffusion models (DDMs). However, some decisions are difficult even given unlimited sampling time, and it is less clear what limits performance in such cases. Here, we studied this problem using a combination of psychophysical experiments in rats and computational modeling. We compared two closely related tasks: odor mixture categorization and odor detection. We found that, as problem difficulty was increased in the two tasks, for the same change in accuracy, the change in reaction time was substantially larger in detection than in categorization (41% vs. 13% increase). This result suggested that difficulty in odor categorization results from non-sensory variability that is not subject to integration. We first explored this hypothesis by introducing a new source of noise in a standard DDM: in addition to the normal fast, within-trial noise (i.e. within the diffusion process) we added a slow, trial-to-trial noise, represented by drift rate variance. We found that fast noise plays the main role in odor detectability, while slow noise is critical for categorization. We hypothesized that one source of drift rate variance may be on-going changes in stimulus-response mapping caused by reinforcement learning. To test this idea, we used an extended delta-rule learning model (DRM) to examine the effect of trial-by-trial updating on performance accuracy. We show that the relative importance of different noise sources in this model shifts depending on the task. While detection performance is limited by stimulus noise, categorization performance is dominated by noise in weight updating. These results provide an account of which sources of noise will dominate in different kinds of perceptual decisions and explain why different tasks will show different susceptibility to integration.

III-56. Optimal integration of multisensory event streams in rats and humans

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In recent years, studies have examined how subjects combine evidence across time within a single sensory modality, and separately how subjects combine static evidence across modalities. We trained rats and humans on a decision task that invited subjects to accumulate sensory information both over time and across modalities. Subjects were trained to discriminate lower- from higher-rate stimuli that consisted of auditory or visual pulses.
separated by short or long inter-event intervals (IEIs). Varying the proportion of long relative to short IEIs in a 1-second trial allowed us to generate audiovisual stimuli over a range of difficulties. Here, we report three novel findings: (1) We now extend to rats our previous finding that when the reliabilities (i.e., signal-to-noise ratios) of auditory and visual stimuli are adjusted to obtain equal performance for both modalities, subjects’ performance on multisensory trials is near the level predicted by statistically optimal (i.e., maximum likelihood) cue combination; (2) When we systematically vary the relative reliability of auditory and visual stimuli and present trials in which the two modalities provide conflicting information, human subjects optimally weight sensory information accumulated over time in proportion to the relative reliabilities of each event stream; and (3) By modeling decision-making using an evidence accumulation framework, subjects’ multisensory performance can be predicted by fitting weights to either modality based upon subjects’ single sensory performance. Together, these findings indicate that subjects are sensitive to cue reliability when integrating sensory information across time and modalities. Furthermore, the ability to optimally integrate information across time and sensory modalities appears to be a general feature of the mammalian brain that is not restricted to a particular species.

III-57. Dissociable Influences of D1 and D2-mediated Frontal Eye Field Activity on Target Selection

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Recent evidence suggests an important role for dopamine in decision making. We explored this possibility by testing the influence of D1 and D2 receptor-mediated activity in the frontal eye field (FEF) on the selection of visual targets for saccades. We manipulated dopaminergic activity in the FEF of monkeys performing a saccadic double-target, choice task. By systematically altering the onset asynchrony of the two targets (TOA) we could measure the bias in target selection toward either target. Next, we manipulated D1R and D2R-mediated FEF activity with local, intracortical infusions of the D1R antagonist SCH and the D2R agonist quinpirole. The effects of these manipulations were fourfold. First, we found that the D1R and D2R manipulations both increased the selection of Tin targets, and to a similar extent; however, neither manipulation changed the sensitivity of the monkeys’ choices to the TOA. Second, the amount of shift in the psychometric function with the D1R manipulation was inversely correlated with the baseline sensitivity to TOA. The D2R manipulation showed an opposite trend. Third, we found that the probability of repeated choices on consecutive trials was reduced by the D1R manipulation, yet it was enhanced by the D2R manipulation. Fourth, we examined how selection on a given trial depended on the choice and TOA on the previous trial and found that relative to the D2R manipulation, the D1R manipulation decreased the preference for targets that appeared first on the previous trial if the target was previously selected. Our results reveal stark differences between the influence of D1R and D2R-mediated activity on target selection and how it is adjusted based on past outcomes.

III-58. Joint probability of independent events is consistent with weighted combination of log probabilities

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In standard probability theory, the conjunctive probability of two independent events is the product of the proba-
Human performance in a conjunction task could be predicted by standard probability distortion models. During each trial, a subject chose between a single roulette wheel and a pair of roulette wheels, displayed on a computer screen. After the subject has chosen, all three wheels were spun simultaneously at different speeds. If the subject chose the single wheel, he won a monetary reward precisely when the wheel stopped with the needle pointing at the orange zone. If the subject chose the pair, he won only when both wheels in the pair stopped in orange zones. Design: There were 12 conditions, each corresponding to a choice of probabilities $P_1$, $P_2$. Across trials, the size of the orange zone of the single wheel was varied by an adaptive procedure to measure the Pe of the single wheel that the subject considered equivalent to each $P_1$, $P_2$ pair. Ten naïve subjects completed the experiment. For all subjects, we rejected the standard model $Pe=P_1P_2$. We considered several distortion functions $w(p)$ and found that subjects treated the larger in each $P_1$, $P_2$ pair differently from the smaller. We relabeled $P_1$, $P_2$ as $P_+$, $P_-$ where $P_+$ is greater or equal to $P_-$, and discovered that data fitted the model: $log(Pe)=(alpha)log(P_+)+(beta)log(P_-)$ with weights alpha and beta. We rejected the hypothesis $alpha=beta$ for each subject individually: subjects assigned different weights to larger and smaller probabilities. The model is readily interpreted neurally but the differential weighting of large and small probabilities is not previously reported.

**III-59. Representation of multiple stimuli in the macaque middle face patch.**

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Face recognition is mediated by specialized brain regions. In the macaque temporal lobe, face selective neurons are aggregated into face selective regions that are tightly interconnected. This functional organization allows for a systematic study of the neural mechanisms of face recognition. Neurons within the face patches have large receptive fields. Consequently, in a natural scene, these large receptive fields will frequently encompass multiple objects. Thus a question central to theories of object recognition arises: how is the representation of a face affected by the presence of other objects? Two psychophysical phenomena lead to opposite predictions: faces have been observed to pop out amongst non-face objects. Thus face representation may not be compromised in the presence of clutter. On the other hand, the “crowding effect”, a reduced discriminability of an object in clutter, affects faces, too. Thus face representations may be impaired by clutter. To address this question, we conducted electrophysiological recordings in the middle face patch MF. For each neuron, the most preferred face stimulus was selected and the receptive field was mapped. Then, the preferred face was presented together with distractor stimuli in several configurations: distractor category (face or non-face), number and spacing were varied to study if and how this would change the representations of the preferred face. We found that a small proportion of neurons in MF showed responses that were largely uncompromised by the presence of distractors, thus potentially providing a correlate of the face pop-out effect. However, the large majority of MF neurons reduced their response to the preferred face stimulus with increasing number of distractors and with increased proximity of distractors. Effects were stronger for face distracters than object distracters. These three findings are consistent with the psychophysics of crowding and might thus represent a neurophysiological correlate of crowding.

**III-60. A neural network model of the primate visuo-motor system**

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Most models of the primate visual system fail to incorporate eye movements. Humans make about three saccades per second, and this is an integral part of how the visual system works. Although binary well separated categoriza-
tion judgments can be made in a single fixation (e.g., Fabre-Thorpe, Ghislaine, & Thorpe, 1998), harder decisions involving many categories may demand many fixations (e.g., Holm, Eriksson, & Andersson, 2008). Moreover, learning new categories requires multiple fixations (e.g., Henderson, Williams, & Falk, 2005). A few simple neural network models of the primate visuo-motor system exist (e.g., Lo & Wang, 2006), but they cannot be used with actual images, limiting their utility for making predictions about cognitive processes and behavior when viewing images.

We created a recurrent probabilistic neural network model that uses a simulated retina to sample its environment. To learn visual features for our retina model, we use independent component analysis (ICA) to acquire sparse V1-like filters from natural images. These features are non-linearly weighted by how rarely they occur in the natural environment (Shan & Cottrell, 2008), with rarer features given greater weight. This is followed by spatial pooling of the visual features over multiple localized regions of the current visual field.

The features acquired in a fixation are compared to compressed object memories using a probabilistic neural network (PNN; Specht, 1990). Unlike the standard PNN model, we have incorporated a form of competitive divisive normalization, which significantly improves performance. A recurrent multinomial logit network is used to make the final prediction, with the recurrent connections used to retain information from fixations across time. A saccade controller determines where to look next.

