

September 12-14 Munich, Germany







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Bernstein Conference 2012

September 12 - 14, 2012

Klinikum rechts der Isar, Technische Universität München Hörsaalgebäude, Einsteinstraße, 81675 München

Program and Abstracts

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Neurovision Film Contest Organization

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PhD Symposium Organization

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Funding

The conference is mainly funded by the German Federal Ministry of Education and Research (BMBF) via the Bernstein Center for Computational Neuroscience Munich, which is part of the National Bernstein Network Computational Neuroscience. In addition, various companies, non-profit organizations and research centers support the conference through donations, either as exhibitors or by supporting specific sessions or prizes that are awarded during the conference.

Participating Institutions

Bernstein Center for Computional Neuroscience Munich CoTeSys – Cognition for Technical Systems Deutsches Schwindelzentrum – IFB German Neuroinformatics Node Ludwig-Maximilians-Universität München Munich Center for Neurosciences – Brain & Mind National Bernstein Network Computational Neuroscience Parmenides Center for the Study of Thinking Technische Universität München

Exhibitors

ALPHA-OMEGA digital GmbH BrainLinks-BrainTools International Neuroinformatics Coordinating Facility Multi Channel Systems MCS GmbH npi electronic GmbH Springer-Verlag GmbH Technologit GbR

Program

Wednesday, September 12

In conjunction with Neuroinformatics 2012 (September 10 to September 12), see also http://neuroinformatics2012.org/program

- 12:30 Lunch
- 14:00 Opening and Presentation of the Bernstein and Braitenberg Awards 2012
- 14:00 Opening (Local Organizers)
- 14:05 Welcome TUM and LMU
- 14:15 Welcome BMBF and Presentation of the Bernstein Award 2012
- 14:25 Lecture by the Bernstein Award Winner
- 15:05 Presentation of the Braitenberg Award 2012
- 15:10 Lecture by the Braitenberg Award Winner: Moshe Abeles (Ramat Gan) Binding activities among cortical areas
- 15:50 Coffee
- 16:20 Neural Circuits: Structure and Signals [G-Node Session]
- 16:20 Moritz Helmstaedter (MPI Neurobiology Munich): Structural Neurobiology: Tools for the dense reconstruction of neuronal circuits
- 17:00 Gaute Einevoll (Aas): How local is the local field potential?
- 19:00 Joint INCF/BCCN Conference Dinner Location: Münchner Künstlerhaus am Lenbachplatz

Program

Thursday, September 13

09:00	Coding
09:00	Alexandre Pouget (Geneva): Probabilistic approaches to coding and computation
09:40	Greg DeAngelis (Rochester): Neural computations underlying optimal multisensory cue integration
10:20	Coffee
10:50	Vision [MCN Session]
10:50	Matteo Carandini (UCL London): Wakefulness, locomotion, and navigation: A look from visual cortex
11:30	Gabriel Kreiman (Harvard): Temporal constraints for visual object recognition: neurophysiological, behavioural and computational approaches
12:10	Tomaso Poggio (MIT): A sketch of a theory of visual cortex
12:50	Lunch
14:00	Network Dynamics and Representations
14:00	Kwabena Boahen (Stanford): Neurogrid: Simulating a million neurons and a billion synapses in real-time with sixteen neuromorphic chips
14:40	Shaul Druckmann (Janelia Farm): Overcomplete representations and neuronal circuit dynamics
15:20	Coffee
15:50	Learning [CoTeSys Session]
15:50	Bernhard Schölkopf (MPI Tübingen): Statistical and causal learning
16:30	Máté Lengyel (Cambridge): Internal models: of ferret and men
17:10	Jochen Triesch (FIAS Frankfurt): Self-organization and unsupervised learning in recurrent networks
18:00 - 21:00	Poster Session I

20:00 Öffentlicher Vortrag – Onur Güntürkün (Bochum): Intelligenz ohne Hirnrinde? Wie Vögel einen eigenen Weg zu kognitiven Höchstleistungen gefunden haben

Friday, September 14

09:00	Decision
09:00	Ranulfo Romo (UNAM Mexico City): Conversion of sensory signals into perceptual decisions
09:40	Zach Mainen (Lisbon): Origins and use of uncertainty in decision-making
10:20	Coffee
10:50	Disease and Cure [IFB Session]
10:50	Quentin Huys: Explaining away emotions. How simple decision dysfunctions might perturb complex cognitions
11:30	Stefan Leutgeb (UCSD): Spatial processing and map learning in the entorhino-hippocampal circuit
12:10	Bernhard Seeber (Nottingham / TU Munich): Improving hearing with cochlear implants in reverberant spaces
12:50	Lunch
14:00	Cognition [Parmenides Session]
14:00	Onur Güntürkün (Bochum): The Left and the Right Side of Visual Discriminations
14:40	Andreas Nieder (Tübingen): Biological precursors of the number sense
15:20	Coffee
15:50	Prizes and Global Perspectives
15:50	Bernstein Movie Award 2012
16:05	Brains-for-Brains Award
16:20	Maryann Martone (UCSD): Big data from small data: A deep survey of neuroscience data via the Neuroscience Information Framework
17:00	Christof Koch (Allen Institute, Seattle): Project MindScope
17:40	Outlook (Organizers of Bernstein Conferences 2012 and 2013)
18:00	Poster Session II

Conference Information

Venue

Scientific sessions will take place at the Klinikum rechts der Isar, the university hospital of the Technische Universität München. Note that the entrance to the lecture hall building is from Einsteinstrasse, near the underground stop "Max-Weber-Platz", not at the main entrance of the hospital at Ismaninger Strasse.

On-Site Contact

event lab. GmbH Catharina Herrmann Phone: +49 (0) 177 2673158

Presentation Instructions

Oral presentations

Oral presentations will be given in Lecture Hall A. Talks are 40 min including discussion. A computer (Windows 7) with common software (MS Powerpoint, Adobe Reader) will be provided for upload of talks, preferably as pdf file, ahead of time via USB. Alternatively, speakers can use their own personal laptop. In any case, please get in touch with session chair and technical staff at least 30 minutes before your session.

Poster presentations

Poster Sessions will be held on Thursday and Friday, 18:00 - 21:00. Poster boards are numbered according to the abstract numbers as they appear in this program book (preceded by T for the poster session on Thursday and by F for the poster session on Friday, respectively). Materials for putting up the posters will be provided. Posters can be mounted starting 8:30h on the day of the respective poster session. Please dismount your poster after the poster session.

Abstracts

Abstracts of this conference, including high-resolution versions of figures, have been published online in *Frontiers* and can be accessed at http://www.frontiersin.org/events/Bernstein_Conference_2012/1661

For the iPhone an abstract viewer application is available. Visit http://www.bccn2012.de/app for more information.



Wireless Internet

During conference hours, an open conference network as well as eduroam will be available.

Food

Coffee and cookies will be provided during coffee breaks free of charge. During poster sessions, finger food will be provided free of charge. Lunch will be served at the venue for those who have purchased lunch vouchers. Note that unfortunately it is not possible to obtain lunch vouchers on site. Several restaurants as well as cafes and bakeries can be found within short walking distance near the venue.



Joint INCF / Bernstein Conference Dinner

The Joint Dinner will provide ample opportunities to meet with participants from both the INCF Congress and the Bernstein Conference at the "Münchner Künstlerhaus". For more than a century, the 'Munich House of Artists' has served as a gorgeous meeting place for artists and the general society alike. Participants will learn more about this historical gem over a welcome drink, after which a buffet-style dinner and beverages will be served. We look forward to a nice late-summer evening and stimulating discussions.

The Joint INCF/Bernstein Conference Dinner will take place at the "Münchner Künstlerhaus am Lenbachplatz", Wednesday, Sep 12, starting 19:00. It will take ca. 15 min from the conference venue to get there. Directions: From 'Max-Weber-Platz' take U4 (direction 'Westendstrasse') or U5 (direction 'Laimer Platz') to 'Karlsplatz (Stachus)'. Follow the signs 'Ausgang Lenbachplatz/ Karlsplatz/ Maxburgstraße'. Outside, turn right and cross the street. You will find the Künstlerhaus at the corner of Maxburgstrasse and Herzog-Max-Strasse. Take the entrance on Maxburgstrasse into the courtyard of the Künstlerhaus.



Special Events

Bernstein Award for Computational Neuroscience 2012

Since 2006, the Federal Ministry of Education and Research (Bundesministerium für Bildung und Forschung, BMBF) annually confers the Bernstein Award for Computational Neuroscience to one excellent junior researcher with outstanding ideas for new research projects. The award is endowed with up to 1.25 million \in over the course of five years and is one of the most highly remunerated research awards for young scientists in Germany. With this funding, the awardees can establish their own, independent research group at a research institution of their choice in Germany.

The Bernstein Awardee 2012 will be publicly announced within the opening session of the Bernstein Conference 2012, on September 12, 2012. Following the award ceremony, the awardee will present his/her current research and future projects to be conducted with the support of the award.

Valentino Braitenberg Award – The Golden Neuron 2012

In honor of Prof. Valentino Braitenberg, one of the founding directors of the Max Planck Institute for Biological Cybernetics in Tübingen, and pioneer of Computational Neuroscience in Germany, who sadly passed away in September 2011, the Valentino Braitenberg Award was created. It will be awarded for the first time during the opening session of the Bernstein Conference on September 12, 2012.

The prize recognizes outstanding researchers who have provided major contributions to our understanding of brain function and who significantly influenced brain research or are expected to do so. Especially considered are studies of the microscopic properties of brain architecture and their functional implications.

The Award 2012 will go to Prof. Moshe Abeles from the Gonda Multidisciplinary Brain Research Center at Bar Ilan University, Israel.

Brains for Brains Awards 2012

The Brains for Brains Awards are an initiative of the Bernstein Association for Computational Neuroscience, supported by external donors. This year's awards were kindly supported by Brain Products GmbH, Gilching, Multi Channel Systems MCS GmbH, Reutlingen, and neuroConn GmbH, Ilmenau.

The Brains for Brains Award honors outstanding young international scientists who achieved a peer-reviewed scientific publication before starting their doctoral thesis. It consists of a $500 \notin$ cash prize and a travel fellowship of up to $2.000 \notin$ covering their trip to Germany, participation in the Bernstein Conference and two individually planned visits to selected Computational Neuroscience labs in Germany. During the award ceremony, the awardees give a brief teaser about their posters that will be presented during the subsequent poster sessions. This wards will go to Loffray Scaly (Columbia University, New York, USA) and Michael

This year's awards will go to Jeffrey Seely (Columbia University, New York, USA) and Michael Eickenberg (INRIA-Parietal, Neurospin, Saclay, France).

Public Bernstein Lecture 2012

The Bernstein Conference touches upon many themes that are of high public interest, from fundamental questions about brain and mind to clinical and biotechnological applications of neuroscience research. To foster the exchange between computational neuroscientists and the interested public and to provide an overview about a specific research topic that is at the focus of research within the Bernstein Network, the Public Bernstein Lecture has been introduced in 2012. To reach a broad audience, the lecture will be given in German, at 20:00 on September 13, 2012.

This year's speaker is Prof. Onur Güntürkün from Ruhr-Universität Bochum. He will talk about the astounding cognitive abilities of birds. Complex thinking without a cortex - certainly a thought-provoking topic.

Neurovision Film Contest

"And what have you discovered?" Every scientist knows the awkward feeling when other people want to know what they work on. Scientific advances catch people's interests, but the complex and abstract details often make communication between scientists and non-scientists difficult. Even more so in areas like neuroscience, where most study subjects, such as cells or brain activity, are invisible and thus not intuitively understood by people outside the field.

To help tackle this problem, for the second time, the Bernstein Conference called for entries to the NeuroVision Film Contest. Without using many words, complex ideas can be transported via strong images or animations. We want to encourage scientists to use their imagination and to express their ideas about neuroscience in this medium. Likewise, we want to raise interest in our field in young filmmakers.

Conditions for entering the contest were straightforward and left possibilities for many different approaches. Importantly, no professional filmmakers were allowed to participate. Submitted films had to deal with neuroscience - subject and way of presentation were up to the filmmakers. Accordingly, the variety of films we received was large, ranging from science fiction to informational science coverage and to an almost poetic tribute.

You want to see the masterpieces? Throughout the conference, all films will be shown in rotation in lecture hall B. You can enjoy other scientists views on their work and also vote for your favourite film there. A ballot for voting is included in the conference bag. Also, a jury composed of media professionals as well as scientists – Markus A. Dahlem (TU Berlin), Robin Greene (On3), Armin Olbrich (Bayrischer Rundfunk), Florian Rau (HU Berlin), Markus Schulte von Drach (Süddeutsche Zeitung) – will elect winners. With the help of our sponsors Assign Group, Elisabeth und Helmut Uhl Stiftung, and Innovations- & Gründerzentrum Biotechnologie, we are able to award two prices: One for the most creative handling of the topic and one for the greatest informational value. Awards will be given during the official award session on the last day of the conference.

NNCN PhD Symposium "Tools and their application to neuroscience research - a student perspective"

VENUE: LMU Biocenter, Ludwig-Maximilians-Universität München, Dept. Biology II, Grosshaderner Str. 2, 82152 Planegg-Martinsried (20 min U-Bahn ride from Munich downtown) TIME: September 15, 2012 09:30 – 12:30 (afternoon session until 18:00)

This year's NNCN PhD Symposium will focus on the application, development and improvement of software tools in neuroscience. Furthermore, it will be combined with the 2nd annual INCF Hackathon, a gathering of developers and users of the very same tools.

The Symposium will feature a set of fast, rich and easily-digestible "Lightning Talks" (5-10 minutes each) presenting diverse tools from our field. You will be able to inform yourself of many ongoing tool developments and foster your knowledge of things that facilitate your research! Also you will be able to interact with the developers of your tool of choice and, in turn, provide inputs on the future developmental direction of your favorite software.

The main Symposium will take place in the morning and refreshments will be served during lunch break. For those interested, the afternoon will feature sessions of social hacking, discussions and small group meetings, which will be arranged in an ad hoc fashion. The whole day will be concluded with us enjoying a warm and sunny Bavarian evening while having drinks and barbecue on the beautiful outskirts of Munich!



Invited Talks

Neural Circuits: Structure and Signals

$\left[O \ 1 \right]$ Structural Neurobiology: Tools for the dense reconstruction of neuronal circuits

Moritz Helmstaedter*

Structure of Neocortical Circuits Group, Max Planck Institute of Neurobiology, Martinsried, Germany * mhelmstaedter@neuro.mpg.de

The mapping of neuronal connectivity is one of the main challenges in neuroscience. Only with the knowledge of wiring diagrams is it possible to understand the computational capacities of neuronal networks, both in the sensory periphery, and especially in the mammalian cerebral cortex. Statistical circuit mapping using a combination of paired intracellular recordings and anatomical reconstructions has provided insight into the connectivity between populations of cells. To move beyond pairwise connectivity statistics, however, dense circuit mapping is required. Our methods for dense circuit mapping are based on 3-dimensional electron microscopy (EM) imaging of tissue, which allows imaging nerve tissue at nanometerscale resolution across substantial volumes (typically hundreds of micrometers per spatial dimension) using Serial Block-Face Scanning Electron Microscopy (SBEM). The most timeconsuming aspect of circuit mapping, however, is image analysis; analysis time far exceeds the time needed to acquire the data. Therefore, we developed methods to make circuit reconstruction feasible by increasing analysis speed and accuracy, using a combination of crowd sourcing and machine learning. We have applied these methods to circuits in the mouse retina, mapping the complete connectivity graph between almost a thousand neurons, and we are currently improving these methods for the application to neuronal circuits in the neocortex.

[O 2] How local is the local field potential?

Gaute Einevoll*

Department of Mathematical Sciences and Technology, Norwegian University of Life Sciences, Ås, Norway * Gaute.Einevoll@umb.no

The local field potential (LFP) usually refers to the low-frequency part (<~500 Hz) of an extracellular potentials recorded inside the brain. It is among the oldest experimental measures of neural activity and has been widely used to investigate network mechanisms involved in, for example, sensory processing and higher cognitive processes including attention, memory and perception. The LFP has also been suggested as a candidate signal for neuroprosthetic devices as it is relatively easy to record and more stable than single-unit activity. Despite its wide use, there is still limited knowledge about the relation between the LFP and the underlying neural activity. The LFP is believed to primarily reflect synaptic activity in a population of neurons in the vicinity of the recording electrode, but there are contradicting reports on the spatial extent of the region generating the LFP.

In the talk I will present recent results from our group where we have used a biophysical forward-modelling approach (Holt and Koch, J Comp Neurosci, 1999) to address this question (Linden et al., Neuron, 2011). Specifically, we have calculated the LFP signal from synaptically activated populations of morphologically reconstructed cortical cells and investigated how various key factors determine the size of the region that an LFP electrode can 'see', in particular, the neuronal morphology, distribution of synapses, level of correlation in synaptic activity, the position of the recording electrode, and the signal frequency. I will further present results for how steeply the LFP signal decays outside an active population and finally suggest some simple "rules-of-thumb"-answers to the question raised in the title.

Coding

[O 3] Not noisy, just wrong: the computational and neural cause of behavioral variability

Alexandre Pouget*

Department of Neuroscience, University Medical Center, University of Geneva, Switzerland * alex@bcs.rochester.edualex@bcs.rochester.edu

Behavior varies from trial to trial even when the stimulus is maintained as constant as possible. In many models, this variability is attributed to noise in the brain. Here, we propose that there is another major source of variability: suboptimal inference. Importantly, we argue that in most tasks of interest, and particularly complex ones, suboptimal inference is likely to be the dominant component of behavioral variability. This perspective explains a variety of intriguing observations, including why variability appears to be larger on the sensory than on the motor side, and why our sensors are sometimes surprisingly unreliable. It also predicts specific patterns of correlations among neurons, which are markedly different from the ones that are currently assumed to exist in cortical circuits.

[O 4] Neural computations underlying optimal multisensory cue integration

Greg DeAngelis*

Department of Brain and Cognitive Sciences, University of Rochester, USA * gdeangelis@cvs.rochester.edu

In many contexts, integration of multiple sensory cues can optimize perception and action planning. Studies of human and animal behavior have demonstrated that different sensory cues are often integrated optimally, consistent with predictions of a Bayesian computational framework. In contrast, traditional electrophysiological studies of multisensory integration have been largely empirical in nature, and have not related the computations performed by single neurons to the optimal performance seen behaviorally. Using perception of self-motion as a model system, our group has bridged this gap between neurons and behavior. We have characterized the mathematical rules that single neurons use to combine visual and vestibular inputs related to self-motion, and we have shown how these neural computations translate to optimal (or near-optimal) performance at the level of population codes. Furthermore, we have demonstrated that many of the empirical observations regarding multisensory integration by single neurons can be explained by a simple computational model in which multisensory neurons perform a weighted linear summation of their inputs followed by divisive normalization at the stage of multisensory integration.

Vision

$\left[O~5\right]$ Wakefulness, locomotion, and navigation: A look from visual cortex

Matteo Carandini*

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Most of what we know on primary visual cortex (V1) comes from experiments performed under anesthesia. Yet visual cortex is typically used by awake animals while they actively navigate an environment. I will describe three studies currently performed in my laboratory to investigate how visual processing in mouse V1 is affected by wakefulness, locomotion, and navigation. The first study, by Bilal Haider, indicates that wakefulness dramatically enhances synaptic inhibition, abolishing the balance of excitation and inhibition typically seen in V1 under anesthesia. The second study, by Asli Ayaz, indicates that locomotion profoundly alters spatial integration, greatly reducing the surround suppression that is common in V1 neurons of stationary animals. The third study, by Aman Saleem, reveals that V1 signals are modulated by virtual navigation, in a way that is ideally suited to code for the visual stimuli created by locomotion in the environment. These results indicate that visual processing in mouse V1 is profoundly affected by wakefulness, locomotion, and navigation, and reinforce the need for studying the cerebral cortex during natural behavior.

[O 6] Temporal constraints for visual object recognition: neurophysiological, behavioural and computational approaches

Gabriel Kreiman*

Children's Hospital, Harvard Medical School, Boston, Massachusetts, USA * gabriel.kreiman@tch.harvard.edu

We can visually recognize complex shapes in a brief fraction of a second in spite of large variation in metric properties such as scale, position, viewpoint or illumination. This remarkable degree of selectivity, invariance and speed in visual recognition is orchestrated by a cascade of computations along the ventral visual stream. In this talk, I will discuss psychophysics and neurophysiological data during recognition of isolated objects that provide strong constraints towards understanding the neural circuits and mechanisms that underlie shape recognition in humans. A simple, bottom-up, hierarchical architecture is consistent with the behavioral and neurophysiological evidence and can provide a good first-order approximation towards describing the initial 100-200 ms in visual recognition. A computational model instantiating this type of feed-forward architecture shows a remarkable ability to recognize objects. I will then try to probe the limits of this feed-forward architecture by considering more complex tasks including recognition of objects in cluttered scenes and recognition of partially occluded objects. Breaking up bottom-up processing provides initial steps towards investigating possible roles of top-down signals implemented via feedback connections.

[O 7] A sketch of a theory of visual cortex

Tomaso Poggio*

McGovern Institute for Brain Research, Massachusetts Institute of Technology, Cambridge, Massachusetts, USA

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I conjecture that the sample complexity of object recognition is mostly due to geometric image transformations and that the main goal of the ventral stream is to learn-and-discount image transformations. The theory provides a simple, biologically plausible one-layer module for learning generic affine transformations in \mathbb{R}^2 and become invariant to them for any new image. It argues that although this approach is likely to have been discovered early by evolution and can deal with a few very important objects, it is too storage expensive to deal with a potentially infinite set of objects. The ability to deal with an unlimited number of objects is obtained by a hierarchical architecture for which we prove local and global invariance of parts and wholes, respectively. With the assumption of online, Hebbian-like learning in various visual areas the theory predicts the tuning of the neurons in terms of the spectral properties of the covariance of the learned transformations for different receptive fields sizes. The theory also predicts that class-specific transformations are learned and represented at the top of the ventral stream hierarchy; it also explains why a patch of mirrorsymmetric tuned face neurons should be expected before pose invariance in the face network. If the theory were true, the ventral system would be a mirror of the symmetry properties of motions in the physical world.

Network Dynamics and Representations

$\left[O~8\right]$ Neurogrid: Simulating a million neurons and a billion synapses with sixteen neuromorphic chips

Kwabena Boahen*

Stanford University, USA * boahen@stanford.edu

Large-scale brain simulations link high-level cognitive phenomena to low-level biophysical mechanisms, helping neuroscientists understand how cognition emerges from the brain's wetware. These simulations use a digital approach to model ion-channels that was pioneered by Hodgkin and Huxley in the 1940s. Computer performance has increased over a billionfold since then (Moore's Law), enabling supercomputers to simulate networks with millions of neurons connected by billions of synapses in real-time. This scale is only about 0.01% of the human cortex, however. And clock speed has plateaued in recent years, putting real-time full-brain simulations out of reach for the foreseeable future-even for the fastest supercomputers. Fortuitously, with the recently developed ability to emulate (i.e., simulate in real-time) various types of ion-channels, the analog technique pursued by neuromorphic engineers over the past two decades has matured. The brain can now be modeled using subthreshold analog computation to emulate ion-channel activity and asynchronous digital communication to route synaptic connections. Neurogrid, an entirely clockless system with sixteen mixedanalog-digital chips created at Stanford, emulates a million cortical neurons connected by six billion synapses. It rivals the performance of 20 IBM Blue Gene L racks on this particular task while consuming five orders of magnitude less energy. By providing an affordable platform to perform large-scale simulations, Neurogrid is helping neuroscientists vet various hypotheses about how the brain works.

[O 9] Overcomplete representations and neuronal circuit dynamics

Shaul Druckmann*

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Our brains are capable of remarkably stable stimulus representations, for instance during working memory tasks. While stimuli are kept in working memory, i.e., during delay periods in working memory tasks, neurons in prefrontal cortex display elevated firing rates and are thus thought to support the memory representation. Surprisingly, the activity of individual neurons during the delay period is constantly changing. Since neuronal activity encodes the stimulus, its time-varying dynamics appears paradoxical and incompatible with stable network representations. Indeed, this finding raises a fundamental question: can stable representations only be encoded with stable neural activity, or its corollary - is every change in activity a sign of change in network representation? Here we explain how different time varying representations offered by individual neurons can be woven together to form a coherent, time invariant, representation. Motivated by two ubiquitous features of Neocortex: redundancy of neural representation and sparse intra-cortical connections, we derive a network architecture that resolves the apparent contradiction between representation stability and changing neural activity. Our theory predicts relations between neuronal functional properties and network architecture. We show that our intuition regarding network representation, typically derived from considering single processes in isolation, may be misleading, and that the complex, time-varying activity of distributed processing in many neural and biological circuits does not necessarily imply that the network explicitly encodes time-varying properties.

Learning

[O 10] Statistical and causal learning

Bernhard Schölkopf*

Empirical Inference Department, Max Planck Institute for Intelligent Systems, Germany * bernhard.schoelkopf@tuebingen.mpg.de

Kernel methods in machine learning have expanded from tricks to construct nonlinear algorithms to general tools to assay higher order statistics and properties of distributions. They find applications also in causal inference, an intriguing field that examines causal structures by testing their probabilistic footprints. However, the links between causal inference and machine learning go beyond this, and the talk will outline a few thoughts how some challenging problems of modern machine learning can benefit from the causal methodology.

[O 11] Internal models: of ferret and men

Máté Lengyel*

Department of Engineering, University of Cambridge, UK * m.lengyel@eng.cam.ac.uk

Our percepts rely on an internal model of the environment, relating physical processes of the world to inputs received by our senses, and thus their veracity critically hinges upon how well this internal model is adapted to the statistical properties of the environment. I will describe two recent studies in which we addressed two fundamental questions about how internal models are adapted to the environment: how are they learned, and what is their neural underpinning?

Theories of learning can be divided into two qualitatively different classes: supervised learning predicts that we develop specialised representations for each task; unsupervised learning predicts general-purpose representations that can be used in a wide range of tasks with different tasks requiring different operations on the same underlying representation. We developed a novel method that can extract complex, multi-dimensional mental representations from behaviour. We showed that the representations of human faces vary dramatically across subjects, but are invariant across tasks within a subject. This provides evidence for a strong unsupervised learning-based representation of faces in humans.

Although a number of behavioural studies have demonstrated that internal models are optimally adapted to the statistics of the environment, the neural underpinning of this adaptation is unknown. Using a Bayesian model of sensory cortical processing, we related stimulusevoked and spontaneous neural activities to inferences and prior expectations in an internal model and predicted that they should match if the model is statistically optimal. To test this prediction, we analysed visual cortical activity of awake ferrets during development. Similarity between spontaneous and evoked activities increased with age and was specific to responses evoked by natural scenes. This demonstrates the progressive adaptation of internal models to the statistics of natural stimuli at the neural level.

[O 12] Self-organization and unsupervised learning in recurrent networks

Jochen Triesch*

Frankfurt Institute for Advanced Studies (FIAS), Germany * triesch@fias.uni-frankfurt.de

Cortical circuits are shaped by a number of different plasticity mechanisms, but it is still unclear how these endow the cortex with useful information processing abilities. Over the last years we have developed recurrent neural network models that self-organize their connectivity under the influence of different plasticity mechanism including spike-timing dependent plasticity and different forms of homoestatic plasticity. These self-organizing recurrent networks (SORNs) can learn about the temporal structure in input time series in an unsupervised fashion and can greatly outperform non-adaptive networks on challenging prediction tasks. Furthermore, these networks can explain a number of features of cortical circuits including the Poisson-like firing of individual neurons, the overall distribution of synaptic connection strength, and the high degree of synaptic turnover and patterns of synaptic fluctuations. In addition, they make testable predictions regarding the distribution of synaptic life times. Finally, they also explain some psychological results on sequence learning in adult subjects. Overall, our results suggest that cortical circuits are shaped by processes of network self-organization through the combined action of multiple forms of neuronal plasticity.

Decision

[O 13] Conversion of sensory signals into perceptual decisions

Ranulfo Romo*

Instituto de Fisiología Celular, Universidad Nacional Autónoma de México, Mexico City, Mexico * rromo@ifc.unam.mx

Most perceptual tasks require sequential steps to be carried out. This must be the case, for example, when subjects discriminate the difference in frequency between two mechanical vibrations applied sequentially to their fingertips. This perceptual task can be understood as a chain of neural operations: encoding the two consecutive stimulus frequencies, maintaining the first stimulus in working memory, comparing the second stimulus to the memory trace left by the first stimulus, and communicating the result of the comparison to the motor apparatus. Where and how in the brain are these cognitive operations executed? We addressed this problem by recording single neurons from several cortical areas while trained monkeys executed the vibrotactile discrimination task. We found that primary somatosensory cortex (S1) drives higher cortical areas where past and current sensory information are combined, such that a comparison of the two evolves into a decision motor report. Consistent with this result, direct activation of the S1 can trigger quantifiable percepts in this task. These findings provide a fairly complete panorama of the neural dynamics that underlies the transformation of sensory information into an action and emphasize the importance of studying multiple cortical areas during the same behavioral task.

[O 14] Origins and use of uncertainty in decision-making

Zach Mainen*

Champalimaud Neuroscience Programme, Champalimaud Centre for the Unknown, Lisbon, Portugal * zmainen@fchampalimaud.org

Complex brains allow organisms to build internal models of the world and thereby make predictions about how to best act to obtain resources and avoid threats. Inevitably, these models and resulting predictions have a degree of uncertainty. This is reflected, for example, in inaccurate decisions in perceptual decision-making tasks. We have been interested in the problem of how these uncertainties arise and how the nervous system makes use of them to optimize behavior.

To investigate these issues, 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. By manipulating the nature of the cues, we can vary the difficulty or uncertainty of the task. Through this approach, together with simultaneous recordings from several brain areas and simple formal models, we have begun to elucidate some of these issues.

In this talk, I will present experiments suggesting 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.

Disease and Cure

[O 15] Explaining away emotions. How simple decision dysfunctions might perturb complex cognitions

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We all have to fight our own selves and know, that in certain situations our impulses will lead us astray. Psychology and related fields have long recognised the parallel existence of multiple decision-making system, and these have been characterised behaviourally, computationally and neurobiologically. While sophisticated approaches have yielded increasingly clear estimates of the extent to which they are separately identifiable, their potential for interaction has been less well explored. Here, I will discuss one such recent finding, showing how behavioural inhibition in the face of losses shapes goal-directed tree search. Based on this, I will discuss the potential for psychiatric comorbidities to arise from the changes at the interface between high-level, goal-directed decision-making and more low-level, Pavlovian, decisions, focussing particularly on the informational exchange between the systems.

[O 16] Spatial processing and map learning in the entorhino-hippocampal circuit

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My laboratory is interested in identifying neuronal mechanisms for long-term memory storage at the systems level. Because specialized hippocampal circuitry is necessary for many forms of memory, we investigate the computations that are performed in a local circuitry that consists of entorhinal inputs to hippocampus and hippocampal outputs to entorhinal cortex. In particular, our research asks which mechanisms generate hippocampal spatial firing patterns and how spatial firing patterns contribute to spatial memory. The input layers of the medial entorhinal cortex to hippocampus contain many cell types with precise spatial firing patterns, including cells with grid-like spatial firing patterns (i.e., grid cells). We found that silencing the neuronal activity in the medial septal area abolishes theta oscillations and grid-like firing patterns in entorhinal cortex. Even though precise spatial and temporal firing patterns in entorhinal cortex and hippocampus are disrupted, we found that the spatial firing patterns of hippocampal cells are partially retained after septal inactivation. We therefore asked whether septal input to entorhinal cortex is particularly important for generating new spatial maps of the environments. We find that the formation of new spatial maps is disrupted to a substantially larger extent than the retention of familiar maps. These findings have important implications for understanding how neurodegenerative processes in the entorhinal cortex can result in a failure to appropriately organize neuronal activity and synaptic plasticity, and thus in the memory problems that are characteristic for Alzheimer's disease.

[O 17] Improving hearing with cochlear implants in reverberant spaces

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Cochlear implants (CIs) are neural prostheses which give a sense of hearing to deaf people by stimulating the auditory nerve. In many users they restore the ability to understand speech in quiet, but noise and reverberation cause severe problems. It seems that implant users have difficulties hearing out one source in a potpourri of sources. This so called "auditory scene analysis" relies, amongst other cues, on information from both ears (binaural) which is degraded with implants. Our work focusses on means to code binaural information in the electric pulses delivered by the implant to improve the perception of sound direction – an important aspect for locating and understanding speakers. Past approaches have generally attempted to reduce the energy of the interfering reverberation or noise. Our novel approach instead aims to increase the perceptual saliency of the cues used to locate sounds in reverberation. In simulations of implant use with normal-hearing listeners we demonstrate that by changing the coding of the target sound to better transmit its binaural cues, it can be localized better in reverberation. The new approach only alters the transmitted envelope signal and can thus be implemented in commercial devices without changing the implanted part.