To assess our model's predictive capability, we evaluate it on computer vision datasets from several domains, including objects (Caltech-256), flowers (Oxford Flowers-102), and birds (CUB-200). Our preliminary results exhibit performance comparable to recent methods in computer vision. We are currently investigating improvements to the model, including training the saccade controller using reinforcement learning, and we intend to compare the model's predictions with human eye movements.

III-61. Short-Term Plasticity Optimizes Synaptic Information Transmission

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Short-term plasticity (STP) is widely believed to play important roles in information processing. This major function of STP has recently been challenged, however, by several computational studies indicating that transmission of information by dynamic synapses is broadband, i.e. frequency independent. Here we developed an analytical approach to quantify time- and rate-dependent synaptic information transfer during arbitrary spike trains using a realistic model of synaptic dynamics in excitatory hippocampal synapses. We found that STP indeed increases information transfer in a wide range of input rates, which corresponds well to the naturally occurring spike frequencies at these synapses. This increased information transfer is observed both during Poisson-distributed spike trains with a constant rate as well as during naturalistic spike trains recorded in hippocampal place cells in actively exploring rodents. Interestingly, we found that presence of STP in low-release probability excitatory synapses leads to optimization of information transfer specifically for short high-frequency bursts, which are indeed commonly observed in many excitatory hippocampal neurons. In contrast, more reliable high-release probability synapses that express dominant short-term depression are predicted not to have optimal information transmission for spike bursts, but rather for single spikes. This prediction is verified in inhibitory hippocampal synapses that exhibit dominant depression and fits well with the observation that inhibitory hippocampal interneurons do not commonly fire spike bursts. We conclude that STP indeed contributes significantly to information transfer and may serve to maximize information transfer for specific firing patterns of the corresponding neurons.
III-62. Stochastic short term depression imposes a frequency-dependent filter on information transmission

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Synapses act as information gates in neuronal networks. Hence, a comprehensive description of neural coding requires an understanding of synaptic dynamics and their impact on signal and information transfer. Recent theoretical studies show that a widely used deterministic model of synapses exhibiting short term synaptic depression (STD) transmits information encoded at all frequencies equally. However, vesicle release and uptake dynamics responsible for STD are known to be stochastic. We use stochastic calculus techniques to derive a compact description of the filtering properties of a deterministic and a detailed stochastic model of STD. Taking synaptic stochasticity into account imposes a frequency dependent filter on information transfer. Using parameters consistent with experimental studies of cortical synapses, we show that a population of presynaptic cortical neurons with stochastically depressing synapses transmits information optimally at frequencies higher than 10Hz. In addition, the postsynaptic conductance induced by these neurons exhibits a power spectrum that is peaked within the beta frequency band even when the presynaptic inputs have a white or broadband power spectrum. Our results have important and general implications for coding in neuronal networks.

III-63. Optimizing online learning capacity in a biologically-inspired memory structure

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To function in a complex world, our brains must somehow stream our experiences into memory in real time as they occur. An “online” memory of this kind must form durable memory traces based on a single exposure to each incoming pattern, while preserving older experiences as long as possible. Using computer models and mathematical analysis, we studied the online learning capabilities of a biologically inspired memory, with the goal to understand how the properties of neurons, dendrites, and synapses interact to determine online storage capacity. A key assumption was that dendrites, rather than whole neurons, are the main representational units used to encode learned information. In previous work (Wu and Mel, 2009), we focused on synaptic plasticity rules and their impact on online storage capacity. In this work, given that learning operates at the level of dendrites, we set out to identify the factors that determine optimal dendrite “size” (i.e. the number of synapses on each dendrite). We show that capacity is maximized when dendrites are of “medium” size, that is, when each dendrite contains a few hundred synapses rather than 10’s or 1000’s of synapses. We show why both short and long dendrites suffer from severe capacity costs: long dendrites lead to wasteful over-representation, while short dendrites suffer from greater susceptibility to noise as well as a previously undescribed problem of “dendrite availability”. We also studied the relationship between optimal dendrite size and properties of the input patterns: increased pattern density and noise both reduced capacity, but denser patterns push for shorter dendrites while noisier patterns push for longer dendrites. Our results can help clarify which morphological changes that occur with aging, stress, neurological disorders, and mental retardation are likely to be most detrimental to online recognition memory, and why. Funding provided by NSF CRCNS grant no. IIS-0613583.
III-64. Prediction error signals in ACC are scaled according to rational adjustments of learning

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Behavior often depends on the ability to update beliefs according to new information. Optimization of this process often requires preferential use of information occurring after likely environmental changes. Here we examined the role of the anterior cingulate cortex (ACC) in this process by measuring behavior in two rhesus monkeys and single-unit activity in one monkey performing a ten-alternative choice task that included both static fluctuations (noise) and abrupt changes (change-points) in the identity of the rewarded target. Subject performance was consistent with an optimal-inference model: they tended to switch choice targets more frequently after errors, most notably for errors that were unlikely to result from noise or that occurred shortly after a change-point. Moreover, they exhibited information-seeking behaviors during the feedback interval that revealed the extent to which feedback would be incorporated into future choices. In particular, the fraction of time searching through target locations and the latency to begin this search process (measured after the rewarded target was revealed visually but before juice delivery) reflected rational adjustments of influence, as reflected in subsequent choice behavior. We recorded the activity of 47 single units in the ACC of one monkey performing the task. Consistent with previous studies, we found units that responded preferentially to either reward or error feedback. To examine how adjustments of influence might affect these responses, we computed an error-response metric specific to each neuron that reflected how much the neural response on a given trial resembled that of the average error trial. This metric was larger for error trials and smaller for correct trials in which the monkey displayed more extreme information-seeking behaviors (e.g. shorter latency to search or larger search fraction), suggesting that ACC neurons scale reward prediction error signals according to the extent that those signals should be incorporated into future beliefs.

III-65. A high-performance, robust brain-machine interface without retraining

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Brain-machine interfaces (BMIs) translate neural activity into control signals for prosthetic systems, such as computer cursors and robotic arms. BMIs strive to offer people with movement disabilities greater interaction with the world. Despite compelling proof-of-concept demonstrations, barriers to translation still remain (Ryu & Shenoy, Neurosurgical Focus, 2009). One such barrier is that without frequent decoder retraining and recalibration by expert technicians, system performance becomes unusably poor over time. We present here a robust BMI that does not require any retraining and can sustain high performance for up to a month. We trained a rhesus macaque (Monkey J) implanted with two 96-channel electrode arrays in M1/PMd to perform a 2D free-paced randomized grid keyboard selection task for a juice reward. A BMI decoder was built using spike threshold crossings (-4.5xRMS) utilizing the ReFIT-KF algorithm (Gilja et al., COSYNE, 2010), which then continuously controlled the on-screen cursor. The decoder's parameters were held constant for thirty consecutive days, and the monkey performed the BMI grid task for thousands of trials each day until satiated. Monkey J successfully achieved high performance, regularly sustaining 3-4 bits per second across hours. Over the course of the month long experiment, nearly 900 kilobits in total were communicated, comparable to the content in a short novel. These results were enabled by the inherent stability of spike threshold crossings across weeks and the high performance offered
by the ReFIT-KF algorithm. These findings demonstrate that without retraining or intervention, a high performing BMI can transmit significant, meaningful information over several weeks. As frequent retraining is untenable for long-term patient use, such robust performance is crucial for the successful translation of BMIs and should further increase their clinical viability.

III-66. Cerebellar granule cell activity during behavior: dynamics in light of the adaptive filter model

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For nearly forty years, the Marr-Albus-Ito model of the cerebellum has provided the dominant framework for understanding cerebellar control of motor learning. In this model and subsequent adaptive-filter models of cerebellar function, the cerebellar granule layer is proposed to separate sensory inputs into a large array of basis functions that can be reinforced by error signals during learning. However, direct tests of the role of granule cells during behavior have been prohibitive due to the miniscule size and close packing of these cells. Here, we overcome this barrier by using two-photon calcium imaging to monitor the activity of GFP-positive granule neurons during the horizontal optokinetic reflex. To quantify the activity of granule cells, the fluorescence time series of each neuron is averaged across optokinetic stimulus cycles and regressed against a linear model incorporating velocity, position, and calcium-buffering components. In total, we examined 44 GFP-positive granule neurons whose activity was well described by model fits \( r^2 \geq 0.7 \). 89% carried signals that were dominated by stimulus velocity (velocity/position: 3.3±2.9). Of these neurons, a third exhibited activity that increased with stimulus velocity irrespective of direction, while the remainder exhibited direction-selective responses. Analysis of the relative sensitivity to leftward vs. rightward directed stimulation as a function of pair-wise distance suggests neighboring granule neurons encode similar information, and direction-specific velocity neurons tend to be more caudal in the zebrafish cerebellum. To describe the dynamics of granule activity, drifts following cessation of stimuli were quantified by fitting the average fluorescence response to a model of the underlying firing rate. The approximated time constants from this study ranged from 5 msec to 6 sec, consistent with the heterogeneity of dynamics hypothesized to be a feature of the granule layer in the adaptive-filter model (n=17 direction-selective neurons).

III-67. Action valuation in multi-effector decision-making

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Models of action selection posit parietal and motor areas containing effector-specific maps that represent values of available motor actions. Effector-specific maps, however, cannot represent the values of actions that involve multiple effectors acting in coordination, so the mechanisms by which values of conjoint movements are represented and used to guide effectors are unknown. One possibility is that effector-nonspecific valuation areas step in to guide action selection via connectivity with motor or motor-planning regions. We investigated multieffector decision-making using model-based fMRI, exploiting the contralateral organization of hand control to contrast choices executed with coordinated bimanual versus unimanual hand movements. Subjects (N=20) performed a
four-armed bandit task, alternating between selecting choices by either pressing one of two buttons on the left or right hand or, in the bimanual condition, simultaneously pressing one button with each hand. Using trial-by-trial estimates of action values derived from a reinforcement learning model fit to choice behavior, we found at choice time activity correlating with chosen option value in the bilateral mid-cingulate cortex, extending into the supplementary motor area (p<0.01, cluster-size corrected). Examining the cingulate ROI for effector specificity, we found a hand-by-hemisphere interaction indicating stronger value representation for actions by the contralateral hand (p<0.05). The medial PFC also showed value-related activity (p<0.05, small-volume cluster-size corrected), but unlike the mid-cingulate, no effector specificity (p>0.5). Testing whether the mPFC influenced motor areas more during coordinated movements, we performed a psycho-physiological interaction seeking areas showing higher mPFC connectivity during bimanual than right or left-handed actions, and identified an area of mid-cingulate cortex (p<0.05, small-volume peak corrected). These results suggest that while effector-specific value maps may drive simpler actions, complex actions involving coordination between effectors implicate top-down control from frontal areas where value is represented over options rather than effector-specific actions.

III-68. Internal metabolic state determines human motor control strategies
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Computational motor control successfully explains human motor coordination in a principled manner by deriving optimal control policies from minimization of cost functions (e.g. Todorov&Jordan,2002). However, little is known about the neuronal implementation of the controllers and their cost functions (Scott et al.,2004). Two possible cost functions stand out as being biologically principled: signal-dependent motor noise (Harris&Wolpert,1998) and metabolic cost. These are evolutionarily sensible: maximizing biological fitness by minimizing task-relevant variability and energetic expenditure. We previously found that the optimal activations of the 6 muscles involved in planar reaching movements differ whether noise or energy consumption are considered, due to their muscle fibre compositions and size (Taylor&Faisal, 2011). Here we test the hypothesis that the internal metabolic state produces trade-offs between energy and noise in motor planning. Ten right handed participants performed center-out reaching tasks under two different metabolic regimes. Participants acted in a low-friction haptic-virtual-reality setup executing reaches to 8 targets 15 cm away (N=800 trajectories). Each subject was tested during the morning on two separate days: 5 subjects fasted from 8pm the evening before the first session and followed their normal nutritional routine for the second session (vice versa for the other subjects, counterbalancing potential learning effects). We find that reaching trajectories changed significantly between high and low metabolic regimes. Controls independent of the metabolic state or velocity profiles showed no significant change. We reconstructed a weighted energy-noise cost function using inverse nonlinear optimal control by fitting the trajectories for both metabolic regimes. As predicted, the energy cost function was consistently dominant in the low metabolic regime. Our findings suggest a change in motor coordination strategies based on internal metabolic state. To our best knowledge this is the first demonstration that internal metabolic state affects neuronal computation strategies.

III-69. A stable, long-range motor pattern in the songbird brain
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Modern neuroscience has uncovered a wide range of machinery for cellular plasticity that underlies the neuron's ability to change. In parallel, an ancient question has become more pressing: how are memories maintained for a lifetime given the plasticity of single neurons? In vertebrate motor learning, a related question is whether
learned neural sequences are stable. A musician may activate muscles in a fast sequence with a remarkable stereotypy that persists for years. However, little is known about the stability of the underlying neural patterns over these time scales. Do the same microscopic (i.e. single cell) or mesoscopic (i.e. multi-unit) patterns of neural activity persist across time at central levels of motor control, or does the brain drift among “degenerate” states that produce the same effective muscle output? The answer to this question will vary depending on the system considered. We continuously monitored neural activity from the cortical pre-motor nucleus HVC in awake-behaving zebra finches both in bilateral and unilateral implants, using minimally invasive carbon-fiber electrodes. The recordings reveal a detailed pattern of neural activity stereotyped on a 5 ms time scale that is synchronous between the two hemispheres. These stereotyped patterns persist for months. Furthermore, after nerve damage to the syrinx (vocal organ), we find evidence that central motor patterns remain unchanged for a minimum of one month, despite disruption of the acoustic form of the song. We conclude that the neural correlates of song include both precise single unit firing and stable mesoscopic, patterns. Here we describe progress towards understanding the relationship between these two levels of motor representation.

**III-70. Are grid-cell responses very low-dimensional?**

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What mechanisms could underlie grid cell activity in rodents is the subject of debate, with different models positing starkly divergent neural architectures and dynamics. One model class is based on the conversion of cellular temporal oscillations into spatially periodic responses, while another is based on strong lateral network connectivity that leads to low-dimensional periodic pattern formation in the neural population, which is then converted into periodic spatial responses. Despite these differences, current analyses of experimental data have not ruled out either model. We examine spikes from multiple simultaneously recorded grid cells, with the aim of elucidating the dynamics underlying grid cell activity. We demonstrate evidence of a 2-dimensional continuous attractor in the response of grid cells to animal location. The responses of grid cells with similar spatial period are identical (up to measurement uncertainty), differing from each other along only 2 dimensions of their response, through translations of their preferred spatial phases. The relationships between grid cell responses — specifically, their relative spatial phases — remain absolutely stable (up to measurement error) over time, even if the responses themselves do not. Relative phases remain absolutely stable when the grids are significantly deformed by anisotropic stretching in response to a rapid resizing of the environment, as well as when the grids uniformly expand in novel environments. The stabilization of relative phase during dramatic changes in single-cell responses cannot be ascribed to input from external cues or from the hippocampus, because we ascertain that relative phases are stable even when these inputs are not. The findings together provide unequivocal support for the hypothesis that the brain computes using low-dimensional continuous attractors. Finally, we assess the implications for proposed mechanisms of grid cell activity, and show that the data specifically support the pattern-forming recurrent network models.
III-71. Scale-dependence of orientation statistics in natural scenes

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Vision evolved to extract information from natural scenes replete with contour and texture elements. However, contour-integration and texture-processing have traditionally been treated as separate phenomena. Here we show that these two universal types of information can be extracted from natural scenes, simply by varying the ratio of two scales of processing: (a) edge-extraction and (b) orientation sampling. We analyzed pair-wise statistics of more than 10^6 image patches taken from natural scenes (van Hateren & van der Schaaf, 1998). We found that contour-like smooth continuation patterns emerge when orientations are sampled at a spatial scale that matches the scale at which the edges were extracted. In contrast, texture-like iso-orientation patterns emerge when orientations are sampled at coarser scales. The relevant scales of processing accord with the dimensions of receptive fields observed in the geniculostriate pathway (Alonso et al., 2001), suggesting that natural selection has endowed the visual system with the capacity to extract contour and texture from natural scenes via a single mechanism. This leads to testable hypotheses about the relationship between the receptive field sizes of visual cortical neurons and the degree to which they exhibit distinct patterns of anatomical connectivity.