Acknowledgements

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Cognition

[O 18] The Left and the Right Side of Visual Discriminations

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Hemispheric asymmetries play an important role in almost all cognitive functions. For more than a century, they were thought to be uniquely human and, consequently, animal models were considered to be nonexistent. Now, an increasing number of findings make it likely that we inherited our asymmetries from common ancestors several hundred million years ago. Thus, studying animal models could provide unique insights into the mechanisms of lateralization. Visual asymmetries in pigeons are an excellent animal model system since all relevant neural properties can be elucidated at a behavioral, anatomical, and electrophysiological level. I will present data of a visual discrimination task that is designed such that the two hemispheres of the animals have to compete. In most cases, the left hemisphere wins. Subsequently I will present a series of experiments that analyze the neuromechanical properties of this left-right difference. These studies show that asymmetrical processing starts with an early attention-mediated shift of processing resources into (mainly) the left hemisphere. Subsequently, a higher number of recruited neurons that also discriminate a higher level are found in the left hemisphere. Finally, commissural interactions are taking place in an asymmetrical manner at the final stage of the motor output, resulting in left unihemispheric control of the response. Thus, brain asymmetry in this animal model is constituted by a cascade of neural processes that finally provide the dominant hemisphere with an advantage in accessing motor output.

[O 19] Biological precursors of the number sense

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The verbal number concept allows humans to develop the superior mathematical skills that are a hallmark of technologically advanced cultures. Recent findings in animal cognition, developmental psychology and anthropology, however, indicate that numerical skills are rooted in non-verbal biological primitives. We investigated the neural foundations of quantitative categories and concepts in behaving macaque monkeys in combined psychophysical/neurophysiological studies. The current data shed light on the question of how the primate brain processes quantity information at an evolutionary early stage.

Global Perspectives

[O 20] Big data from small data: A deep survey of neuroscience data via the Neuroscience Information Framework

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Understanding the brain strains the limits of current human ingenuity. Perhaps more than any other organ system, the problem of understanding the brain is fundamentally multiscale, with relevant data derived from spatial and temporal scales spanning many orders of magnitude. Because of the complexity and breadth of these networks, unraveling functional circuits underlying complex behaviors or pinpointing the locus of disease processes, even where the genetic defect is known, has confounded scientists, who by the limitations of experimental methods glimpse only a pinhole view of a vast interconnected landscape. Many scientists are calling for new computational and data driven methods to help accelerate translation of brain circuitry and chemistry into effective therapeutics. Since its first production release in 2008, the Neuroscience Information Framework (NIF; http://neuinfo.org), the NIF has grown into the largest source of neuroscience resources (data, tools, materials and services) on the web. Through the NIF, we have been involved in a deep survey of the neuroscience resource landscape and have acquired a global perspective on currently available resources. NIF currently provides deep query over 150 different data sources, collectively comprising 350 million records. We have recently begun to employ powerful analytics tools to analyze the current resource landscape, using workflow engines and other analytics packages. In this presentation, I will present the results of these analyses, discussing the types of resources currently available, and the extent to which neuroscience can assemble a large, coherent data set from the "long tail of small data".

[O 21] Project MindScope

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The Allen Institute for Brain Science is engaged in a ten year project to study the principles by which information is encoded, transformed and represented in the mammalian cerebral cortex and related structures. The goals of MindScope are to provide a quantitative taxonomy of cell types and their interconnections in visual cortex and associated brain regions, to observe their dynamics under physiological conditions in behaving mice, to construct cellular models of how their dynamics and function arise from the structural description, and to understand how this function relates to visual perception. This is a large-scale, in-house team effort to synthesize anatomical, physiological and theoretical knowledge into a description of the wiring scheme of the cortex, at both the structural and the functional levels. The fruits of this cerebroscope will be freely available to the public.



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US-German Collaboration in Computational Neuroscience

$\left[T \ 1\right]$ Phase Space Analysis of a Ionic Model for Cortical Spreading Depression

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The local dynamics of cortical spreading depression (SD) are analyzed in a simplified mathematical neural tissue model. We give an analysis of the model's phase space structure to gain insights about SD ignition and the relevant parameters. The membrane contains Hodgkin-Huxley-like ion channels with dynamic concentrations of sodium, potassium, and chloride ions that vary according to the transmembrane currents via active and passive channels as well as pump

currents maintaining ion gradients between intra– and extracellular space. Extracellular potassium is further regulated by diffusion and glial buffering. The dynamical regimes for different applied currents, potassium bath concentrations and buffering strengths contain stable fixed point dynamics, seizure-like bursting, and SD trajectories. We investigate the transition from a stable resting state to seizure activity and also the transition from seizure to SD. Frequencies and amplitudes are analyzed to characterize the type of excitability connected to both patterns.

$\left[T\ 2\right]$ Characterizing Spatial and Auditory Responses in the Gerbil Hippocampus

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The goal of our project is to identify how spatial and auditory stimulus sequences are encoded within the hippocampus of the Mongolian gerbil, a rodent with a highly developed auditory system. As a first step, we asked whether the mechanisms of spatial coding of other rodent species are also present in gerbils. We characterized the spatial firing patterns of hippocampal cells by training gerbils to search for randomly scattered food in an open arena. The walls of the arena were flexible so that they could be configured as a square (diagonal = 115 cm) or a circle (diameter = 102 cm). In addition, gerbils were trained to run on a 1- or 1.5-meter linear track. After gerbils were well-trained, we began to record the firing responses of hippocampal cells. In each box and on the linear track, we found principal cells in the CA1 and CA3 subfields of the hippocampus that showed place fields that were spatially stable and precise.

In order to measure movement-theta in the gerbil, we also recorded the local field potential (LFP) and computed its time-frequency spectrogram. As in other rodents, the LFP shows high power in the theta range (7-11 Hz). In gerbils, the peak frequency is approximately 8.5 Hz. We looked at the relationship between spiking and theta for different cell types. Putative interneurons are phase-locked to theta, firing preferentially near the trough of the theta rhythm. The power spectrum of autocorrelograms also shows that interneurons are tightly locked to the 8.5 Hz frequency. Conversely, putative principal cells show oscillation frequencies that are higher than the predominant LFP frequency. As in other rodent species, such disparity

between the oscillation frequencies of cells and of the LFP is indicative of theta phase precession, which was also directly evident in cells with place fields on the linear track. Taken together, our results show that the spatial coding mechanisms in gerbils correspond to those in other rodents, in particular to those of rats.

In addition, we performed experiments to look for hippocampal responses to auditory stimuli. When the gerbil passed specific locations while running on the linear track, we played a corresponding tone. We found that the cells that showed spatial esponses during this experiment tended to have their firing fields located near the tone locations. This suggests that place field responses may be shaped by auditory stimuli. These findings indicate that gerbils can be used as a model organism to compare spatial and auditory sequence coding. Whether identical cell populations in the hippocampus can support both mechanisms remains to be determined.

Acknowledgements

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[T 3] Synaptic and extrasynaptic influence of astrocytic glutamate uptake on orientation selectivity in primary visual cortex

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One of the most prominent response features in primary visual cortex is orientation selectivty. In an in-vivo study in Ferrets Schummers et al. [1] investigated the importance of rapid glutamate uptake by glutamate tansporters situated on the astrocytic membrane in close vicinity to the synpatic cleft for sharp orientation tuning. With TBOA they blocked the astrocytic glutamate uptake and observed an increased response for preferred orientation along with broadend orientation tuning. The experiment, however, was unable to determine wether the broadend orientation tuning derives from changes in synaptic transmission via slowed down gluamate clearance or if the underlying mechanism is a change in neuronal excitability due to increased amibent glutamate concentration. In the computational study presented here we investigate which of the two possible mechanisms better explains the observed data. The synaptic as well as the somatic mechanism are incorporated independently in a recurrent 2d-model for ferret primary visual cortex [2]. The model consists of two populations, one excitatory and one inhibitory, of Hodgkin-Huxley point neurons. The total recurrent input received by these cells are stronger than the total afferent input, which leaves the network poised to a balanced regime. In the 2d-model orientation tuning is organized in a pinwheeldomain structure. The somatic mechanism is incorporated as an additional gluamate driven receptor current. Here the level of ambient glutamate represents how strong gluamate uptake is reduced. For the synaptic mechanism, synaptic NMDA and AMPA receptors were described by detailed models with several conformational receptor stages [3]. Theses receptors are driven by a bi-exponential glutamate concentration. Its decay constant is modified by the astrocytic gluamate uptake and decay is prolonged in the presence of TBOA [4]. Motivated by the significant difference in synaptic geometry for excitatory to excitatory and excitatory to inhibitory synapses as well as the difference in glutamate transporter density in the vicinity of these two types of synapses, we selectively vary the glutamate decay constant along these two types of connections. We find that both mechanism can achieve an increase in the preferred response along with changes in orientation tuning. However, the synaptic mechanism with the differentiated increase in decay times for both types of connections yields a better agreement with the experimental observations.

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$[\top 4]$ Higher-order feature detection in olfactory bulb - Integration in the granule cell-mitral cell network

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Odours stimulate input to multiple olfactory bulb (OB) glomeruli, exciting large populations of mitral cells. The first major point at which these multiple dimensions of olfactory input can be integrated is in the olfactory bulb's extensive mitral cell-granule cell (MC-GC) network. ~500,000 GCs interconnect the ~30,000 MCs, receiving excitatory dendrodendritic synapses from MCs and making inhibitory dendrodendritic synapses both reciprocally and onto many other MCs. We aimed to better understand olfactory cross-channel integration by characterising the integration rules of the MC-GC circuit.

Firstly, we infected the GC layer (GCL) with AAV-ChR2, and investigated how light stimulation of the GCL summed with synaptic stimulation mediated by action potentials (APs) in mitral cells. We recorded the resulting GC output by recording, in whole cell voltage clamp, the IPSCs received by mitral cells. As might be expected, light and synaptic stimulation of the GCL given together resulted in significantly supralinear increases in evoked IPSCs in 20/63 cells. Unexpectedly, however, in 23/63 cells light could lead to a significant reduction in inhibitory postsynaptic currents (IPSCs). Notably, light stimulation that was too weak to evoke IPSCs in recorded MCs could block AP evoked recurrent IPSCs (n = 9/17 cells). Further, pairing APs in one MC with current-injection evoked AP stimulation in a second MC lead to supralinear IPSC increases in only 4/49 cells, but IPSC suppression of $37 \pm 24\%$ in 26/49 cells. Further characterisations of this surprising suppression of GC mediated inhibition were consistent with GCs being inhibited, potentially via deep short axon cells.

A second approach is being developed to investigate synaptic integration in GCs themselves. Using a transgenic mouse in which ChR2 is expressed in olfactory receptor neuron axons (Smear et al, Nature [2011], 479:397), glomerular input has been stimulated via light activation and its summation measured by current clamp recordings from GCs. Preliminary experiments indicate that this will allow us to measure how many independent glomerular inputs are required to trigger GC APs.

Together these experiments provide key data that can be used model the GC mediated crosstalk between MCs.

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$\left[T\ 5\right]$ Integration of bottom-up and top-down signals in visual recognition

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In a collaboration of Harvard Medical School and University hospital Freiburg we study visual perception and memory in the human brain with high spatial and temporal resolution. Subjects are epilepsy patients who are implanted with depth electrodes and/or intracranial surface electrodes to localize the seizure focus for potential surgical resection. In parallel with field potentials we record single neuron spiking activity using microwires inserted in depth electrodes. The goal of this collaborative effort is to understand the interaction and integration of bottom-up and top-down signals through the combination of neurophysiological recordings at high spatial and temporal resolution in the human brain, computational data analysis and modeling. The properties of hierarchical and feed-forward theories of visual recognition provide a quantitative framework to examine information processing in the feedforward path along the ventral stream to account for ultra-rapid complex object recognition. One of the main limitations of these models is that they do not take into account the massive backprojections that convey information from higher cortical areas back to the lower areas. In order to explain everyday visual perception, we need to incorporate a quantitative and computational description of top-down control of sensory processing derived from frontal and parietal cortex as well as medial temporal lobe memory structures.

In our study we examine progressively more complex tasks that include both bottom-up and top-down components in order to shed light on the dynamical integration of feed-forward and feed-back signals in the human ventral visual cortex. One type of information that can be fed back is the temporal relationships among visual events in an episodic memory. In order to investigate memory function involved in object recognition, we have subjects perform tasks that involve the learning of image sequences while we record from temporal lobe structures including hippocampus. These tasks offer the potential to reveal functions of the hippocampus in the learning of temporal relationships, such as prospective/anticipatory coding of upcoming images and/or learning of associations among temporally-linked images. In particular, we test the involvement of the hippocampus in learning the temporal component of episodic memories, beyond simple association of the events which are members of the episode. Here, we dissociate the learning of which images are members of a particular sequence from learning of temporal order by asking patients to memorize sequences, then testing either their memory of the sequence members or memory of the temporal relationships among sequence members. Finally, replaying of the order of activation of place cells that together constitute a trajectory to a reward location during and after training occurs in the rodent hippocampus, and is believed to play a role in memory consolidation. We test whether such replay occurs in non-spatial cognitive domains in the human hippocampus.

Acknowledgements

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$[T\ 6]$ Generation of computer models of dendritic signal processing and synaptic plasticity mechanisms in hippocampal nerve cells by high-resolution microscopy

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Neuronal dendrites constitute an elaborate web of branching processes, excitatory and inhibitory synapses, neurotransmitter receptors and voltage-gated channels. How can we visualize these components, determine their spatial relationships, and reveal their functional interactions? If we can see the component parts at high resolution, we can then use this information to generate more accurate computational models of dendrites and the complex integrative functions they perform.

We propose to combine two high-resolution imaging methodologies: two-photon microscopy, which provides high-resolution functional imaging in living tissue, and array tomography, which provides even higher resolution and the ability to identify the location of molecular constituents of the dendrite. These experiments will provide a view of the dendritic tree with unprecedented structural and functional detail. Using these data, we will then develop improved computational models of the dendritic tree that combine and integrate this underlying organizational complexity.

A focus of the proposal is the distribution of synapses over a vast dendritic tree. Of the tens of thousands of synapses on a single CA1 pyramidal neuron, many are located electrically far from the site of action. Furthermore, there is abundant evidence that the size and properties of excitatory synapses vary according to their dendritic position. Likewise, inhibitory synapses that target dendrites are diverse in their location, molecular markers, and functional properties.

Our multidisciplinary, collaborative approach will use the hippocampus as a model system for studying this neuronal complexity at the level of cells, synapses and molecules, but the results will provide working hypotheses and approaches that can be applied in future studies to other types of pyramidal neurons, such as those in the neocortex. In our view, this is an important step, because understanding the intricacies of neurons and their connections is a necessary component of understanding complex neural circuits. The two

experimental approaches we will employ – two-photon uncaging and array tomography – are both relatively new and both provide sub-micron resolution regarding synaptic structure and function. The results of our experiments will be used to develop computational models, which will be used to generate and test hypotheses regarding the complex integration of synaptic inputs that occurs in the dendrites of hippocampal pyramidal neurons.

$[\top 7]$ How dynamic is encoding? State-dependent feature-selectivity in thalamo-cortical circuits of the rat whisker system

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The dynamic association of computations performed by almost identical repetitive microcircuits across neocortex is the basis for the generation of highly flexible 'states' that give rise to vastly different behaviors. The key to reaching an understanding of cortical processing, therefore, is to study how it adapts signal processing to these different states. It is generally believed that the relevant mechanism for adaptive processing lies in interactions of thalamo-cortical loops, and in view of the repetitive outlay across neocortex may generalize across states. Therefore, our project compares thalamo-cortical coding in bottom-up (sensory driven), top-down (cognitive), and vigilance related states. The rat tactile whisker system is a model system that offers a broad knowledge base of connectivity and neuronal processing and a superior accessibility of thalamo-cortical representations. The specific aims of our project are to 1) assess feature selectivity of thalamic and cortical neurons in range of states using encoding models, based on white noise analysis, and 2) study behavioral tasks with different perceptual requirements to assess whether behavioral discriminability is correlated with (and thus possibly caused by) the ability to dynamically adjust feature selectivity. Thus far, we have developed some of the computational tools based on spike-triggered analysis, using simulation and data from the anesthetized rat. In parallel, we have developed the behavioral framework necessary to integrate the work across the two laboratories. We will present preliminary work on both the acute and behavioral sides of the project.