III-72. Population decoding algorithms for change detection and discrimination

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Over what timescales is neuronal activity informative about both constant, and changing, stimuli? To explore this issue, we recorded from MT and MST neurons in two macaque monkeys performing a task requiring the detection and discrimination of unpredictable speed changes. Previously, we have reported that on timescales of tens of milliseconds, the activity of single neurons encodes the sign of the speed change and can be decoded to predict the animals' behavioral judgments. Here, we examine maximum-likelihood methods of decoding the responses of a population of neurons in order to predict the precise timing of speed changes. We focus on how the raw spike trains of each neuron in the population might be filtered, or pre-processed, to facilitate change detection and discrimination on behaviorally relevant timescales. For example, spike trains might be low pass filtered, or converted to an instantaneous spiking rate, or spike-rate derivative. The most successful decoder, which had similar performance to the animal's behavior, was designed to simultaneously categorize recent speed variations using two independent change detectors: faster versus not faster, and slower versus not slower. The decoder was unable to extract information about veridical speed throughout a trial, and only performed at levels better than chance if the raw spiking times were pre-processed to give a spike rate derivative. This derivative was formed by taking the difference between spike trains convolved with exponential functions with short and long time constants. The optimal prefilter time constants were 20 ms and 120 ms, with these times critically affecting discrimination performance, the rate of false detections (noise susceptibility), and the timing of when changes were correctly detected. Our results demonstrate that stimulus changes, but not veridical stimulus properties, can be reliably decoded from short (<100 ms) timescales of activity across a population of MT/MST neurons.
III-73. Adaptive Gating of Information Flow to Cortex

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A ubiquitous property of sensory pathways is that they continuously adapt to changes in the properties of the sensory input. Adaptation is not simply fatigue or attenuation of neural activity, but instead can fundamentally change the features to which the sensory pathway are sensitive and thus changes what the pathway encodes. We have recently shown that through multi-site, multi-electrode recording in the thalamocortical circuit that adaptation through ongoing tactile stimulation in the rat vibrissa system induces a fundamental change in what behaviorally relevant features the cortex encodes: from detection of a tactile contact to discrimination between different speeds of the tactile/whisker input (Wang et al., Nat. Neurosci., 2010), and does so through the desynchronization of the projecting thalamic inputs. To what extent this observation is general and whether it manifests perceptually has not been well studied. Using ideal observer analysis of voltage sensitive dye imaging of cortical activation, we now show that adaptation produces an enhanced spatial acuity at the level of S1 at the expense of a degraded detectability of tactile inputs. Further investigation reveals a frequency dependent enhancement of discriminability that reflects a tradeoff involving restricting spatial extent of cortical activation while maintaining good signal-to-noise. A separate behavioral paradigm reveals that these phenomena manifest perceptually. Adaptation degrades detectability of vibrissa contact, consistent with our observations that detectability is increased in the absence of self-motion. Discriminability, on the other hand, is enhanced by adaptation, improving spatial acuity as measured in a go/no-go discrimination task using deflections of individual whiskers. Taken together, we believe these results provide a compelling framework for switching between coding of different kinds of information when behaviorally relevant.

III-74. Detection of weak sensory signals by molecular dynamic transformations of interspike interval sequence

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Spike-activated molecular-dynamical processes are common in neural systems, including both neural adaptation and synaptic transmission. These molecular processes form a dynamical representation of the fine-timescale pattern of interspike interval sequences that can be used to decode sensory information encoded in afferent spike trains. A recent theoretical discovery by our lab has shown how negatively correlated interspike interval (ISI) sequences common to sensory afferents paradoxically induce molecular activation patterns in the intracellular adaptation processes that are statistically independent from spike to spike (Nesse et al., 2010). Here, in our most recent work, we put the above theoretical discovery to the test by stimulating sensory afferents of the weakly electric fish Apteronotus with weak stimulus intensities near known behavioral detection thresholds. Negatively correlated afferent ISI sequences recorded from afferents in vivo were then transformed into a spike-activated model-based molecular-dynamic code. This dynamical code was discovered to exhibit the independence property predicted in Nesse et al. (2010). Moreover, the molecular-dynamic code was able to achieve the known behavioral detection levels for the fish, and exhibited distinct advantages over more conventional firing-rate-based models of
sensory detection.

Because independent and identically distributed (IID) data allow for computationally efficient statistical analyses, our discovery that a putative intracellular adaptation process underlying in vivo spike trains may exhibit such an IID property from correlated ISI sequences suggests a plausible theory into how neurons, sensory afferents in particular, may efficiently represent sensory information in their internal molecular states and transmit information onward through synaptic dynamics.

III-75. Multisensory integration in the rat - behavioral benefits and neural correlates in parietal cortex

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The complementary information provided by our different senses greatly enhances our ability to perceive and interact with the environment. Rodent models offer the possibility to study the underlying neural mechanisms and computations using a range of methodologies. However, suitable behavioral tasks and cortical candidate areas for the rodent remain to be elucidated. We developed a two-response forced-choice stimulus detection paradigm where rats (Long Evans) were required to detect lateralized audio-visual targets presented in either uni- or multisensory configuration. After training, the animals exhibit faster reaction times and enhanced detection rates in congruent multisensory conditions and this multisensory response enhancement is strongest for weak unisensory stimuli. These multisensory behavioral benefits mirror those described for similar tasks in humans. To localize target areas of multisensory convergence, we performed high-resolution intrinsic imaging experiments in urethane anaesthetized rats. We found a consistent overlap of responses to visual, somatosensory and auditory stimuli in an elongated region which had the cytoarchitectonic properties of an association area (sparse layer IV) and which overlapped well with parietal region PtA, as defined by the Paxinos atlas. Laminar recordings confirmed the functional convergence of unisensory inputs both in current source densities and multi-unit activity. These recordings also demonstrated multisensory response interactions and the magnitude and sign of response enhancement / suppression was dependent on temporal stimulus order. Control experiments confirmed the specificity of the multisensory response patterns to the parietal region (in comparison to visual cortex). We developed a rodent model of behavioral multisensory integration similar to paradigms known from human psychophysics and we show the presence of key criteria of multisensory processing in a region in the parietal cortex. Ongoing experiments directly study the neural underpinnings of behavioral benefits for enhanced stimulus detection in the behaving animal.

III-76. Multisensory calibration with external feedback is contingent on cue-reliability

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Accurate perception of a dynamic environment requires continuous multisensory calibration. When present, external feedback is particularly beneficial for multisensory calibration, since it serves as a “teacher”. However, the principles of interaction between external feedback and relative cue-reliability, and their combined influence on multisensory calibration are currently unknown. Five monkeys were trained to perform a heading discrimination task in which they were required to report whether self-motion was to the right/left of straight ahead. Stimuli comprised either visual (optic-flow), vestibular (motion platform) or combined (visual-vestibular) passive motion. For each experimental session, coherence of the visual stimulus was manipulated such that either visual or vestibular reliability was relatively higher. A systematic heading discrepancy was introduced between the visual and vestibular stimuli and external feedback was congruent with either the more-reliable or less-reliable cue. When external feedback was aligned with the more-reliable cue, the less-reliable cue shifted towards the feedback, and the more-reliable cue (which was already accurate) did not shift. However, when external feedback was aligned with the less-reliable cue, a surprising form of calibration occurred: cues were yoked and shifted together in the same direction. Hence, whilst the more-reliable cue shifted to become more accurate, the less-reliable cue simultaneously shifted away from the external feedback, becoming less accurate. We propose two different mechanisms of multisensory calibration: 1) cue-specific (local) calibration, and 2) reference-frame (global) calibration. When the more-reliable cue is incongruent with external feedback, the entire reference frame (zero) is considered to be inaccurate. Hence cues are yoked and shift in conjunction. When the more-reliable cue is congruent with external feedback, the global reference frame is considered accurate and the less-reliable cue is calibrated individually/locally. These results suggest that the Bayesian-optimal cue-combination is used to assess global accuracy.

III-77. Odors sum linearly in time in the rat olfactory bulb

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Odor stimuli in the natural environment travel away from the source via turbulent carriers. At the sensory end, signals from multiple sources thus arrive intermittently, varying both in intensity and duration. Computational models show that significant information about the location of the source can be extracted from the temporal dynamics of this signal (Hopfield 1991, Murlis et al. 1992). However, it is unknown how these time-varying odor inputs are represented in the rodent olfactory system. To this end, we studied responses of mitral/tufted cells (output neurons of the olfactory bulb) to precisely controlled, time-varying patterns of 9 odors and their binary combinations, in anesthetized, tracheotomized rats using extracellular single unit recordings. We find that individual cells (n=76) modulate their firing rate in synchrony with the odor waveform, in a surprisingly linear manner. The response to an arbitrary odor waveform is accurately predicted by convolving the estimated “impulse response” (response to a brief stimulus) with the odor waveform (measured by a photo-ionization detector). Excitatory and/or inhibitory responses evoked by two odors sum arithmetically upon concurrent presentation of the two odor patterns (n=36). Further, we compared responses across free breathing and tracheotomized conditions. We show that the phasic, respiration-tuned responses of cells (n=12) are explained by simply convolving the “odor impulse” with the respiration waveform (measured by a pressure sensor). This summation of responses at the mitral cell level is striking and unexpected, given the complex wiring diagram of the bulb and the richness of inhibitory interactions. Contrasting observations in the insect olfactory system (Broome et al. 2005, Geffen et al. 2009) suggest that different mechanisms of information processing may be used in the mammalian and invertebrate olfactory systems. This may be attributed to inherent differences in circuit architecture and/or odor sampling behavior.
III-78. Noradrenergic control of long-term cortical synaptic receptive field plasticity

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Neuronal networks of the cerebral cortex are plastic, maintaining the capacity to reorganize throughout life. While neuromodulator release is required for cortical plasticity, it is uncertain how subcortical neuromodulatory systems, such as the noradrenergic locus coeruleus, interact with and refine cortical circuits. Here we determine the dynamics of cortical receptive field plasticity at the synaptic and spiking levels using in vivo whole-cell recording. Adult rats were anesthetized, stimulation electrodes implanted in the locus coeruleus, and a craniotomy performed over the primary auditory cortex (AI). After mapping AI, whole-cell and cell-attached recordings were made from AI neurons, and pure tones of varying frequencies and intensities were presented to the animal to characterize tonal receptive fields. Pairing sensory stimulation (pure tones) with locus coeruleus activation (to release noradrenalin) dramatically changed the tuning properties of AI neurons. In most cases, pairing induced large increases of tone-evoked synaptic and spiking responses. While in some cases, these changes could be stimulus-specific, in most other cases the magnitude of tone-evoked responses was greatly increased across all stimuli, de-tuning AI receptive fields. This degradation of frequency tuning was observed immediately after pairing, before emergence of new stimulus preference occurred 30+ minutes later. Unlike the effects of nucleus basalis pairing (Froemke et al., Nature 2007), locus coeruleus pairing seemed to enhance tone-evoked excitation and inhibition together. Multiple cell recordings from the same animal for hours after pairing suggested that these changes in AI tuning could persist for 10+ hours. We hypothesize that such changes to cortical tuning curves have important implications for the detection and/or discrimination of different sensory inputs. In particular, increased excitability could make it easier for a network or animal to detect the presence of a stimulus, in exchange for reduced discriminative abilities.

III-79. Real-time changes in single neurons during auditory object recognition learning

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Adult sensory systems do not maintain a static representation of the external world, but instead modify their response properties as a function of experience and real time behavioral demands. In the auditory system, studies of adult experience-dependent plasticity have been generally limited to responses to artificial stimuli, and usually the effects of experience are compared between animals or at discrete time points. Here, we expand the scope of these studies by investigating changes in single neurons as animals performed ethologically realistic behaviors mediated by natural stimuli. We recorded extracellular action potentials from single neurons in an avian analogue of auditory cortex while European starlings learned to classify sets of novel auditory objects (segments of starling song) in a vocal recognition task. Across the population, recently learned objects elicited stronger neural responses on average than did objects for which birds had extensive training. In addition to these longer-timescale population effects, by maintaining single unit isolation while new objects were introduced (sessions lasted between one and four hours) we were able to observe changes in the same neuron over the course of learning. Here, responses to newly learned objects changed more than responses to over-trained reference objects presented in the same behavioral session. On average, neuronal firing rates for all stimuli decreased during a learning session, and this decrease was largest for the set of newly learned objects. Our results support a model in which natural experience leads to progressive sparsening of representations in the auditory system. We propose that initial learning is tied to a period of over-representation of multiple stimulus features followed by
selective retention (or suppression) of responses tied to subsets of features that are more (or less) informative for natural behaviors.

III-80. Encoding of motion onset by retinal ganglion cells

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Sudden onset of motion signals changes in the environment that can have great behavioral significance. Recent psychophysics studies have shown that motion onset is especially effective at capturing attention and is more salient than smooth motion itself (Abrams and Christ, Psych. Sci. 2003, Christ and Abrams, Vision 2008). Here, we investigated whether the retina contributes to the recognition of sudden motion onset. Using multi-electrode array recordings, we found that a subset of salamander ganglion cells, fast OFF cells, respond significantly more strongly a bar’s motion onset than to smooth motion. This was despite aligning our stimuli such that once motion onset began, the smooth motion and motion onset stimuli were exactly identical. Using stimuli with motion of only one edge as well as pharmacology, we found that the OFF pathway dominates the response to motion onset. We explored different computational models of the motion onset effect. The classical receptive field model (LN model) failed to predict a larger response to motion onset than to smooth motion, sometimes predicting no response or even an inhibitory response. Next we considered a model with rectified bipolar subunits within the ganglion cell’s receptive field, as for a Y-type cell (Victor and Shapely, J. Gen. Phys. 1979). Although the subunit model correctly predicted excitation for motion onset at all locations on the receptive field center, this model was unable to produce a stronger response to motion onset than to smooth motion, sometimes predicting no response or even an inhibitory response. Finally, we added contrast gain control mechanisms (Berry, Nature 1999) to both the bipolar and ganglion cells of the subunit model. This Adaptive Cascade model could reproduce all of the qualitative features of the ganglion cell responses to smooth motion, motion onset, and bar appearance over a range of contrasts and speeds.

III-81. A wide-field neuron enhances visual contrast sensitivity in the fly

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Peripheral visual circuits are highly adapted for efficient coding of image contrast. However, the mechanisms by which retinal circuits maintain contrast sensitivity across diverse luminance conditions are not well understood. We identified a new class of wide-field feedback neurons in the fly lamina that contributes to visual contrast sensitivity. Silencing these lamina wide-field (lawf2) neurons decreased the fly’s ability to detect low contrast visual motion stimuli. Using targeted whole-cell patch-clamp recordings in vivo, we found that lawf2 neurons encode low frequency luminance fluctuations, and that their excitability increases when the fly is flying. Application of the neuromodulator octopamine mimicked flight conditions, suggesting that octopamine release during flight alters
the coding properties of lawf2 neurons. These data suggest that lawf2 neurons enhance contrast sensitivity by providing feedback to the lamina, and that the quality of this feedback depends on the behavioral state of the fly. Behavioral state modulation of peripheral visual circuits may compensate for the shift in image statistics experienced during self-motion.

**III-82. Perceptual relevance of neurally-inspired natural image models evaluated via contour discrimination**

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A key hypothesis in sensory system neuroscience is the idea that sensory representations are formed by the statistical regularities in sensory signals and thus acquire knowledge about the outside world (Barlow, 1997). In vision, several probabilistic models of local natural image regularities have been proposed which intriguingly replicate neural response properties (Attick & Redlich 1992, Bell & Sejnowski 1997, Schwartz & Simoncelli 2001, Karklin & Lewicki 2009). To evaluate how such models relate to functional vision, we previously measured their perceptual relevance using a discrimination task pitting model image patches against true natural image patches (Gerhard, Wichmann, Bethge, 2011). Observers were remarkably sensitive to the regularities of grayscale patches, even for patches as small as 3x3 pixels. Performance relied greatly on how well the models captured luminance features like contrast fluctuation. Here we focus on how well the models capture local contour information in natural images. In a two-alternative forced choice task, observers viewed two tightly-tiled textures of binary image patches, one comprised of natural image samples, the other of model patches. The task was to select the natural image samples. We measured discrimination performance at patch sizes from 3x3 to 8x8 pixels for 8 models spanning the range from low likelihood to one among the current best in terms of likelihood. We compared human performance to an ideal observer with perfect knowledge of the natural distribution for patch sizes at which we could empirically estimate the distribution and tested potential texture cues with a classification analysis. While human performance suggested suboptimal strategies were used to discriminate contour statistics relative to grayscale statistics, observers were well above chance with binary 4x4 pixel patches and larger, meaning that neuronally-inspired models do not yet capture enough of the contour regularities in natural images that functional human vision can detect, even in very small natural image patches.

**III-83. Continuous Time Infomax Models of Oculomotor Control**

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Recent models of oculomotor control have been successful at describing saccade velocity profiles using optimal control principles. Some models postulate that the eyes minimize the expected deviation from a target end point (Minimum Variance models). Other models postulate that eye movements minimize the time required to reach the target point (Minimum Duration models). These models have a common assumption that the goal of oculomotor control is to reach target points. Not surprisingly, much of the empirical data used in these models is based on tasks in which the explicit goal is for the eyes to move to predefined target end points. However, such tasks seldom occur in daily life. Instead, the eyes typically play a supportive role, providing other actuators (e.g., the hands) with the information they need to efficiently achieve their goals (e.g., grasp objects). Here, we use a rapid-pointing task to study eye movement in different conditions where the eyes serve either a supporting role (where the reward...
depends on the hand endpoint) or an executive role (where the reward depends on the fixation endpoint). Our results suggest that Minimum-variance and Minimum-duration models cannot account for key properties of the eye movements observed in our data. To address this issue, we present an alternative class of models (Infomax models) in which the eyes move to maximize the information needed to achieve goals. The approach relies on a novel algorithm (PIC2) developed at our laboratory to find approximate solutions to continuous time partially observable stochastic optimal control problems. We present our progress solving Infomax Control problems and show how they explain the complex saccadic movements observed in our experiments.