Acknowledgements

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Neurons, networks, dynamical systems

$[T\ 8]$ Universal principles of topology governing both of structural and effective connectivity

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Since the era of Hebb, the importance and mysterious role that neuronal ensembles play in has been a main concern of the neuroscience [Hebb, 1949]. Recently, much work using structural connectivity has revealed patterns of synaptic connections in neuron ensembles [Bock et al., 2011]. Structural connectivity information is extremely valuable, as it indicates pathways through which one neuron could possibly influence spiking in another. In contrast, effective connectivity aims to describe the pathways through which influence actually occurs. The concept of "effective connectivity" was initially described in regard to local neuronal networks [Aertsen et al., 1989]. However, almost all research on "effective connectivity" has been done in macroscopic dynamics recorded using fMRI, MEG, and EEG [Friston, 1994]. Furthermore, even out of the studies on microcircuits, almost no work has been done on effective connectivity in local cortical networks at the timescale of typical synaptic delays within the cortex (1-20 ms). This is unfortunate, as direct influence between neurons would be expected to occur at these time delays. Structural connectivity studies have shown that groups of 3-7 cortical neurons are more likely than chance to be synaptically connected to each other if they have synapses onto a common neighbor neuron [Perin et al., 2011]. This led to the question whether effective connectivity also shows this pattern. In order to investigate these topics, we used a 512 electrode array system to record spontaneous activity in 9 slice cultures that included neocortex and portions of hippocampus. On average, we recorded over ~120 neurons from each culture for 1 hr or more. Although many metrics of effective connectivity have been proposed, we selected transfer entropy because several studies found it to compare favorably in accuracy to other metrics. Structural connectivity studies have shown that groups of 3-7 cortical neurons are more likely than chance to be synaptically connected to each other if they have synapses onto a common neighbor neuron [Perin et al., 2011]. This led to the question whether effective connectivity also shows this pattern. In the comparison between the topological properties of structural neuronal networks and the topological properties of the reconstructed effective connectivities, we could find universal principles of topology governing both of structural and effective connectivity.

[T 9] Nonlinear predictive coding in early sensory circuits

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Early sensory systems, such as retina and olfactory bulb, face a challenge of quickly and accurately transmitting information about the world to higher brain areas through a limited bandwidth channel ("Barlow's bottleneck"). This can be addressed by a strategy, known as predictive coding, whereby predictable components are subtracted away from incoming stimuli and only the difference is transmitted. Indeed, it was proposed that a linearly computed prediction is subtracted by retinal interneurons (Srinivasan et al. 1982). Here, we advance the predictive coding view by solving the non-linear dynamics of a simplified model of early sensory networks. We demonstrate that due to their non-linearity inhibitory interneurons afford a representation that develops over time from highly sparse and more robust, to less sparse and more accurate. These representations are not transmitted directly to higher brain areas (due to the large number of axons this would require) but are subtracted from the sensory signal in projection neurons to generate the residual. We demonstrate that the transmission of the residual by the projection neurons indeed ameliorates the bandwidth limitation. The proposed neural circuit implementation of the predictor module using sparse representations in inhibitory interneurons solidifies predictive coding as a conceptual framework of early sensory processing.

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[T 10] Brain Graph - Style Information Processing for Mobile Robot Control

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A Brain Graph is a model of the connectome of a nervous system, which interconnects processing nodes through a set of communication edges. Such a representation originated in the research domain Graph Theory, and shares many similarities with probabilistic graphical models: (a) nodes are computational units within a distributed system that are functionally separable from each other; and (b) interactions between such nodes become continuously less meaningful the more similar the nodes are to each other. In machine learning, probabilistic graphical models are used for computing uncertainty and for the generation of actions based on perception, which provides a unified framework for graph theory and probabilistic reasoning in complex real-world settings. This has lead to the development of a framework to generate intelligent behavior in a fashion similar to neural computation in the brain: a massively parallel distributed computing system, in which overall performance comes from independent computation of local units that communicate with a subset of neighboring nodes. Today, many neuroscientists use Brain Graphs as a way of modeling the human brain connectome, by abstractly defining the nervous system as a set of computational nodes and interconnecting edges. In such Brain Graphs nodes represent collections of similar neurons (in terms of structure and function), while edges represent structural - and hence functional - connections between those nodes.

In our research we model Brain Graphs for sensory perception and motor action generation in the setting of a simple autonomous mobile robot that interacts in its environment. We investigate Factor Graphs (a subclass of Graphical Models) to represent relations between observable sensory signals, possible hidden states, and desired motor output. Belief propagation updates (also known as Sum-Product Message Passing) perform inference between those variables by calculating marginal distributions for unobserved nodes, conditional on available observed sensory data.

Using this mechanism, we develop the following probabilistic reasoning framework and apply it on a 3-wheel omnidirectional mobile robot to infer adequate motor commands given sensory input. In our model, we define several random variables as nodes in the graph: current velocity (V), desired velocity (D), motor acceleration (A), and motor command (M). The

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network computes marginalizations over certain nodes by message passing. Currently, our model handles each motor separately, but can be extended to simultaneously cover all motors of the robot under consideration, which involves probabilistic computation such as likelihood maximization or maximum a posteriori to estimate unobservable model parameters. Initial experiments indicate that reasoning in this graphical system yields comparable results to standard conventional control approaches.

Acknowledgements

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[T 11] Ornstein-Uhlenbeck-process joins and extends different theories of correlations

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Different models are in use for to investigate neuronal reccurent networks and their resulting structure of covariances. The diversity of models brings up the question, which features of correlations are generic properties and which are peculiarities of the often abstracted neuronal dynamics. Currently, it is unclear how different neuron models relate to each other and whether and how results carry between models.

In this work we present a unified view on pairwise correlations in recurrent random networks. We consider binary neuron models, leaky integrate-and-fire models, and linear point process models. We show the equivalence between each of these models after linear approximation to the Ornstein-Uhlenbeck (OU) process [2]. The above mentioned models split into two groups, which are distinct from each other only in a matrix prefactor scaling the noise and the choice of variables interpreted as neural activity.

The known closed form solution of OU processes [2] holds for both classes. This approach enables us to map results obtained for one model to another, in particular we extend the theory of correlations of all considered models to the presence of synaptic conduction delays, and present a simpler derivations for some established results [4].

The approach is applicable to general forms of connectivities, and for the purpose of comparison to direct simulations, population averaged results are presented. The method of linearization required to map non-linear models to the OU process employs elements of a mean field approach. Furthermore, it takes into account neuron input distributions around mean field values, increasing the accuracy of the results and showing the influence of fluctuations on effective system parameters that determine e.g. the presence and parameters of oscilations. The theoretical population averages are exact for fixed out-degree network architectures and approximate for fixed in-degree. The latter, however, are beneficial for non-linear models, allowing a simpler linearization based on mean-field arguments.

Finally we show that the oscillatory instability known for networks of integrate-and-fire models with delayed feedback [3] is a model-invariant feature of any of the studied dynamics: We find that an identical pole structure of the cross spectra determines the population power spectra in different models and we explain the class dependent differences between covariances in time and frequency domain.
Acknowledgements

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[T 12] Cellular Distributions for Cortical Network Models: A fast approach for in-vitro characterization and translation of single-cell data into simple neuron models

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There is a growing interest in large-scale network simulations that capture the cellular heterogeneity and variation observed in real cortical tissue, as more and more experimental information becomes available on the role of cellular diversity in cortical dynamics and computation [1,2]. Both developing (fitting) and simulating such a diversity of cell models which capture the spiking behavior of their real-cell counterparts in sufficient detail can be computationally guite demanding. It may therefore be desirable to have single cell models which, on the one hand, are simple enough to allow for fast fitting to experimental data and relatively short simulation times, but which on the other hand are still physiologically highly valid in the sense that they can reproduce and predict a number of spiking characteristics of the real cells. In preparation for a physiologically detailed prefrontal cortex (PFC) network model, we characterized in vitro in adult rodent PFC >200 pyramidal and inter-neurons from various layers with standard electrophysiological protocols. For the purpose of translating these data efficiently into single cell models, we derived closed-form expressions for onset and steady-state f-I curves (firing rate over step current) for a simplified version of the adaptive exponential (AdEx) [3,4] and for the adaptive leaky (aLIF) integrate-&-fire model. These expressions allowed for a fast and completely automatized procedure which tightly fits these cell models to their experimental counterparts. Although the model neurons have been fitted solely on standard experimental f-I and sub-rheobase V-I curves, it is shown that they still can predict the spiking behavior (timing and rate) of their experimental counterparts to in-vivo-like fluctuating current inputs very well within the bounds of physiological reliablity.

This approach was then used to translate our pool of adult rodent PFC slice recordings into a variety of physiological cell types and distributions of cellular parameters for the construction of a large-scale realistic PFC network model from which first results will be shown. This approach may therefore offer a promising tool for developing physiologically valid yet still simple and relatively fast to simulate neuron and network models.

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$\left[T \ 13\right]$ Input-dependent decorrelation of neuronal activity in rat barrel cortex

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The barrel cortex of mouse and rat is a highly topographically organized cortical structure with each barrel corresponding to exactly one individual whisker. Recently, it became possible to record membrane potentials of neurons in a barrel in awake behaving animals and correlate these measurements with the whisker movements and spiking activity [1,2,3]. If the animal sits quiet, membrane potentials show slow oscillations (~1-5 Hz) and high pairwise correlations, while during whisking these oscillations get reduced and membrane potential correlations decrease [3]. In particular, during quiet wakefulness spiking of excitatory neurons is hardly correlated and driven by individual depolarizing inputs, whereas the spiking of inhibitory cells is clearly correlated and coincides with the depolarized phase of the membrane oscillation. In response to sensory input it appears that it is predominantly the spike correlations between excitatory and inhibitory neurons that get reduced, while excitatoryexcitatory spike correlations stay low and uneffected [4]. This decorrelation of barrel activity is believed to enhance the signal processing and decoding of sensory input [5]. In [4,5] both simplified rate models as well as spiking neuron network simulations were presented that explain the decorrelation in response to sensory input by feedforward inhibition and spike threshold non-linearities.

Here, we study recurrent spiking neuron networks that comply with the measured connectivity, neuron parameters, and synaptic weight statistics for layer 2/3 and 4 of barrel C2 of barrel cortex [6,7], and analyze under which circumstances these networks produce the observed membrane potential and spike correlations in different input regimes.

From a theoretical point of view it is noteworthy that the barrel cortex networks appear to be much denser and more strongly connected than commonly assumed in the oft-applied theory of balanced random networks [8,9], and that rates of individual neuron types are very disparate, with excitatory neurons firing at much smaller rates (\sim 1/s) than inhibitory neurons (\sim 10/s) [3].

Thus we will moreover analyze, if a reduced population model akin to the one derived in [10] to explain the observed decorrelation in balanced random networks [11] can be employed in the more heterogeneous barrel network as well.

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[T 14] Weak Perturbations in Large-Scale Cortical Network Models

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The importance of the occurrence and timing of a single action potential in cortex has remained unresolved. Given the number of neurons and the weak and unreliable nature of cortical synapses, it has been argued that individual action potentials carry little significance. In contrast, recent experimental and modeling studies suggest that individual action potentials have a measurable effect on the subsequent evolution of the overall network dynamics [1-3]. It is unknown under what circumstances cortical networks exhibit such sensitivity to weak perturbations. In particular, it has remained unclear how the sensitivity of cortical networks to very small perturbations depends on network connectivity and overall network state (e.g. awake versus anesthetized).

We here used large-scale simulations of Izhikevich neurons [4] to determine the effect of weak perturbations on the overall network activity structure. Specifically, the model consisted of a two-dimensional layer of excitatory pyramidal cells (PYs) and a two-dimensional layer of fast-spiking inhibitory interneurons (INs). Fast, excitatory synapses connected PYs to PYs, and PYs to INs whereas INs provided fast inhibitory input to PYs. The connection topology for the PY-PY connections was chosen to be either local, small-world, or global random. Perturbations to the membrane voltage were applied by injection of weak currents. We assessed how weak perturbations propagated through the network as a function of the network configuration and what perturbation parameters enabled transitions between different macroscopic activity states. Understanding the effect of weak perturbations will help to elucidate sensory processing where sensory input has to overcome ongoing spontaneous network activity that may dominate overall activity structure in the awake animal. Furthermore, more refined brain (micro-)stimulation paradigms may be designed to specifically exploit regimes of high sensitivity to efficiently modulate pathological network dynamics as a treatment of neurological and psychiatric disorders with underlying functional pathologies in cerebral cortex.

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[T 15] Feasibility of long-range synchronization with zero phase lag in a relay network

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The long-range synchronization of neuronal activity between brain areas is now well established experimentally, in particular for the beta (14-30 Hz) and gamma (40-80 Hz) frequency bands. It is remarkable that some of the reported synchrony appears to have zero phase lag, given the synaptic and conduction delays inherent in the connections between distant brain areas. This has led to speculations about a possible functional role of zero-lag synchrony in neuronal communication, attention, memory and feature binding (Fries, 2005). However, recent studies using single-unit and local field potential recordings point to synchronization with non-zero phase lags (Uhlhaas et al., 2009). Hence we ask here under which conditions zero-lag synchrony can occur in the brain.

Several theoretical studies have argued that mutual pulse-coupling with delays and excitatory synapses cannot easily lead to zero-lag synchrony (Zeitler et al., 2009). This study therefore uses the second simplest network for interacting neuronal populations: two synchronizing oscillators which interact via a relay oscillator (Fischer et al., 2006; Vicente et al., 2008), where the relay could for example represent the thalamus (Gollo et al., 2010). Analytical results and computer simulations were obtained for both type I Mirollo-Strogatz and type II Hodgkin-Huxley neurons. A main result of our study is that synchronization is easier to achieve with the latter than with the former. Furthermore, we have investigated various types of synaptic coupling and find that alpha synapses with short rise times (typically less than 2 ms) are more suitable for achieving zero-lag synchronization.

We have also considered the potential impact of Spike-Timing Dependent Plasticity (STDP) for various learning windows. In agreement with Knoblauch and Sommer (2003), we found that with STDP the network converges to zero-lag synchronization at a faster rate and for a larger range of synaptic strengths and delays times. However, when the delay times between the two synchronizing oscillators and the relay oscillator are different, zero phase lag is easily lost. Furthermore, adaptation of the synapses often took quite some time (in general more than 500 cycles); considerably more than the observed time range of 200 to 250 ms to generate zero-lag synchrony in the gamma frequency range in visual perception (Rodriguez et al., 1999). Considering the actual conditions present in the brain, our study hence suggests a cautious re-evaluation of the proposed functional role of zero-lag synchrony.

Figure 1: Influence of synaptic rise times. For different conduction delays τ (normed to the intrinsic period) and synaptic weights ε , (A)-(C) show synchronization quality and (D)-(F) convergence promptness, respectively, for Mirollo-Strogatz neurons. The rise time of the alpha synapses is set to 1 ms in (A) and (D), 2 ms in (B) and (E), and 3 ms in (C) and (F).



Figure 1

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[T 16] Modelling homeostatic control of intrinsic excitability in single neurons

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Intrinsic excitability in neurons is controlled by a number of homeostatic mechanisms, among which are the modulation of conductances in voltage-dependent ion channels and the modulation of the distance of the axon initial segment (AIS) from the soma. Due to their large size and good accessibility in slice experiments, a useful model system for these forms of homeostatic regulation are principal neurons of the medial nucleus of trapezoid body (MNTB) in the auditory brainstem. These act as relay neurons, receiving excitatory input and transmitting inhibitory signals to the auditory nuclei involved in sound localisation. One form of homeostasis of intrinsic excitability has been shown to be mediated by Nitric Oxide (NO), which is released by MNTB neurons in an activity-dependent manner and modulates Kv3 and Kv2 potassium channels conductance. We have investigated this homeostatic regulation

in a multi-compartment MNTB neuron model, incorporating the localisation of ion channels in the soma and the AIS. The analysis of the model showed that the main effects of NO synthesis, a reduction of excitability and concomitant changes in action potential shape as observed in vitro (Steinert et al., Neuron, 2008, 2011), can be accounted for by increasing Kv2 conductances. Moreover, we found that the localisation of ion channels in the AIS, as opposed to the soma, results in a significantly faster action potential onset, with this effect increasing as the AIS is located more distally to the soma. Consistent with previous reports (Grubb & Burrone, Nature, 2010), the latter also increased neural excitability. We currently investigate how NO synthesis and AIS location affect the integration of synaptic inputs for different average activity levels and other statistical features of the input.

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[T 17] Large scale neural model of the human cortex functional connectivity based on empirically derived resting state networks

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Resting state functional connectivity (FC) between region pairs in the whole brain exhibits complex spatio-temporal patterns, which are organized into so-called resting state networks (RSNs). It is commonly assumed that underlying anatomical connectivity shapes spatial properties of the RSNs. However, strong FC between two cortical regions observed even without direct axonal connections implies that FC cannot be understood in terms of anatomical connectivity alone. Here, we aim to address the question of the FC between anatomically unconnected areas by simulating large-scale neural networks of resting state FC of the human cortex. Our model is based on an empirically derived FC network from resting state fMRI data, as adapted from the study of Kiviniemi et al., (2009). This network is comprised of 64 network nodes/regions of interest (ROIs), which are chosen from all over the cortex. There are 30 pairs of inter-hemispheric homologues, and 4 additional ROIs are chosen along the midline. We explore topology and dynamics of the network supported by the large-scale connectivity matrix, which entries indicate temporal correlations between the pairs of the network nodes. We investigate how networks topologies change for different correlation thresholds and how they differ from comparable random networks. Similarly, networks dynamics simulated for different spatio-temporal networks, obtained after thresholding the correlation matrices, enable us to characterize parameters important for the emergence of the coherent fluctuations in the network. In our model the local node level is described by nonlinear models such as a population of FitzHugh-Nagumo systems and network dynamics is modelled with different

parameters for each node and different time delays to account for the finite signal propagation times between the nodes. From a stability analysis we demonstrate that time-delay plays a significant role in emergence of different functional state networks.

[T 18] Dynamical causal modeling reveals modulation of prefrontal-hippocampal connectivity by a genomewide significant schizophrenia variant

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Recently developed data analysis techniques such as Dynamical Causal Modelling (DCM) move beyond classical "static" approaches by proposing generative models of fMRI data that have physiological interpretability [1, 2]. Such nonlinear models of neural ensemble dynamics are now frequently used to infer on effective connectivity between brain regions. Altered interactions between brain areas have been proposed to underlie several psychiatric disorders. In schizophrenia, abnormal coupling between dorsolateral prefrontal cortex (DLPFC) and hippocampal formation (HC) has been demonstrated, but the relevance of these changes for heritable risk is unclear [3]. We used DCM to investigate relations between genetic risk variants for schizophrenia and effective connectivity between DLPFC and HC and examine the robustness of these relations across three different German samples . Here we report effects of a polymorphism on ZNF804A (rs1344706), a genome wide significant risk variant for schizophrenia [4], on brain connectivity in 180 participants. Subjects performed an N-Back working memory task which activated the right DLPFC and deactivated the left HC. We constructed a systematic set of DCMs describing interactions between both regions. To test whether endogenous fluctuations had an important effect on the task we estimated our DCMs considering two different approximations: classic, assuming that brain connectivity is only driven by the task, and stochastic, assuming that brain connectivity is driven by the task and also by some endogenous fluctuations independent of the task that are included in the model as noise. Our preliminary results show that self-connection in right DLPFC and connection between right DLPFC and left HC are modulated by genotype leading to different connectivity between risk allele carriers and non-risk allele carriers. This study illustrates how one can establish the functional significance of specific genetic polymorphisms for disease mechanisms and thus help identifying potential targets for the development of new treatments.

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$\left[T \ 19\right]$ Stimulus driven correlation gain modulation in neuronal networks

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In order to analyze the response of a neuronal network to an external source of correlated inputs it is useful to divide the input correlations into "between" and "within" correlations (Yim et al. 2011). The "between" correlations (B) are defined as the mean pairwise correlation between spike trains from the presynaptic pools of different neurons, whereas "within" correlations (W) refer to the mean pairwise correlation between spike trains belonging to the same presynaptic pool. In a random network the two types of correlations are same, however, in inhomogeneous networks W and B may differ strongly (Lindsay et al. 2012). From an abstract point of view, neurons in a recurrent network receive just two different sources of input, one coming from outside the network and the other coming from the network itself, each of these sources may have a different structure in terms W and B and the interplay between these two structures will define the correlation gain of the network. Correlation gain of a network can be adequately studied using a reduced two-neuron model. Here, we consider the case of two neurons receiving correlated inputs corresponding to the external and local network input. We show that the interplay between the correlation structure of local and external inputs provides a flexible mechanism to dynamically modulate (increase or decrease) network correlations. The correlations W and B are shaped by both the structure of the connectivity as well properties of the input. Thus, beyond proposing a mechanism to modulate correlations our findings clearly suggest that it is highly important to know the connectivity structure of the input projections as well that of the receiving network in order to correctly predict the impact of sensory and/or top-down inputs on the neural activity.

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[T 20] Site of spike initiation changes with functional context in coincidence detector neurons

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Principal cells of the medial superior olive (MSO) are very fast coincidence detectors in the auditory brainstem that encode interaural time differences by their firing rate. Their enormously low time constant of only a few hundred microseconds is caused by the very low input resistance of about 5M Ω at rest [1], which arises from the expression of low-voltage-activated potassium channels (KLVA) and hyperpolarization-activated unspecific cation channels (HCN). Spike initiation is generally assumed to occur in the axon's initial segment (AIS). However, in neurons with very low input resistance, as in the MSO, this may no longer hold true, because the soma constitutes an enormous current sink. Moreover, these cells receive a huge amount

fast excitation and slowly-decaying inhibition at rates up to 2 kHz, such that their input resistance in vivo is even much smaller than at rest. Hence the questions arise: how are these cells able to elicit action potentials (APs)? And, how are these cells able to uphold their biological function?

By using a multi-compartmental model of an MSO cell and its axon, we found that, at rest, the spike initiation segment (SIS) in the model is indeed the AIS, because the electrotonic independence of the AIS from the leaky soma results in an input resistance of the axonal segments that is considerably higher than at the soma. For higher input conductances, as they are obtained by simulating naturalistic synaptic activity, the SIS can also be found further distal in the axon. This is because the excitatory and inhibitory conductances by themself and via opening KLVA and HCN channels, respectively, reduce the excitability of the AIS, while more distal axonal regions are much less affected.

We conclude that, although in cases where the AIS itself is not excitable, the deeper axon is, and enables the cell to convey information downstream. We show that the cells ability to initiate spikes distally enhances the dynamic range of the generated rate code. Moreover, the model suggests that especially the low rate part of the code is mostly established by distally initiated AP responses.

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$\left[T\ 21\right]$ Theory for the spiking statistics of a neuron driven by stochastic oscillations

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The spontaneous activity of neurons as well as the neural variability in response to repeated stimuli cannot be understood without taking into account various sources of noise. To assess the effect of fluctuations, simplified stochastic models have been suggested, for which the spiking statistics can be calculated analytically. Most of these models generate spike trains with independent interspike intervals (ISIs) – so-called renewal point processes. In recent years, however, a number of studies have reported pronounced correlations between ISIs for various types of neurons, thus providing experimental evidence for non-renewal spiking [1,2]. For such neurons, analytical techniques to compute the relevant firing statistics are scarce.

Here, we discuss one specific source of non-renewal spiking, namely, a stochastic input current with a pronounced periodicity (stochastic oscillation). For a perfect integrate-and-fire model driven by such a stochastic oscillation, we calculate the ISI density and the serial correlation coefficient (SCC) extending previously developed analytical methods [3, 4]. These results are used to explain the complex spike patterns of electrosensory afferents in paddlefish [5] that receive stochastic input with a strong oscillatory component. By fitting the theoretically obtained SCC to the data, we are able to extract unknown biophysical parameters such as the quality of the oscillatory driving. Our theoretical results can be extended to Gaussian input currents with arbitrary correlation function and may be thus helpful to analyze the spiking statistics of neurons stimulated by signals with a complex temporal structure.

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$[T\ 22]$ Complex network structure can affect the balance of excitation and inhibition in large directed networks of cortical neurons and synapses

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There are two fundamentally important aspects of brain network connectivity about which very little is known. The first is whether complex network structure is embedded in microscale neuronal networks, where nodes represent individual neurons, and edges represent synaptic connections between neurons. The second unknown is how complex network structure at the micro-scale impacts on neuronal dynamics in terms of aspects such as plasticity, synchronization, hyperexcitability and learning.

These two questions are unanswered because current imaging techniques are unable to resolve the sufficiently large numbers of individual neurons, and their 1000s of synaptic connections, and these are needed to create a mathematical network model. In the absence of such information, many simulations of large cortical networks and their electrical activity assume simple random connectivity.

Here we highlight how large networks of spatially embedded neurons in the cortex exhibit a unique set of features that are unparalleled in other network models beyond neuroscience. A key feature is the presence of two main classes of neurons: excitatory and inhibitory. We propose new methods that are specifically tailored for simulating and statistically characterising such networks and describe simulation results that employ these methods in order to study hypothesised "non-random" connectivity in both visual cortex area V1, and in the primary olfactory cortex.

It is demonstrated that incorporation of a variety of complex structural features, such as directed clustering, can unexpectedly influence the balance of excitatory and inhibitory activity amongst the neurons in the network. In particular, we present results on networks that exhibit population oscillations due to sparse synchronization, and show that hyper-excitability (an indicator of epilepsy) that is not present in random networks can be induced when the network is instead highly clustered.

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$[T\ 23]$ Two types of adaptation currents differentially affect the firing rate dynamics and spiking variability of large recurrent neuronal networks

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A prominent feature of many types of cortical neurons is spike-frequency adaptation, shown by a decrease in spike rate during prolonged stimulation. This behavior is typically mediated by slow potassium currents through voltage-dependent low-threshold or calcium-activated high-threshold channels, both of which are susceptible to cholinergic modulation [1]. Here we describe how such adaptation currents affect spike rates, spiking variability, and oscillatory activity in large recurrent networks of sparsely coupled excitatory and inhibitory neurons, depending on the strengths of external feed-forward and recurrent excitation.

To allow for large numbers of conductance based synaptic inputs with realistic efficacies, we take a mean-field approach based on the Fokker-Planck (FP) equation complemented by large network simulations. The FP equation provides a useful tool to analyze the dynamical properties of large neuronal networks as has been demonstrated using the leaky integrate-and-fire model [2]. We apply the experimentally verified adaptive exponential integrate-and-fire neuron model [3,4], which incorporates voltage-sensitive subthreshold and spike-dependent adaptation, respectively, representing the two types of slow potassium currents.

We find that an increased subthreshold adaptation current causes the network to become silent after a transient period of activity unless external or recurrent excitation is sufficiently large. When the adaptation current is spike-triggered on the other hand, up-and-down states occur in regimes where recurrent excitation dominates inhibition as well as the feed-forward input. Interestingly, both adaptation mechanisms oppositely affect spike train variability. Subthreshold adaptation increases the coefficient of variation of inter-spike intervals while spike-triggered adaptation leads to more regular spiking. For balanced networks we further show how spike rate oscillations in response to rhythmic external inputs are modulated. At lower frequencies adaptation currents lead to phase advances, whereas without adaptation we observe only phase delays. At high frequencies on the other hand these currents mediate spike rate resonance. Our results emphasize the influence of spike-frequency adaptation on network activity and indicate that its specific effects strongly depend on the type of adaptation.

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$\left[T \ 24 \right]$ Transcranial electrical stimulation accelerates sleep homeostasis in humans

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During sleep the human electroencephalogram (EEG) shows large scale oscillations of approximately 0.75 Hz. These slow-wave oscillations (SWO) are considered a marker for sleep pressure and homeostatic recovery from wakefulness. Here we show that a short period of weak transcranial electrical stimulation can accelerate the normally occurring decay of SWO in the course of the night. This work combines human sleep EEG data with a multi-scale computational model of SWO and electric stimulation. In addition to providing insight into the mechanisms of sleep homeostasis, this empirical finding of accelerated slow-wave decay suggests that it is possible to increase the efficiency of sleep.

Sleep pressure is reflected in the power of slow-wave oscillations observed in the human EEG: Power is high after extended wakefulness and gradually decays during sleep [Borbély et al., 1981]. Transcranial stimulation with oscillating currents matched in frequency can entrain SWO and transiently increase their power [Marshall et al., 2006]. Here we show in humans that 25 minutes of oscillating stimulation at the beginning of sleep attenuates the natural decay of SWO in the remainder of the night. Both the decay in power as well as the spatial coherence of SWO is reduced (N = 10 participants, p=0.016, p=0.009 respectively). The analysis to the EEG data was motivated by predictions from a multi-scale computational model. On the macroscopic scale a finite element model estimated electric field intensities using realistic anatomy of the human head and brain. On the microscopic scale, SWO were modeled with a network of synaptically connected spiking neurons. The network was tuned to exhibit periodic transitions between active and quiescent states resembling "UP" and "DOWN" states which are known to underlie SWO [Steriade et al., 1993]. The electric fields couple with the network by incrementally polarizing the membrane of excitatory cells following established biophysics [Fröhlich et al., 2010, Reato et al., 2010]. This polarization results in increased or decreased network firing rates depending on polarity. With transcranial stimulation in humans the folding of the cortical surface leads to a mix of stimulation polarities across cortex. The model shows that despite this mixed-polarity stimulation there is a net increase in firing rate as a result of entrainment of the network SWO with slow-oscillating stimulation. It has been hypothesized that homeostatic synaptic downscaling underlies the homeostatic decay of SWO naturally observed in the course of the night [Riedner et al., 2007]. When homeostatic plasticity is taken into account, the model predicted that the increased firing rate would speed up synaptic downscaling and thus accelerate the decay of SWO during stimulation. As a direct consequence of this faster decay during the stimulation, the decay in the hours following the stimulation is reduced. This is precisely what we observed in the human EEG data. More specifically, the size of the subsequent decay correlated with the predicted values which varied across different electrode locations as a result of the differing cortical polarization (p=0.02, N=11 electrodes). Thus, the multi-scale model not only provided a mechanistic explanation for the observed accelerated homeostatic decay of SWO, but it quantitatively predicted the size of the effect across different cortical locations.

The combined experimental and modeling results support the hypothesis that electrical stimulation can accelerate synaptic homeostasis, and thereby influence a putative process of sleep regulation. The ability to accelerate the homeostatic function of sleep may have important practical implications. For instance, it will be interesting to determine in future studies if such acceleration results in increased sleep efficiency and improved human behavioral performance.

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$[T\ 25]$ Brute force parameter fitting for a simulation of an in vitro neuronal network

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We developed a pulsing model called INEX [1] which simulates neuronal activity as observed in neuronal networks cultivated on multielectrode array (MEA) neurochips. In an in vitro experiment approximately 500,000 cells of the frontal cortex of embryonic mice are cultivated on such a MEA neurochip (experiments are carried out by NeuroProof GmbH, Rostock, Germany). Circa 10,000 neurons and 90,000 glia cells of the total amount survive.

The INEX model is based on an inhomogeneous Poisson process [2] to simulate neurons which are active without external input or stimulus as observed in neurochip experiments. It is accomplished using an Ising model [3] with Glauber dynamics [4] and has four parameter types: basic activity c, the excitatory weights w_e of the synapses which have positive values, the inhibitory weights w_i of the synapses which have negative values and a factor f indicating the varying probability for the occurrence of spikes depending on the previous activity of the neuron. Using an automated fitting method, these four parameter types were chosen in the following way: First, the ranges for the four parameter types were set. Then we simulated twenty times a neuronal network with 800 excitatory and 200 inhibitory neurons with parameter type values in different intervals but within the range. For each spike train twelve activity describing features were calculated. The same features were calculated from the spike trains of twenty MEA neurochip experiments with cell cultures originated from frontal cortex of embryonic mice after 28 days in vitro. Per experiment 15 to 50 spike trains were available. The simulated and the experimental spike strains had a length of 30 minutes. The mean value and the standard deviation were calculated for all features. The parameter fitting was considered as successful if the calculated features of the simulated spike trains lay within the standard deviation of the MEA neurochip features.

The parameter types are scalable. For the choice of the parameter range we developed a heuristic based on spike rates and burst rates observed in experiments and the dependency between the parameters. The described brute force parameter fitting was applied within the intervals according to the derived parameter dependency. Results were shown in several isoline 3D plots depending on the value of f with the mean basic activity of all 1,000 neurons on the xaxis, the mean inhibitory weights on the y-axis and the mean excitatory weights on the z-axis.

The simulated spike trains show typical synchronous spike and burst patterns as known from MEA neurochip experiments with frontal cortex neurons. Calculated features adapted from spikes and bursts indicate that the presented model simulates neuronal activity similar to activity as observed on MEA neurochips.