III-84. Dissection of cortical microcircuits by single-neuron stimulation in vivo

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A fundamental process underlying all brain functions is the propagation of spiking activity in networks of excitatory and inhibitory neurons. To understand how spikes are routed in cortical circuits in vivo, we used two-photon calcium imaging to monitor ensemble activity and targeted patching to stimulate a single neuron in layer 2/3 of mouse visual cortex. Here we show that burst spiking of a single pyramidal neuron can drive spiking activity in both excitatory and inhibitory neurons nearby. For inhibitory neurons, ~30% of the somatostatin interneurons can be reliably activated by a burst of ≥5 spikes. In contrast, parvalbumin interneurons showed no detectable responses to single-neuron stimulation, but their spiking is highly correlated with the local network activity. Our results demonstrate the feasibility of mapping functional connectivity at cellular resolution in vivo and reveal distinct operations of two major inhibitory circuits, one detecting single-neuron spike bursts and the other reflecting distributed network activity.

III-85. Selectivity of neurons in area MT to complex motion features

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Visual perception is constructed from successive computations on visual stimuli by a hierarchy of cortical areas. The computations in a given area can be estimated from spiking responses to stimuli that are sufficiently complex to activate the appropriate combinations of excitatory and inhibitory afferents to a given cell. In this work we have used a naturalistic, continuously varying optic flow stimulus to explore the responses of neurons in the middle temporal area (MT) of the alert macaque monkey. These responses were interpreted using a hierarchical model that took into account the nonlinear properties of the V1 neurons that likely provide direct and indirect inputs to MT. In this rich stimulus context, the putative inputs to MT are rectified, resulting in each being only excitatory or inhibitory. While the resulting model’s excitation is generally spatially localized, its inhibition is direction-tuned, and appears to be distinct from typical surround suppression and normalization, which are largely not direction selective and can be separately identified. Roughly half of MT neurons have motion opponency, although inhibition usually did not spatially overlap with excitation completely. In other MT neurons, inhibition has similar direction tuning to excitation, or is orthogonal, and is usually not spatially co-localized. Taking these additional features into account lead to better cross-validated performance in every case. The observed direction-tuned inhibition can
result in selectivity to more complex features of natural motion stimuli, such as motion boundaries and particular types of optic flow. In total, considering MT neurons in a complex stimulus context reveals a diverse set of computations likely relevant for perception in the behaving animal.

III-86. Compressive spatial summation: a characteristic of extrastriate computation

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The visual system pools image features across increasingly large extents of the visual field, from small receptive fields in the retina to very large receptive fields in anterior temporal cortex. We studied pooling using simple contrast patterns and fMRI measurements of human visual cortex. Subjects viewed a systematic set of contrast patterns occupying different portions of the visual field. In extrastriate cortex the response to a contrast pattern is substantially less than the sum of the responses to individual parts of the pattern presented on separate trials. We modeled this sub-additivity using a compressive power-law nonlinearity that is applied after linear summation of contrast across the visual field. We find that the amount of compression grows larger in anterior extrastriate maps and cannot be explained by increased receptive-field size. An important prediction of the compressive spatial summation (CSS) model is that the more compressive the nonlinearity, the more tolerant the response is to changes in the position and size of a viewed object. In independent datasets we measured responses to objects varying in position and size and confirmed that the CSS model accurately predicts the size and position tolerance exhibited by extrastriate cortex. The CSS model is largely consistent with HMAX, an influential object recognition model that also seeks to explain position and size tolerance. A key feature of HMAX is hierarchy, and we demonstrate through simulations that the CSS model can be re-expressed in hierarchical form. Furthermore, there is an interesting parallel between compressive spatial summation and the observation that responses in visual cortex saturate with increasing stimulus contrast. We are currently developing a general model that quantitatively accounts for both the spatial and contrast nonlinearities. This model can be viewed as a specific instantiation of the canonical cortical circuit model proposed by Kouh and Poggio (2008).

III-87. Direction selectivity within large receptive fields in a three-layer visual cortex

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Cortical direction selectivity emerges de novo in neurons of mammalian primary visual cortex (V1), i.e. direction selectivity is not derived from retinal responses; instead it emerges from computations made in V1. Since its discovery some 50 years ago, elucidating the cellular mechanisms subserving directional selectivity in V1 continues to be an important area of intense research. Cortical direction computation starts in V1 and becomes increasingly complex in higher cortical areas (V2, MT, MST); directional information is combined to produce neurons sensitive to complex motions, such as rotation, expansion, and contraction. The increased complexity is paralleled by an increase in the size of the receptive fields. In MSTd, the receptive fields can cover most of the visual field. We investigate direction selectivity in the three-layer cortex of turtle, which serves as a model to study the circuit mechanisms of distributed processing in primary visual cortex (V1). In contrast to the six-layered structure of
mammalian neocortex, the turtle V1 contains a monolayer of pyramidal neurons, which receive sensory inputs from Lateral Geniculate Nucleus (LGN) axons, excitatory inputs from other pyramidal neurons, and inhibition from GABAergic interneurons. We characterize visual response properties of neurons in turtle visual cortex in an eye-attached whole-brain preparation. We use single electrode extracellular recordings to record both isolated units and multiunit activity while presenting visual stimuli to a hemisected eye. We find that individual neurons respond to motion (small black spot, 2 deg diameter) in distinct regions spanning the entire visual field and to all directions (8 tested). These regions show strong directional tuning, but this tuning varies greatly from region to region. In summary, a subset of units in turtle visual cortex display large nonconcentric receptive fields, reminiscent of higher cortical areas in mammals, with mixed direction-sensitive structure when probed with moving spots.

**III-88. Trial-to-trial variability of MT neurons reveals the nature of their engagement in a motion discrimi**

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We have recently shown that neurons in the motion processing area MT and in the prefrontal cortex (PFC) are actively engaged in all stages of a task in which monkeys compare two directions of motion, S1 and S2, separated by a delay. Neurons in both areas showed direction selective responses, were active during the delay, and showed comparison effects that correlated with perceptual decision. In the PFC, this engagement was also reflected in trial-to-trial variability of spiking activity (Fano Factor, FF) of putative pyramidal neurons, a likely source of top-down influences on MT. The FF tracked consecutive task components and was predictive of the upcoming neuronal events, dropping with stimulus onset, decreasing prior to salient events and flagging neurons participating in sensory comparisons. Here, we report that the variability of spiking activity in MT during the same behavioral task followed a similar pattern. The FF showed a typical rapid drop with stimulus onset, which was present even for stimuli that appeared remotely from the neuron’s receptive field, revealing that even in the absence of overt activity MT neurons were engaged in discrimination. The FF also reflected stimulus identity during several trial components, even in the absence of selective spiking activity. With time in delay, variability of many neurons increased, the pattern opposite to that observed in PFC, suggesting possible interactions between the two areas in preparation for comparison stimulus. Towards the end of the delay, variability of neurons with future comparison effects decreased, an effect analogous but delayed relative to that observed in the PFC, suggesting its possible top-down influences on MT neurons participating in sensory comparisons. Our results demonstrate that the FF provides a sensitive measure of the engagement of MT neurons in motion discrimination tasks and suggest the nature of their interactions with PFC during such tasks.

**III-89. Reductions of correlated firing arise from attention-dependent depolarization in a spiking network**

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Recent studies have found that spatial attention reduces the variability of neuronal responses (Mitchell et al, 2007; Cohen et al, 2009; Mitchell et al, 2009). Variability arises both from sources specific to individual neurons, such as the tendency to fire in bursts, and to sources shared across populations, such as spreading waves of activity. In particular, reductions in variability shared across neurons can lead to large improvements in sensory read-out and behavioral performance (Cohen et al, 2009). These correlated fluctuations in firing rate occur both in awake and anaesthetized animals, and have slow dynamics from tens to hundreds of milliseconds (Bair et al, 2001; Smith
and Kohn, 2008; Mitchell et al, 2009). While previous models of attention have done well at explaining the mean firing rate modulation observed with spatial attention (Lee and Maunsell, 2009; Reynolds and Heeger, 2009), they are ill suited to explain realistic sources of firing variability. Here we introduce a model cortical circuit that exhibits realistic noise fluctuations, and show that depolarization introduced by attentional feedback reduces the magnitude of these fluctuations. The network is implemented as a two-dimensional grid of spiking units that are recurrently connected with shift-invariant center-surround antagonism. The spiking units use a reduced parameter neuron model introduced by Izhikevich (2003) that captures a wide range of behaviors including burst firing. In the absence of input, the network exhibits spontaneous activity that is marked by brief bursts and slower correlated waves of activity resembling those seen in array recordings (Smith and Kohn, 2008). Attentional feedback is modeled as a weak excitatory input that depolarizes units at the attended location. This modest depolarization leads to the increases in firing rate typically observed with attention, and also reduces correlated fluctuations, leading to improved sensory coding.

**III-90. Dynamics of correlated variability in evoked and spontaneous responses of V4 neurons**

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The activity of nearby cortical neurons is correlated on both short and long time scales, measured by both synchronous spiking and correlated trial-to-trial response variability (rsc). In primary visual cortex (V1), the spatial and temporal characteristics of this correlation are well characterized, although the structure and magnitude of neuronal correlation has recently been a topic of debate (Cohen & Kohn, 2011, Nat Neurosci). In area V1, a number of studies have found that correlation is larger in spontaneous activity than in evoked responses. In extrastriate cortex, however, this issue has not been studied in detail. In area V4, a pair of recent studies demonstrated that correlation is modulated by attentional state (Cohen & Maunsell, 2009, Nat Neurosci; Mitchell et al, 2009, Neuron). However, the detailed spatial and temporal structure of correlation in V4 is unknown. We recorded from populations of neurons in area V4 of two awake, behaving macaque monkeys performing a fixation task. We used a chronically implanted 100-electrode “Utah” array, which consists of a 10 x 10 grid with 400 micron spacing between adjacent electrodes (each 1.0 mm in length). We presented drifting sinusoidal gratings stimuli that varied in orientation but were fixed in spatial frequency, temporal frequency, and size, and recorded all waveforms that exceeded a threshold for offline sorting. We analyzed data from pairs of well-isolated single units recorded on different electrodes. We found that the spatial and temporal structure of neuron correlation in V4 was strikingly similar to that we observed in V1, although roughly one-third the magnitude. In a fixation task with no stimulus (spontaneous activity), the value of rsc was roughly two-fold higher than in the evoked condition. These results indicate that the structure of neuronal correlation is likely governed by features of neuronal circuits that are shared across visual cortex.
III-91. The mesencephalic locomotor region modulates layer-specific activity in V1 independent of locomotion

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Behavioral state is known to affect sensory processing. Our previous study in awake, head-fixed mice demonstrated a cell-type specific effect of locomotion on visual processing—when an animal began to walk or run, responses to visual stimuli in layer 2/3 of mouse V1 more than doubled, accompanied by an increased LFP in the gamma range, but spontaneous activity and tuning did not change. Our more recent experiments have also revealed that locomotion has different effects on layer 5, primarily resulting in increased baseline firing. However, the source of the signal modulating cortical responsiveness is unknown. In order to investigate the neural circuits underlying this change with behavioral state, we measured the effect of optogenetic stimulation of glutamatergic neurons in the mesencephalic locomotor region (MLR), which includes the cholinergic pedunculo-pontine tegmental nucleus (PPTg) and has both descending projections to motor pathways and ascending projections to the thalamus and other cholinergic areas. Above a certain threshold, stimulation of the MLR in awake, head-fixed mice induced walking and then running, as stimulation frequency increased, along with the same effects in visual cortex as we previously described for spontaneous locomotion. Surprisingly, stimulation at a frequency below the threshold for locomotion also induced similar effects on visual responses, suggesting that the MLR acts directly to modulate cortical responsiveness via a pathway that is independent of locomotion. Furthermore, the effects of MLR stimulation varied by cortical layer exactly as did those of spontaneous locomotion, with superficial layers showing increased gain while deep layers showed primarily changes in spontaneous firing rates. These findings demonstrate that a midbrain cholinergic region can control both ongoing and evoked activity in primary visual cortex in a layer-specific manner.

III-92. Probing motion perception with spatiotemporal reverse correlation

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We used psychophysical reverse correlation to gain insight into the mechanisms of motion processing in human observers. Specifically, we investigated whether short-range stroboscopic (apparent) motion processing can be explained by canonical motion processing mechanisms, or by a template-matching mechanism tuned to the apparent-motion stimulus. Observers were asked to detect a 3-step apparent-motion bar embedded in spatiotemporal Gaussian white noise. Half the trials contained the signal bar plus noise; the other half contained only noise. The ideal observer for this task consists of a linear template matched to the expected space-time locations of the white bar, followed by a threshold. To probe the mechanisms underlying human performance, we estimated a linear kernel for each observer, using the maximum a posterior estimate under a generalized linear observer model (GLM), with a prior encouraging smooth and sparse filters. (These estimates were significantly better at predicting responses on held-out data than filters fit by “classical” psychophysical reverse correlation). We also estimated a second-order psychophysical kernel that operated on the squared stimulus pixels. The resulting model is insensitive to the sign of stimulus contrast (white vs. black), and exhibits an accelerating nonlinear response to absolute
pixel luminance. Surprisingly, this model provided a more accurate description of observers’ data than the linear
GLM. The observed quadratic kernels exhibited compelling direction selectivity (i.e., spatiotemporal orientation)
and integrated smoothly across a larger range of space-time locations than the actual apparent motion signal.
These results reveal that motion-energy processes (Adelson & Bergen, 1985) are likely involved in the detection
of apparent motion, and also demonstrate the feasibility of extending reverse correlation methods for analyzing
nonlinear mechanisms of motion processing in both psychophysics and physiology.

III-93. Dissociating interneuron types in frontal cortex by firing variability and
spike timing specificity

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To understand how a neocortical microcircuit transforms input to output it is pivotal to elucidate the functional
roles of specific neuron types within the circuit. Previous studies have critically implicated three separable types
of inhibition participating in this processing: (1) Modulatory, inhibitory control that sets the tone for excitability and
responsiveness to input (relying on dendritic targeting ‘CR’ interneurons); (2) localized dis-inhibition of pyrami-
dal cells (through I-to-I interactions relying on ‘CB’ interneurons); and (3) widespread (per-somatic) gain control
of pyramidal cell firing through fast spiking ‘PV’ interneurons. The implicated interneuron types are particularly
well characterized anatomically within prefrontal cortex, but their electrophysiological identification is largely lack-
ing. We set out to identify subtypes of putative interneurons in extracellular recordings within lateral and medial
prefrontal cortex of two awake macaques. We identified 92 putative interneurons - among 420 recorded highly
isolated neurons (21%) - by their unique narrow width of action potentials. We used a measure of ‘Local vari-
ability’ (Lv) to index spiking activity as regular (Lv<1), irregular Poisson-like (Lv∼1), or bursty (Lv>1). Conjointly
with average firing rate, Lv reliably separated three interneuron types that were validated by higher dimensional
k-means clustering. Analysis of spike timing to the local field potential revealed that 90% of neurons showed a
highly consistent phase of firing with varying spectral/timing specificity: Large subsets of putative interneurons
synchronized significantly (and more likely than broad spiking neurons) at 12±1 Hz, or at 30±5 Hz, with a subset
displaying clock-like, regular spike train patterns. Smaller subsets (~15% of interneurons) displayed either highly
specific preferences to synchronize at either 8±1 Hz, at 21±3 Hz, or had two apparent peaks at 5±1 Hz and
45±5 Hz. These findings distinguish putative interneurons, which may correspond to separable anatomical cell
classes and/or relate to separable inhibitory regimes within the cortical microcircuit.