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[T 26] How intrinsic neuronal heterogeneity shapes the cross-correlation functions between spike trains

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Neurons of the same type are intrinsically heterogeneous, showing diverse output firing rates and imprecise spike timing in response to identical fluctuating input currents (Padmanabhan and Urban, 2010). These experimental observations can be reproduced in a population of leaky integrate-and-fire (LIF) model neurons. By rescaling the dynamic equations of the LIF neuron, mathematical relations between multiple neuronal parameters and input noise have been derived, and an identical input to heterogeneous neurons can be conceived as an identical noise with neuron-specific mean and variance (Yim et al., 2011). We further investigated the response relation of pairs of heterogeneous neurons receiving identical input by studying the cross-correlation function (CCF) between their spike trains. We find that the symmetry of the CCF is broken if the rescaled mean of the input to the two neurons is different. The neuron with the higher mean has a higher firing rate and tends to spike earlier than the other one. This is consistent with the previous theoretical finding that a pair of neurons with different firing statistics can exhibit an asymmetric CCF (Ostojic et al., 2009; Tchumatchenko et al., 2010). On the other hand, the symmetry of the CCF is preserved for neurons with different rescaled variances, even when their firing rates differ. This suggests, among other things, that more excitable neurons do not necessarily respond faster to common input.

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$\left[T \ 27 \right]$ Reconstruction of connectivity in sparse neural networks from spike train covariances

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The inference of causation from correlation is in general highly problematic. Similarly, it is difficult to infer the existence of physical synaptic connections between neurons from correlations in their activity. Covariances in neural spike trains have been the subject of intense research, both experimentally and theoretically. Linear models present a direct way to characterize the influence of recurrent connections on covariances in a resting state of asynchronous activity. The effect of direct connections is then described by a matrix of linear coupling kernels. However, as indirect connections also give rise to covariances, the inverse problem of inferring network structure from covariances can generally not be solved unambiguously.

Here we study to which degree this ambiguity can be resolved if the sparseness of neural networks is taken into account. To reconstruct a sparse network, we determine the minimal network of linear couplings consistent with measured covariances by minimizing the L1 -norm of the coupling matrix under appropriate constraints. Counterintuively, after stochastic optimization of the coupling matrix, the resulting estimate of the underlying network is directed, even if only a symmetric matrix of count covariances is known.

The performance of the method is best if connections are neither exceedingly sparse nor dense, and it is easily applicable for networks of a few hundred nodes. Time dependent coupling kernels can be obtained if the full matrix of covariance functions is known, as is demonstrated from simulated spike train data.

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[T 28] Firing rate mismatch can lead to inphase synchronization of neurons coupled by delayed excitatory synapses

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Synchronous firing of neurons has received much attention in relation to the generation of brain wave rhythms and information processing at various aspects in the neuronal systems [1]. It is shown that with inhibitory synapses, inphase firing of neurons is possible in presence of the finite time of transmission of signals between the neurons [2, 3]. Such time-delayed

coupling between neuronal oscillators arises naturally from the neurophysiological origins in processes such as synaptic transmission and axonal propagation of the action potentials.

For the type-I neural oscillators with non-negative phase resetting curve, zero-lag synchronization with excitatory synapses is possible only if the synapses are instantaneous, i.e. the communication delay is ignorable [4]. Otherwise, as noted above, inhibition not excitation can synchronize neural firing.

Presence of inhomogeneity in the network of neural oscillators also destabilizes synchrony [5, 6]. In principle coupled oscillators can overcome mismatch in intrinsic firing rate and match their frequencies, but with certain phase lag. Can the delay (synaptic and axonal) in signaling compensate for mismatch-induced phase lag? We follow this hypothesis by numerical study of two coupled dissimilar type-I model neurons. We show that inphase firing of the neurons is possible with delayed excitatory synapses for certain range of delay time. The investigation is repeated by different configuration of the excitatory and inhibitory couplings between two neurons. The main results are: 1- In presence of mismatch, the neurons can not be synchronized with coupling via inhibitory synapses. 2- With finite delay in communication, mismatch in firing rates of the two neurons can enhance synchrony and 3- Presence of excitatory coupling from the fast neuron to the slow neuron is mandatory to achieve zerolag synchrony. Parameters of the reverse coupling (from slow to fast) are less effective in the dynamics of the system.

Figure's caption: Density plots show cross-correlation of the membrane voltages of two coupled neurons as a function of firing rate mismatch and delay time. In the left (right) panel an excitatory synapse is present from fast to slow (slow to fast) neuron. In the middle panel couplings are bidirectional with equal strengths and the same delay time. Larger correlation appears as brighter color. In the right panel complete synchronization can be achieved just with zero mismatch which can not be clearly seen. The model neurons are type-I Morris-Lecar neurons with mainly positive phase reset curves [7]. Delay time is measured in the units of the intrinsic inter-spike interval of the slow neuron and the mismatch is defined as the difference of the external current normalized by the current of the slow neuron.



Figure 1

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[T 29] The Function and Fallibility of Visual Feature Integration: A Dynamic Neural Field Model of Illusory Conjunctions

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Objects are composed of various surface features such as color and shape. The visual system codes many of these features in distinct neuronal populations. Yet we normally perceive objects as coherent wholes rather than seeing aggregations of unrelated features. This suggests the existence of an integrative process conjoining visual features. Psychophysical studies indicate this integration process to be fallible, however, as it sometimes erroneously combines features from different objects. These errors are referred to as illusory conjunctions [1]. For example, when subjects briefly view a multi-letter display containing a green 'T' and a red 'X', they might report having seen a green 'X'. Illusory conjunctions provide a valuable test case with respect to the functional mode of visual feature integration.

We developed a neurodynamic model of the processes involved in integrating visual features into multi-feature objects, based on the framework of Dynamic Field Theory [2]. We then tested it using a typical illusory conjunctions task. The model consists of several coupled neural field representations with lateral interactions, organized into three modules: First, a low-level representation of the visual stimuli, capturing feature information and location; second, a spatial pathway, dealing with spatial attention and the read out of item location; third, a surface feature pathway, dealing with feature attention. The surface feature pathway additionally includes a feature representation that can either retain feature information of one item in the form of sustained activity or read out an item's feature information. The model includes two instances of both the low-level representation and the surface feature pathway, one for color and one for shape. The two low-level representations are connected only through the spatial pathway. When information about a feature of one item is retained in the surface feature pathway, it exerts a biasing effect on the other parts of the model. As a consequence, the spatial location of the respective item is selectively attended. As this location also contains the item's second feature, it can be extracted from the low-level representation. The resulting pattern of activation then fully captures the item's feature and location configuration. In the process, illusory conjunctions may emerge due to the coarse nature of featural and spatial selection mechanisms.

Our model captures several key findings reported in the behavioral literature. Namely, illusory conjunctions occur more often between spatially close stimuli [3] and between stimuli that share similar features [4]. Additionally, the illusory percept tends to be located at the midpoint between the two involved stimuli [5]. These parallels with psychophysical findings suggest that the model provides a robust theory of feature integration in early vision, particularly supporting the notion of a shared spatial frame as the basis for visual feature integration.

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[T 30] How ion-channel cooperativity can influence neuronal activity

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Individual stochastic units, so-called ion channels, are responsible for electrical signaling in the brain. Despite accumulating evidence for additional interactions between ion channels [1-2], the prevailing assumption is that ion channels act independently. Since Hodgkin and Huxley's model of action potential (AP) initiation, it is supposed that channels change their open probability in response to a common signal such as the membrane voltage, but do not directly influence each other.

Enhancing or hindering interactions between channels are known to exist and therefore consequences for neuronal spiking dynamics can be expected. Nevertheless, they have so far received relatively little attention in the analysis of excitable membranes. Naundorf et al. [3] have shown that cooperativity of sodium channels may explain the rapid onset dynamics of APs. Here, using bifurcation analysis and stochastic simulations of an extended Morris-Lecar model, we investigate from a theoretical perspective how cooperative and anticooperative gating between ion channels changes basic sub- and suprathreshold voltage dynamics [4]. The effects of channel interactions include the modification of the range of sustained firing and cell-intrinsic noise, the prolongation of AP duration, the occurrence of multistability and type-3-like firing. In contrast to modifications in channel number (insertion or blocking of ion channels), the system that modulates interactions between ion channels can maintain the same peak conductances but still drastically change its dynamics. We therefore hypothesize that channel interactions could be an efficient mechanism to regulate the neuronal activity and voltage noise.

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[T 31] A Fast-Slow Minimal Model for Medium Spiny Neurons: A Geometrical Perspective

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The role of basal ganglia in motor control is well-known [1,2], but it also takes part in high order cognitive processes, such as reward-related learning, goal-directed behavior or selective attention [3-5]. The complicated and creative information processing ability of basal ganglia makes it home for decisions amongst available competitive choices. Dysfunction of this sub-cortical network, along with the related neurotransmitters (e.g. dopamine), causes neurodegenerative diseases as Parkinson's Disease or Huntington's Disease [6,7]. D1 and D2 type dopamine receptors have a modulatory effect on this network by controlling the GABAergic signalling from the basal ganglia main input station, striatum, to the direct and indirect pathways. The striatal medium spiny neurons (MSNs) play key role in the formation of the antagonistic functions of direct and indirect pathways. We focused on the state-space behavior of the conductance-based computational model of MSNs which is constituted with nonlinear dynamical systems' approach.

The typical behavior of the striatal MSNs is bursting activity as claimed in [8] and these neurons play a role in synaptic plasticity. Since the conventional Hodgkin-Huxley neuron model is not suitable for modelling the striatal MSNs, L-type Ca+2 (high threshold calcium), Kv1.2-containing K+, Calcium activated Calcium and Calcium activated Potassium (afterhyperpolarization) ion channels are also considered in connection with the role of dopamine receptors in MSNs. The bursting activity that is appeared in torus canards [9] of the proposed MSNs minimal model is explained via the qualitative theory of fast-slow dynamical systems with a significant ratio of time scale parameter (eps«1). In the model we proposed, the generation of bursting pattern depends on two different current mechanisms. Slow current system (sodium) is responsible for the bifurcation branch between equilibrium point and the limit cycles (Andronov-Hopf Bifurcation) by effecting the fast current system (afterhyperpolarization). At the same time, fast current system has a role in spiking activity of the bursting patterns (saddle-node of periodic orbits). A torus bifurcation also appears in the full system. The Subhopf/Fold Cycle type bursting activity of the proposed model is an example of Ca2+ gated inactivation of an inward current [10] and it depends on fold limit cycle bifurcation. Besides codimension-1 bifurcations, period doubling and torus bifurcation are also observed with numerical continuations.

The proposed model is capable of explaining how dopamine release modulates the functions of striatum. The geometry of the phase portraits, imported from significant bifurcation points, allow us to understand the ability of the proposed model. Thus, the whole architecture of the proposed model is shown to be captured by bifurcation analysis.

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[T 32] Critical dynamics and asynchronous rate propagation in homogenous feedforward networks

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Recent experimental and computational evidence suggests that the brain may operate at a critical state characterized by complex dynamics, significant higher-order correlations, and optimal computational properties. We investigate the emergence of critical activity in a homogeneous, feedforward network of McCullochs-Pitts neurons. By applying an eigenstructure analysis of a mean-field Markov chain model, we explain the emergence of persistence, complexity, and higher-order correlations characteristic of criticality. We extend our analysis from an initial treatment of purely excitatory networks to more complex models that include inhibition and noise: excitatory-inhibitory networks display enhanced robustness of the critical state, and noisy networks exhibit stochastic resonance as the addition of some noise mitigates the effect of harsh thresholding.

[T 33] Dynamic Neuronal Excitability

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Neurons generally show two types of excitability [1,2]: Type I neurons support arbitrary long inter-spike-intervals, while type II neurons start firing with a non-zero frequency upon current injection.

Here we show that a transition from type I to type II can be dynamically controlled in a large number of conductance-based neuron models (including Wang-Buszaki, Morris-Lecar, Connor- Stevens, Erisir et al.), e.g. by an increase in leak conductance. We mathematically prove that the bifurcation structure of this transition is organized by a degenerate Bogdanov-Takens-cusp bifurcation point of co-dimension 3 [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 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.

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[T 34] Comparing developmental approaches to generate neuronal morphologies for pattern recognition

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This study compares two different developmental approaches for generating neuronal morphologies, one presented previously in [1, 2], and the other being EvOL-Neuron [3]. Both of these approaches are used to optimize neurons for a pattern recognition task. The difference between the two approaches is that in the first approach [1, 2] the dendritic morphology is represented as a pre-structured genome where the branching pattern of the dendritic tree is denoted by partition trees in the genotype, which can result in only one phenotype, while EvOL-Neuron [3] uses a probabilistic branching approach, which can create a range of phenotypes from a single genotype. During the evolutionary process, the probabilistic branching approach needs to select a genotype such that all the resulting phenotypes perform well. The hypothesis is that this change to the developmental approach for the mapping between genotype and phenotype will produce different selective pressure. In order to facilitate a fair comparison between the neurons produced by the two different algorithms, in an initial study EvOL-Neuron [3] has been modified to generate dendritic trees with a fixed number of terminal points and compartments. The number of terminal nodes, compartments, membrane capacitance, membrane resistance and axial resistance are set to the values used in [1, 2] respectively. A number of input patterns, with a pattern size that equals the number of compartments in each neuron, are stored by using a simple learning rule that is based on long-term potentiation of active synapses [1, 2]. The stored and novel patterns are then presented to the neurons and the fitness of the neurons is determined by calculating a signal to noise ratio over the amplitudes of the resulting excitatory postsynaptic potentials (EPSPs). Each individual neuron in a generation undergoes ten trials of pattern recognition where ten different novel and stored patterns are presented to the neuron and the fitness of the neuron in each case is determined. The average of the ten trials is taken as the actual fitness of the neuron. In both algorithms it was noticed that symmetric trees performed better than asymmetric trees in the pattern recognition task. Also, trees with shorter mean path length performed better than trees with longer mean path length. The best and the average fitness values produced by both algorithms lie in the same range. The main result of using the probabilistic branching approach was that there was additional selective pressure for the algorithm to select more symmetric trees which was not seen in the pre-structured genome approach [1, 2]. We are currently extending our study by optimizing active conductances in addition to dendritic morphologies.

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$[T\ 35]$ Phase shifting in a network of cortical circuits and its implications for communication through coherence

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Everyday tasks, like shifting attention between sensory stimuli, require a highly dynamic communication structure in the brain. Changes in anatomical connections are too slow to meet those requirements. Locally connected populations of neurons can synchronize their activity, giving rise to synchronous oscillatory behavior in the gamma band (30-80 Hz). Changes in the degree of synchrony of network activity and the phase of the oscillations can be achieved faster than changes in the underlying synaptic connections. The Communication Through Coherence hypothesis (CTC) states that two circuits are more likely to communicate effectively if their oscillations are in phase, hence phase changes affect information flow in a network of local circuits. CTC sets specific requirements for the neuronal system, because the phase of a population's oscillation should be adjustable independent of the rest of the network. We develop models to study mechanisms of phase shifting in networks of local circuits and their consequences for information transfer.

We modeled two regions of interconnected Hodgkin-Huxley type neurons. The local circuit in each region consisted of 400 pyramidal cells and 100 interneurons. The neurons were connected by GABA- and AMPA-type synapses, with short axonal delays. Connections between neurons were made randomly with probability p, which reflected the anatomical data for the pre and postsynaptic population. A region can show both synchronous and asynchronous activity, where synchrony increases with the level of depolarization of the neurons. Furthermore, the phase of local circuits can be shifted by applying brief synaptic inputs to either the pyramidal cell population or the interneurons. The new phase is determined by the strength of the pulse and its timing relative to the oscillation.

When two local circuits are connected by excitatory synapses, we find that synchrony can be achieved between these circuits. Synchrony arises when both regions have similar oscillation frequencies or if one projection dominates the other, hence it depends on the strength of the feedforward and feedback connections and the level of depolarization in either region. Axonal delays cause a phase difference between the regions, which can be modified by applying short pulses to one of them. This changes the information flow in the network, as assessed by the mutual information between the spike densities of the two regions.

Taken together, these results show that in the context of networks of spiking neurons, rapid modulation of the direction of communication, as predicted by CTC, is feasible.

[T 36] Grid cells, adapted to a small world

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Individual medial entorhinal cortex (mEC) 'grid' cells provide a representation of space that appears to be essentially invariant across environments, modulo simple transformations, in contrast to multiple, rapidly acquired hippocampal maps; it may therefore be established gradually, during rodent development. The possibility is currently being explored of running experiments in which rodents develop, during the critical period for grid cell formation, between P15 and P35, on a revolving sphere, with virtual reality provisions that should give them the visual impression of living and running on the surface of a tiny planet – literally a small world. What grid cell firing maps would we expect to observe after such a training protocol? Our single-cell adaptation model predicts a sequence of spherical harmonics, each of which is the optimal asymptotic solution for the self-organizing adaptation process, within a certain range of the world radius.



Figure 1

$\left[T\ 37\right]$ Morphological properties of neurons in the honeybee auditory system

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Honeybees use a specialized symbolic communication, the waggle dance, for sharing information about remote food sources in the colony by vibratory signals. These signals, consisting of 20 ms sound pulses with a carrier frequency of about 265 Hz (Kirchner et al. 1988), are detected via the antennae and processed by neurons in the auditory system (Ai et al. 2009).

Using preliminary data of one nurse (young) honeybee and of one forager (older) honeybee, we analyzed the morphological and physiological properties of the DL-Int-1 (or AMMC-Int-1, Ai & Itoh 2012) interneuron in the honeybee auditory system which is thought to be involved in the processing of the acoustic communication signals (Ai et al. 2009). The neuron's dendritic arborizations shows a conspicuous dichotomy forming a dorsal branch (DB) and a ventral branch (VB).

For metric analysis, we determined surface area, volume, number of branch points, mean dendritic diameter, distance of terminal tips, and total cell length based on swc representations of the neuron morphologies. We used a Python tool for automated analysis of morphological data (https://github.com/G-Node/Morphjongleur). With respect to the determined parameters, the VB in the forager neuron showed reduced values as compared to the nurse neuron. This reduction was strongest for the volume (down to 68%) and, interestingly, strong for the mean distance of terminal tips (down to 76%). In contrast, there were no significant differences in the DB parameters between forager and nurse neurons.

For analysis of electrophysiological properties based on the neuron morphologies, we used the NEURON simulator (Hines 1993) with multi-compartmental models built from detailed reconstructions made with SIGEN (Minemoto et al. 2009). We simulated stimulation by sinusoidal current injections at single dendritic terminal tips, with frequencies ranging from 10 Hz to 700 Hz while observing the membrane potential at a putative axon hillock at the center of the soma. As expected, damping of the membrane potential oscillations measured at the soma increased with frequency. For the individual neurons, the damping of VB inputs was lower than that of DB inputs, despite the facts that DB terminal tips (and thus the stimulation sites) were much closer to the recording site and that both dendritic branches showed similar mean cross sections (difference: <1%). This result can be explained by the higher number of branching points in DB, which were twice as numerous as in VB.

Our results indicate systematic differences between the two dendritic branches of these interneurons, suggesting a specialization of the neuron morphology. Furthermore, our results point to slight developmental differences which could reflect adaptations to different signal processing demands in nurse (younger) and forager (older) bees.

Acknowledgements

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[T 38] Response properties in a detailed model of pyramidal neuron action potential initiation

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The axon initial segment (AIS) controls the transformation of dendrosomatic synaptic input into spike output and the backpropagation of action potentials into the dendrites due to its lower spike initiation threshold. Channel density and kinetics can both contribute to this low threshold. However, the nature of such threshold differences is unknown and topic of current debates (Kole et al. [2008], Fleidervish et al. [2010], Dulla and Huguenard [2009]).

Dynamical response properties give a constraint on the AIS function. Here we study the dynamical response properties of a detailed multi-compartment NEURON (Carnevale and Hines [2006]) model that well reproduces the sodium concentration changes in the AIS and soma generated by action potential firing in a layer 5 pyramidal cells (Fleidervish et al. [2010]). We investigate how its properties depend on the ion channel density ratio between soma and AIS.

To study this properties, we inject different current stimuli into the soma. These are constant currents, Gaussian noise currents and sinusoidal currents with superimposed Gaussian noise as studied in Higgs and Spain [2009] and Köndgen et al. [2008]. We vary the sodium and potassium channel densities at the axon initial segment as well as mean, variance and frequency of the input current. We then calculate the dynamic rate response of a population of independent neurons. This is described at linear order by a filter function with frequency dependent gain as done by Higgs and Spain [2009].

The f-I curves show that the neuron model under investigation is of type I. This holds true for all channel ratios tested. The cut-off frequency appears insensitive to AIS channel density.

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$[\top\ 39]$ Analyzing chaotic activity in a balanced network of Type II neuronal oscillators

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The chaotic nature of balanced-state network dynamics for networks of integrator neurons has been actively investigated in recent years[1–3]. Chaos in such systems plays a prominent role in how external inputs are processed [4]. A particularly relevant measure in this case is the rate of information loss due to the chaotic dynamics, which is related to the stability metric known as the Lyapunov spectrum. Methods for its accurate calculation in large networks were recently developed[3] and applications thus far have focused on cortical network models of neurons with integrator (Type I) excitability. Networks of resonator (Type II) neurons are nonetheless relevant for cortical interneuron networks and the olfactory bulb. In the latter structure, the population of mitral cells exhibit intrinsic subthreshold membrane potential oscillations characteristic of Type II excitability[5]. These oscillations increase phase-locked spiking and can contribute to gamma-band network oscillations whose power correlates with learning in measurements across phylas[6, 7]. Despite the regularity in the population spiking, the individual mitral cells display irregular, yet precisely-timed activity during the excitatory sensory drive from the olfactory mucosa. With the strong and inhibitory recurrent input,

the scenario suggests a type of balanced state. In order to investigate this scenario, here we present an approach to perform a Lyapunov spectrum analysis of a balanced resonator network.

We studied networks of units described by a generic 2-dimensional linear threshold neuron model. The first neuron dimension is a somatic voltage variable, while the second takes on the role of a synaptic current or a somatic resonant current depending on the parameters, producing integrator or resonator[8] single neuron dynamics respectively. We couple these neurons through an inhibitory connectivity matrix, which at this initial stage we choose to be random, and set the form of the coupling between neurons to delta-pulses. Each neuron is additionally driven by some external excitatory input. For evolution between spikes, we have obtained the analytic solution to the neuron model and implemented an efficient and machine-precise root finding algorithm to obtain the next threshold-crossing time. Using this, we can perform numerically exact, event-based network simulations, iterating from one spike in the network to the next. We also analytically calculated the single-spike Jacobian of this iterative map, which describes how perturbations evolve between spikes and that we use to compute the full Lyapunov spectrum. The spectra converge in time and across initial conditions. Spectra for networks of up to 10,000 neurons appear feasible.

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$[T\ 40]$ Quantitative network features of the basal ganglia and connectome based population simulations

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The processing of motoric information in the basal ganglia and thalamic nuclei of the rat is related to 11 regions (primary motor cortex (M1), caudate putamen complex (CPu), substantia nigra compact part (SNC), substantia nigra reticular part (SNR), medial globus pallidus (MGP), lateral globus pallidus (LGP), subthalamic nucleus (STh), ventrolateral thalamic nucleus, ventromedial thalamic nuleus, parafascicular nucleus (PF), mediodorsal thalamic nucleus) and sometimes the ventral tegmental area (VTA), accumbens nucleus (AC) and habenular nuclei are considered. These regions have been selected in the rat connectome of the rat connectome (state in mai 2012: 15346 regions, 212823 directed and weighted connections) project realized in neuroVIISAS. The adjacency matrix of these 14 core regions of extrapyramidal motoric processing has large a line density of 67% and a low mean pathlength of 1.3 edges in average. The cluster coefficient is also large (0.735), however, the modularity is low (0.079) indicating that all regions have connections to most others. The CPu has the most inputs (12) and lowest Shapley rate (-0.23) followed by the SNR (input: 11,

output: 11), MGP (input: 10, output: 11), SNC (input: 9, output: 12), subthalamic nucleus (input: 10, output: 11) and VTA (input: 8, output: 13). The frequency of 2 to 14 regioncycles (path where source is the same as target region) indicated that the caudate putamen is involved in most cycles followed by the substantia nigra reticular part and subthalamic nucleus. The statistical analysis of 13 directed 3-motifs and 199 directed 4-motifs in 1000 rewiring simulations offers a significant more frequent appearance of the completely reciprocally connected 3- and 4-motifs. The CPu, STh and SNC are involved in these completely reciprocal motifs most frequently. Interestingly, the latter regions (beside PF) have also local maxima in the communicability matrix. The connections that leads to the large vulnerability of the network is the projection from the ventrolateral thalamic nucleus to the CPu, from the CPu to SNC, VTA, LGP and AC. Using this 14 node network in a population simulation (NEST) containing 1000 IAF neurons per region (20% inhibitory, 80% excitatory, synaptic delay 0.1 ms, total frequency of spike injection into the primary motor cortex: 10 kHz) different patterns of oscillatory responses of different regions were found (Figure 1, column 1 (c 1): distribution of spikes, c 2: # of IAF / region, c 3: # of spikes, c 4: spikes / neuron, c 5: first spike appearance [ms], c 6: distance from spike injection region, c 7: # of firing IAF, c 8: mean interspike interval, c 9: standard deviation of ISI, c 10: coefficient of variation of mean ISI). The spike distribution of the LGP shows the the largest similarity with 8 other regions of the 14 node network, however, the MGP and SNR possess the largest average similarity of spike distributions.

In conclusion, the 14 node network possesses global and local network features that can not been simulated by different randomizations. Not all regions in this network that seem to be highly important with regard to network parameters (CPu) does not generate largest coherency in simulations.

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Figure 1

Neural encoding and decoding

[T 41] Role of excitation and inhibition in regulating spiking correlations of pairs of cortical neurons

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Spike correlations in cortical networks play a fundamental role for processing information between neurons. Previous studies showed that correlated excitatory (E) input converging into pairs of modeled "postsynaptic" cells generates strong output correlations, whereas the simultaneous presence of correlated inhibition (E+I input) limits output correlation [1]. Here we tested these predictions using real neurons recorded in mouse cortical slices. Using dynamic clamp, presynaptic trains of spiking activity with different degrees of correlation were modeled and the corresponding postsynaptic conductances were injected in simultaneously recorded pairs of neurons. Correlated synaptic input was delivered in the presence and absence of a high-conductance (HiG) state resulting from a stochastic, in vivo-like synaptic noise, known to affect temporal process capabilities of neurons [2]. In pairs of layer 2/3 pyramidal neurons (PNs), output spike correlation was high when both neurons received a correlated E input. However, combined E+I correlated input decreased output firing correlation of the same PN pairs. Interestingly, the presence of a HiG state decreased output correlation in both cases (E and E+I input). By varying the number of presynaptic modeled neurons and/or the frequency of input spiking, but keeping fixed the degree of input paired correlation, the output correlation of the two recorded neurons changed dramatically. This was due to higher-order statistics of presynaptic spike distributions. Moreover, the levels of output correlation between real neurons were lower than those reported in theoretical studies, but closer to the physiological range reported in vivo. We are currently testing different postsynaptic pairs composed by PN-fast spiking (FS) and FS-FS cells. This approach allows testing complex theoretical predictions in real neurons, thereby helping the comprehension of the temporal processing capabilities of the brain.

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[T 42] What information does the eye send to the brain? Recording the entire visual output at a single retinal location

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Right at the first synapse in the mammalian retina, the stream of incoming visual information is split into multiple parallel information channels, preprocessed in the retinal network and relayed to the brain via different types of retinal ganglion cells (RGCs). About 20 different morphological RGC types have been described, with each RGC population tiling the retinal surface with its dendritic arbors. Here, we simultaneously record from all RGC types at one retinal location to obtain a complete sample of the information sent to the brain and to understand how the representation of spatio-temporal information in a local image patch is distributed across different RGC types. Here show that retinal ganglion cells can be clustered into functionally defined classes based on their Ca2+-responses to simple light stimuli.

We recorded light-evoked Ca2+ activity at single-cell resolution from groups of more than 500 neighboring RGCs loaded with synthetic Ca2+ indicator dyes in whole-mounted mouse retina using two-photon (2P) microscopy. We used a simple full-field light stimulus composed of luminance changes and a temporal frequency chirp. Over 80% of the cells responded reliably to the full field stimulus. Single cell activity patterns could be clustered into more than 15 functionally distinct types using a simple k-means algorithm, yielding about 40% ON cells, 25% ON/OFF and 15% OFF cells, in agreement with previous reports.

In addition, presentation of spatially modulated stimuli such as moving bars and checkerboards allowed us to quickly and reliably identify different previously described functional types such as direction selective GCs. We will further verify the functional clustering by morphological identification or patch-clamp recordings. This is possible because the imaged RGCs remain accessible to microelectrodes and, thus, can be dye-filled for morphological identification or targeted for patch-clamp recordings, in contrast to multi-electrode recordings.

We now aim to refine our battery of simple stimuli to be able to functionally cluster all >20 morphologically described RGCs in the mouse retina. Our approach allows us to create an inventory of all retinal ganglion cells present at a single retinal location. This local retinal "information fingerprint" should be very informative, not only for our understanding of neuronal computations in the healthy retina, but also as a research tool for evaluating specific functional deficiencies in diseased or degenerating retinae.

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$[T\ 43]$ A computation neuroscience stresstest for coding strategies in cochlear implants

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Although modern cochlear implants (CI) are able to restore speech perception to a high degree, there is still a large potential for improvements e.g. in music perception and speech discrimination in noise. To evaluate and optimize novel coding strategies, we have developed a toolbox which codes sound signals into spike-trains of the auditory nerve. We have previously developed a model of the intact inner ear, which we have complemented with detailed models of a CI speech processor, channel crosstalk and spiral ganglion neuron models. With our toolbox we present qualitative comparisons of neurograms elicited by different coding strategies with the situation in the healthy inner ear. Moreover, we conducted quantitative evaluated speech discrimination using a noisy database. ii) With the methods of information theory we quantified the transmitted information coded in neuronal spike trains, which allows us to evaluate especially well how well temporal information is coded. The major advantage of our approach is that we are able to evaluate both spectral and temporal aspects of novel coding strategies before we conduct extensive clinical studies.

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$[\top \, 44]\,$ Two methods of change point detection to identify strong changes in neuronal population activity

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The visual cortex relies on spikes of retinal ganglion cells (RGC) as the only source of information about the visual environment. In contrast to the experimenter, the nervous system generally does not have information about the exact time points of stimulus changes and needs to infer them from the RGC population activity. Here we introduce two different methods, a population average method and a classification method, to identify strong changes in population activity, called population events.

Our data set consists of multi-electrode recordings of RGC. The retina was stimulated with a dot pattern, which moved with one of nine different velocities along one axis of the electrode array. The velocity remained constant for 500 ms and then changed abruptly.

Both algorithms detect population events by computing the moving average of a smoothed population activity.

In the population average method a time point is detected as a population event if the population activity deviates from the moving average by a pre-defined number of standard deviations.

The idea of the classification method is to use a training data set to learn the statistical properties of the population activity during constant stimulation and in response to stimulus changes. The moving average and the population activity are classified into different categories arsing from the quantiles of the respective distributions. By comparing the categories of the test set to the categories of the training set, the probability of a stimulus change is calculated for each millisecond. A time point is identified as a population event if the probability of a stimulus change is greater than a pre-defined threshold, e.g. 0.5.

Both methods showed similar results for the fractions of correctly detected stimulus changepoints (e.g. 0.75) and of false positive change-points (e.g. 0.3). In both methods the moving average time window and the classification threshold have a strong influence on the event detection performance, while the other parameters are less critical for the classification performance. In contrast to the population average method, the performance of the classification method does not improve when information about the standard deviation is added.

Comparing both methods, the advantage of the population average method are that less assumptions and no training set are required and that a lower number of parameters (4 instead of 8) need to be optimized. On the other hand, the classification method does not require the calculation of the standard deviation and uses a physiologically more plausible average time window of approximately 100 ms instead of the very long 400-450 ms time window needed by the population average method.

In summary, both methods have different advantages but show in agreement that stimulus changes can be detected reliably based on the population activity of RGCs.

[T 45] Online Stimulus Reconstruction from Noisy Spike Trains

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The framework of stimulus reconstruction has been used very frequently in the study of neural population codes [1, 2, 3]. In [2] and [3] it the optimal unimodal tuning functions were derived for a stimulus reconstruction task. Most of these studies, however, have either been done under the assumption of static stimuli or with a batch processing paradigm. Furthermore, a frequent assumption in analytical studies is that the population firing rate is independent of the stimulus, which often simplifies calculations [4, 3]. Relaxing this assumption leads to a full filtering problem as stated in [5]. Here, we apply this framework to the case of inhomogenous Poisson processes. We derive the optimal filter equations and study their dynamics.