III-94. Transient motion analysis reveals differential motion dynamics of synap-
tic vesicle populations

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Central synapses typically contain a very small number of release-competent vesicles and synaptic function thus
critically depends on an efficient vesicle recycling program to sustain and control neurotransmitter release. De-
spite several decades of research on synaptic function, the basic vesicle cycling mechanisms remain poorly understood due to the relative inaccessibility of central synapses to conventional recording techniques. Although recent advances in high-resolution microscopy techniques has permitted tracking of single synaptic vesicles, the quantitative analysis of vesicle motion has been limited by the transient nature of the motion, challenges of detecting rapid changes in vesicle behavior in noisy tracks and wide range of timescales at which the motion occur, spanning from tens of milliseconds to tens of seconds. Here we describe a novel transient motion analysis approach that allows identification of rapid changes in vesicle motion and detection of directed motion episodes within vesicle trajectories. The analysis is based on directional correlations between subsequent steps over short time scales and estimation of vesicle mobility based on the traveled distance. The time resolution obtained by this analysis offers a major improvement over the currently available mean square displacement analysis. We demonstrate the application of our motion analysis approach to synaptic vesicle motion during their recycling process in hippocampal neurons. We compared the dynamic properties of vesicles endocytosed via different pathways, specifically, via fast, slow and spontaneous forms of retrieval and found that vesicles recycled by different retrieval pathways exhibit differential motion dynamics, particularly the ability to engage in cytoskeleton-based directed motion. We further combine single-vesicle imaging and pharmacological tools to link specific forms of vesicle motion to identified cellular mechanisms, particularly motor-based cytoskeletal transport.

**III-95. A mobile imaging system to monitor the cortex in behaving rodents**

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Optical monitoring of electrical activity has benefits over traditional electrode-based methods of recording neuronal activity. Electrode arrays have limited, inaccurate spatial resolution and penetrating electrodes damage brain tissue. Most optical studies of neuronal activity in rodents are performed on anesthetized and/or head-fixed animals. These restraints have dramatic effects on all levels of neuronal function, and behavioral performance is substantially altered. There are published head-mountable optical systems for rodents, but they are limited in temporal resolution (< 100 Hz) and signal to noise ratio (< 40 dB). Therefore, a novel imaging system is necessary to measure rapid cortical activity over a wide cortical area using optical probes in behaving rodents.

We have designed a miniature microscope system that measures neuronal activity over a wide area (> 2 mm) with high temporal (> 400 Hz) and spatial resolution. This system is light enough to be mounted on a head of a rodent, and generates little to no heat. Thus, only our system is suitable to record neuronal activity over a wide area at high speeds in freely moving animals with high spatial and temporal resolution without damaging the brain. We present the challenges encountered when designing such a system, in both the imaging circuitry and microscope. We also present what types of dynamic information can be collected by the system to allow scientists to observe neuronal activity in the cortex generated by voltage-sensitive optical probes.

**III-96. Relating patterns of EEG activity to natural scene categories**

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Our ability to categorize natural scenes is essential for visual tasks such as navigation or the recognition of objects in their natural environment. Using functional magnetic resonance imaging (fMRI), we have previously shown that spatial patterns of brain activation in the parahippocampus and throughout visual cortex are specific for natural scene categories (Walther et al. 2009, 2011). Several recent fMRI studies have attempted to illuminate the complex interactions between scene and object perception (e.g., MacEvoy and Epstein 2011; Kim and Biederman 2011). However, its low temporal resolution limits the use of fMRI for exploring the dynamics of these interactions. Electroencephalography (EEG) with its high temporal resolution may serve as a complementary technique. Here we present a first step in this direction. We recorded EEG signals from scalp electrodes while participants viewed images of natural scenes from six categories (beaches, city streets, forests, highways, mountains, offices). We then employed partial least-squares analysis in order to identify activity patterns in the (time x frequency x scalp location) space that significantly contributed to the discrimination between these six categories. Significance of activity patterns was assessed using permutation analysis. We found a cluster of significant activity around eight parietal and occipital electrodes in the theta band (4-8 Hz) between 172-192 ms after stimulus onset. In remarkable consistency with our prior fMRI results, the activity patterns that we found were more pronounced when participants viewed line drawings than when they viewed color photographs of the same types of scenes. Our results illustrate the potential of using EEG for measuring precise time information of neural activity related to natural scene categories. This opens the door to further exploration of scene categorization and its interactions with object perception.

III-97. An open-source system for combining multi-electrode recording with closed-loop feedback

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The advent of optogenetic techniques has driven neuroscience toward experiments which attempt to demonstrate the causal role of particular cell populations in behavior. Such experiments often involve detecting network-level phenomena in awake, behaving animals and intelligently perturbing neural circuits in real time. To this end, we have developed a low-cost, open-source hardware and software solution for multi-electrode recordings in rodents. Our system is not merely a more affordable version of existing commercial products; it goes beyond anything currently available by prioritizing low-latency control of feedback devices in response to neural events. Data acquisition is performed via hardware built around head-mounted amplifier chips (Intan Technology). Digitization is coordinated by an FPGA with custom firmware, which uses USB for high-speed data transfer to and from standard computers. Our open-source hardware and software will allow users to customize all aspects of the data-processing pathway, but we also aim to provide an out-of-the-box solution down the road. Our graphical interface, written in C++, not only enables the user to view and record spikes and LFP, but also provides event-triggered visualizations and an intuitive system for configuring signal processing chains on the fly. We hope this system will become a flexible platform for developing online feedback algorithms that can be easily shared, eliminating the need for redundancy between labs. The software, firmware, and hardware designs are freely available, and we invite and encourage all members of the community to make use of them and contribute to their development. One of our first applications will be online detection of sharp-wave–ripple complexes in the hippocampus. Through stimulating electrodes in the ventral hippocampal commissure, this approach enables us to selectively disrupt ripples with millisecond latency in order to test their role in memory processes.
III-98. Fast methods for mapping the full dendritic synaptic connectivity

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A detailed understanding of the organization of local neural circuits requires determining not just which neurons are interconnected, but also the exact location and strength of synaptic interactions in the dendritic tree. To achieve this goal, we can combine the ability to stimulate individual presynaptic neurons with simultaneous imaging of postsynaptic neurons at subcellular resolution. In this work we develop fast methods to filter voltage measurements and determine the location and strength of synaptic dendritic connections. For this we use two types of data: 1) anatomical measurements of the postsynaptic neuron’s shape and dendritic arborization, used to build a dynamical model of the cell, 2) voltage-sensitive fluorescence observations at subcellular resolution, sampled at several controlled, changing locations, which provide the key dynamical variable, the spatiotemporal subthreshold voltage. The relatively low signal-to-noise ratio of imaging methods implies that optimal filtering methods are needed in order to fully exploit the measurements. We formulated the problem in a Bayesian state-space framework. Under reasonable assumptions, determining the synaptic weights becomes a convex optimization problem. To enforce sparseness, we used an $l_1$ prior with coefficient $\lambda$. For Gaussian noise, we get a quadratic program with a solution path piecewise-linear in $\lambda$, which we obtain by adapting known $l_1$ methods to exploit the structure of this problem and enforce the excitatory/inhibitory nature of the synapses. A major computational challenge comes from the large number of compartments ($N \sim 10^4$) of the dendritic arbor and the $O(N^3)$ computational cost of the exact solution. Using previously developed fast approximation ideas, we find the location and strength of the synapses in $O(Nk + k^3)$ time, where $k$, the total number of synapses, is determined using model selection techniques and generally $k \ll N$. We illustrate our results on simulated measurements in toy and real neurons for different sampling techniques.

III-99. Casting light on the interplay between perception and decision making in active sensing

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Active sensing couples motor responses to sensory processing in feedback loops that can be challenging to investigate experimentally. We combined high-resolution behavioral analysis, electrophysiology, modeling, and optogenetics to dissect the sensorimotor integration underlying chemotaxis in Drosophila melanogaster larvae. When exposed to a static odor gradient, larvae orient through a series of runs punctuated by turns. The timing and directionality of turning events proceed from active sampling. Runs are elongated when the larva moves up-gradient. Turns are facilitated when the larva moves down-gradient. Prior to turning, the local gradient is resolved through side-to-side head movements (casts). Larvae genetically engineered to retain function in a single olfactory sensory neuron (OSN) demonstrate the same basic orientation strategy. We reconstructed the sensory dynamics that the larva experiences at key decision points during unconstrained chemotaxis. Using electrophysiology,
we recorded the responses of the single functional OSN to a replay of the stimulus time course. Two types of signals were characterized in detail: rapid fluctuations in concentration associated with sub-second head casts, and slower odor ramps detected during runs lasting several seconds. These neural responses constitute the mechanistic basis for a model underlying the spatiotemporal integration of dynamical olfactory inputs and its conversion into orientation responses. Our sensorimotor model was tested in a closed-loop tracker where the behavioral state of a larva is classified in real-time. Using light sequences to trigger controlled activity patterns in a single-functional OSN expressing channelrhodopsin, we can induce predictable changes in behavior in response to well-defined sensory inputs delivered during specific behavioral states. We exploited this closed-loop paradigm to establish a relationship between the neural integration of sensory evidence and the probability of implementing stereotyped motor responses (timing of runs, directionality of turns). Overall, our work clarifies how a simple brain uses active sensing and decision making to direct behavior.
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