The derived filtering equations can also be applied to the case of adaptive neurons with spike frequency adaptation. Put simply, we model spike frequency adaptation by a modulating term in the Poisson rate with an exponential recovery to 1 with characteristic time τ and a constant lowering δ after each spike. The filtering equations are essentially the same as before and can be used to derive a particle filtering approach to stimulus reconstruction.

Finally, we study the case of a Gaussian Process distribution over stimuli, which allows for several simplifications. Namely, when the prior over stimuli is Gaussian, Gaussian or exponential tuning functions can be treated in this formalism, allowing for a number of results on the mean-squared-error of filtering of spike trains. These tuning functions encompass a class of Generalized Linear Models, which have been of great interest in the neural coding community. We also derive a mean-field self-consistent equation for the equilibrium variance of a Gaussian filter as an upper bound on the MSE of the optimal filter, analogous to what has been done in [6].

The application of filtering methods to the study of optimal neural coding is a very interesting avenue of research, as it allows us to study the mean-squared-error of stimulus reconstruction with a number of methods from statistics and physics. Particularly the application of particle filtering methods to these studies provides an interesting approach, as these methods are known to converge to the optimal Bayesian estimator in the limit of large number of particles [7]. This allows us to study the best-case performance of neural codes faced with complex stimuli in a dynamic way. This paves the way to a thorough study of optimal population coding of dynamic stimuli with realistic stimulus ensembles and neuron models.

Acknowledgements

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[T 46] Professional instrumentalists excel at musical anomaly detection: Possible evidence for embodied cognition from single-trial EEG discrimination

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We are extremely good at detecting anomalies in our sensory input. For example, while listening to a piece of Western-style music, we can often detect a forced key change or an out-of-key pitch, even if we are not musicians. Here, we investigate differences between musical experts and non-experts in terms of the underlying neural signatures of musical anomaly detection. Experts had 32.6 ± 10.0 years of cello performance experience among a range of ages covering 41.6 ± 10.6 years, while non-experts at 0 years of cello performance experience among a comparable range of ages, though some non-experts had played musical instruments in the past. Specifically we analyzed the electroencephelograms (EEG) of five expert cello players and five non-cello players while they listened to excerpts of J.S. Bach's Prelude from Cello Suite No.1. All subjects were familiar with the piece, with experts having extensive experience playing the piece. Subjects were told that anomalous musical events could occur at random within the excerpts of the piece and to count the number of such events, reporting the number after each excerpt. Subjects were instructed not to move while listening to the excerpts and this was verified via visual monitoring.

Experts had significantly better behavioral performance (i.e. correct counts) than non-experts, though both groups had mean accuracies of >= 85% (experts' accuracy fraction = 0.94 ± 0.03 , novices' mean accuracy fraction = 0.85 ± 0.12). To analyze the EEG data, we trained a logistic regression classifier and assessed its single-trial performance with a leave-one-out (LOO) analysis, using the area under the receiver-operator characteristic (ROC) curve as a metric of accuracy (i.e., the value of Az). In analyzing the EEG this way, we found significant neural correlates only post-stimulus (Bonferroni corrected, p < 0.01), indicating the subjects' neural response to the anomaly. In particular, we summarized each subject's neural discrimintation with the maximum value of Az. We found that each subject had the same relative detection accuracy and significance across groups as seen in the reported behavioral counts, though overall the accuracy from neural correlate based detection (experts' Az = 0.86 ± 0.04 , novices' Az = 0.75 ± 0.06) was approximately 10% less than behavioral accuracy.

Using the subject specific timing we found for the maximum discriminating neural correlates, we performed source reconstruction and compared significant differences between cello players and non-players. We found significant differences (p < 0.01) that included a right lateralized source distribution in experts consistent with the cortical representation of the left hand– i.e. the hand a cellist would use to generate the anomalous key-changes while playing. Together these results suggest that when detecting anomalies in a musical stream, experts with experience performing the piece generate activity in sensory-motor centers that would be involved in executing the action needed to generate the anomaly. Conversely significant activation in non-experts was seen in the left superior temporal gyrus, which has been implicated in general perceptual decision-making tasks. Together, these results suggest that sensory anomalies detected by experts may in fact be partially a result of an embodied cognition, with a model of the action for generating the anomaly playing a role in its detection, while novices' anomaly detection is not embodiment-dependent.

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$[T\ 47]$ Layer specificity of phase coding in entorhinal grid cells for 2-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 and these regions form a hexagonal lattice. As the animal traverses one such 'firing field', spikes tend to occur at successively earlier phases of the theta oscillations in the local field potential ("phase precession"). Phase precession has been demonstrated for both, runs along a linear track and in the open field. Here, we investigate whether phase precession differs for grid cells in different cortical layers by analyzing spike trains individually for each field traversal and relating theta phase with traveled distance.

In open 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. We study the effect of those running statistics on phase precession for grid cells from different cortical layers. We find that phase precession correlations are significantly reduced for layer III grid cells. Interestingly, shorter runs lead to steeper phase precession, as opposed to long and winding runs. This effect is observed for grid cells from all entorhinal layers. Such results refine our view on the layer specificity of entorhinal phase precession.

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[T 48] Information theoretic analysis of rate to phase encoding

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The degree of synchronization between neurons or their relative time delay has long been postulated to carry information [1,2]. When a background oscillation is present, the times at which a neuron fires can be assigned a phase relative to the oscillation. Experimentally, one can observe entrainment to the oscillatory local field potential (LFP) in the olfactory bulb, synchrony binding in the visual system, and phase precession in the hippocampus. Once information is encoded into the relative phase of firing, it can be used to facilitate phase based computations [1], influence the dynamics of spike timing based learning rules, or be converted back into a firing rate using bursting neurons [4].

The performance of a rate-to-phase encoder in the hippocampus was assessed by analyzing recorded data and an integrate & fire model [3]. We extend the analysis to a more general class of models, i.e., phase oscillators that are reduced from conductance based models. The frame work also allows one to investigate the hampering effects of various noise sources.

Our analysis shows, that the exact shape of the distribution of phase differences between spikes emitted by the encoding neuron and LFP depends on the interplay between the neuron's phase response curve and the frequency content of the LFP. When the background input is a simple oscillation, only the lowest frequency component of the PRC matters. Yet neurons that have simple resonances have a PRC whose first Fourier coefficient is zero-the phase of spiking of such a neuron will not encode information. Only neurons that integrate over their synaptic inputs are good phase encoders. The phase encoding is summarized by the vector strength, which is related to the circular mean and variance of the phase distribution. This is calculated numerically by an efficient continued fraction method. Deterministic coding, in which noise is absent, restricts the phase to one half of the oscillation cycle. In a population of identical neurons, noise extends the dynamic range of encoding, even though the phase of individual neurons "slips" outside of the classical entrainment regime. In addition, we make use of the Arimoto-Blahut algorithm to estimate the optimal input statistics for a given rate-to-phase encoder. The boundaries of the entrainment region turn out to be particularly suitable for precise coding.

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$[T\ 49]$ Non-invasive characterization of individual neurons with Continuous dynamic photo-stimulation

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Understanding information encoding by individual central neurons requires characterization of their input-output functions under near-natural input conditions, e.g. in the fluctuation driven regime, characteristic of cortical circuits. Controlling the input and registering on the order of 10.000 - 100.000 spikes as output, one can compute transfer metrics which are critical for collective network dynamics, such as dynamic gain, correlation gain or spike frequency vs current (FI-) curves. So far now such data are exclusively obtained in sharp electrode or patch-clamp recordings, where the input to the cell body and therefore to the spike trigger zone in the axon initial segment is directly controlled. Due to the limited number of spikes obtained in invasive recordings, characterization of individual neurons is often not possible, dynamic gain curves, for instance, are averaged over tens of neurons.

We recently developed an alternative, non-invasive method for neuronal characterization. Spikes are recorded by an array of extracellular electrodes. Well-defined, fluctuating stimuli are delivered via light-activated channelrhodopsins to pharmacologically isolated neurons. Careful characterization of channelrhodopsin's transfer function warrants precise control over the waveform of the induced conductance. An 8x8 array of high-power LEDs provides local (50 µm) stimulation. Spot intensities of up to 30 mW/mm² are independently modulated at several kHz. The non-invasive nature of the experiment enables characterization of many individual neurons for many hours, up to few days. The setup delivers orders of magnitude more data than previously possible in the field of input-output characterization. Neuronal responses were stable, measurement of intracellular pH showed only minor acidification under continuous stimulation. Comparison of our results with dynamic gain measurements and FI-curves obtain with traditional methods establishes the equivalence of the non-invasive, high-throughput method.

Preliminary experiments show that the method is also applicable to slices.



Figure 1

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Sensory processing and perception

[T 50] Amplitude Dependency of Synchrony Codes

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Synchronous activity among neurons in a population is usually associated with the occurrence of specific features in the common stimulus. We investigate the synchrony code in the context of the encoding of electrosensory information in the weakly electric fish Apteronotus leptorhynchus.

Middleton et al., 2009 showed that the extraction of synchronous spikes from a population of input neurons shifts the range of encoded signals to higher frequencies and thus can be understood as a way to separate coding channels. In the electrosensory world this separation roughly matches the frequency ranges used for the two purposes of active electrosensation, i.e. navigation and prey detection, in the lower range, and communication in the high frequency range.

Here, we compare experimental results from in vivo recordings of p-unit electroreceptors with predictions from linear response theory in the limit of weak stimuli. Analytical expressions are derived for the coherence of both the synchronous spikes, as a coincidence detector would read them out, and the integrated spike trains. The theoretical results show how the synchrony code depends on stimulus amplitude and the power-spectrum of baseline firing.

Theory predicts that any cell that has a regular baseline firing rate and contains a certain amount of intrinsic noise can employ a synchrony code and thus separate coding channels. Furthermore the separation of the frequency bands of integrated and synchronous responses dependes on the stimulus intensity. Weak stimuli lead to a clear separation that becomes weaker with increasing stimulus intensity.

Our experimental results from the electrosensory systems of the weakly electric fish support these predictions. In irregular spiking P-units of the active electrosensory system the observed separation of the coding channels indeed shows the predicted stimulus dependency. On the other hand, ampullary receptors of the passive electrosensory system exhibit a much more regular baseline firing rate than those of the active system. Here the coding ranges of the synchronous and integrated responses are not shifted relative to each other. Thus, the receptors of the passive system do not have a sufficient level of intrinsic noise, although a distinction of synchronous and non-synchronous spikes is still possible. Again, these results are in line with the predictions of the theory.

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$[T\ 51]$ Comparative study on the encoding of communication signals in two species of weakly electric fish

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Communication signals play an important role in separating sympatric species. In particular, mating signals of closely related species often differ dramatically and thus ensure a reproductive barrier. The question arises how sensory systems provide the necessary flexibility to appropriately encode these quickly evolving signals. We here investigate this topic on the example of chirping behavior and its encoding in two closely related species of Gymnotiform weakly-electric fish – a well established model system for studying sensory processing on the cellular level.

Weakly electric fish generate an electric field around their body by producing weak electric discharges with a specialized organ in their tail. Electroreceptors distributed over their body they are able to sense this field and distortions of it. The quasi-sinusoidal electric organ discharges (EOD) are used by the fish for navigation, electrolocation and communication purposes. Here we focus on the communication behavior. When two fish meet, there individual EODs interfere and lead to an amplitude modulation (AM) of the EOD, the beat. Since EOD frequencies are sexually dimorphic (male and female fish have higher or lower EOD frequencies, or vice versa depending on the species) the beat frequency carries information about the nature of the encounter. During such interactions the fish produce stereotyped communication signals, so called chirps. These consist of transient increases of the EOD frequency affecting the AMs of the EOD in distinct ways.

In behavioral experiments we studied the chirping behavior of two different wave-type species of weakly-electric fish, Apteronotus albifrons and Apteronotus leptorhynchus. In so called chirp chamber experiments fish were stimulated with sinusoidal, EOD like stimuli mimicking the presence of a conspecific to induce chirping behavior. We observed several differences between the chirps of both species. A. albifrons generally emits chirps of longer duration and sometimes larger complexity than A. leptorhynchus.

In a second step electrophysiological playback experiments were performed in which the recorded chirps were used as stimuli. We analyzed how these are encoded in the responses of one population of electroreceptors, the P-units, that in particular encode AMs of the EOD. Chirps of both species are encoded in the same way by the P-units of either species. The differences in the chirps, however, evoke quite different responses, so that they can be potentially well distinguished by the animals. Species specific adapations thus must occur on high levels of information processing.

$\left[T\ 52\right]$ Temporal adaptation enhances efficient contrast gain control on natural images

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The redundancy reduction hypothesis postulates that neural representations adapt to sensory input statistics such that their responses become as statistically independent as possible. Based on this hypothesis, many properties of early visual neurons-like orientation selectivity or divisive normalization-have been linked to natural image statistics. Divisive normalization, in particular, models a widely observed neural response property: The divisive inhibition of a single neuron by a pool of others. This mechanism has been shown to reduce the redundancy among neural responses to typical contrast dependencies in natural images. Using recent advances in natural image modeling, we show that the previously studied static model of divisive normalization achieves substantially less redundancy reduction than a theoretically optimal redundancy reduction mechanism called radial factorization. This optimal mechanism, however, is inconsistent with the existing neurophysiological observations. We suggest a new physiologically plausible modification of the standard model which accounts for the dynamics of the visual input by adapting to local contrasts during fixations. In this way the dynamic version of the standard model achieves almost optimal redundancy reduction performance. Our results imply that the dynamics of natural viewing conditions are critical for testing the role of divisive normalization for redundancy reduction.

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$[T\ 53]$ Decoding of V1 responsiveness to component motion predicts higher-level responsiveness to pattern motion

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We study the perceptual representation and model the neural representation of pattern motion. Lacking quantitative characterizations of neuronal responsiveness in area MT, we derive theoretical predictions from the responsiveness of motion-selective neurons in area V1, which are comparatively well characterized (Geisler & Albrecht, 1997). Given a quantitative model of responsiveness (tuning and variability) to component motion, we have previously predicted the responsiveness (tuning and variability) to pattern motion, assuming statistically efficient integration of Fisher information. These theoretical results predict that sensitivity to the speed and direction of pattern motion should vary with the constitutive component motions (Lehmann, Pastukhov & Braun, ECVP 2011). We now report psychophysical threshold measurements that quantitatively confirm these predictions. Five observers viewed composite arrays of two types of component Gabor-motion wavelets, reporting either the direction or the speed of pattern motion (t2AFC). To reveal the differential contribution of different motion components, we varied the angle between component wavelets. Thresholds for direction of pattern motion decrease, whereas thresholds for speed of pattern motion increase, with the angle between component wavelets. In conclusion, we can predict neural responsiveness at the level of pattern motion (presumably in area MT) from psychophysical measurements and from neural responsiveness at the level of component motion (area V1). These predictions make no assumptions about neural circuits but simply assume statistically efficient integration of Fisher information.

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$[T\ 54]$ A Neurologically Motivated Computational Architecture for Real-Time Object Recognition

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For decades research could be separated into two camps. The analytical side which has been investigating the structure and functionality of the human brain and the synthetical side which built technical systems from scratch, focusing on very specific tasks. Only recently researchers draw attention to the enormous potential of neurobiological findings for the development of new technical models, which are able to exceed the capabilities of state-of-the art systems. We aim to close the gap between the analytical knowledge about the structure and functionality of the brain and the development of intelligent cognitive systems like humanoid robots.

By emulating the structure of the brain, we hope to provide a more plausible understanding of its functionality.

We propose a neurologically motivated computational architecture for processing information and apply the architecture to realize real-time biologically-inspired object recognition. In contrast to other systems, we emphasize the temporal aspect of sensory input and the importance of rapid processing for agile interactions with the environment. Our object recognition system is based on HMAX, initially proposed by Serre, Wolf and Poggio, which models the ventral pathway in the areas of the visual cortex V1, V2 and V4 and its hierarchical feedforward structure. We enhanced this model by an adaptive information theoretic approach, based on the investigations of the role of entropy in the sensory information processing in the human brain.

The architecture and functionality of our system is motivated by the highly parallel anatomy of the primate visual system and the way information is processed between the neurons. Following the biological archetype, the computational architecture's focus lies on multiple strategies: The hierarchical processing, the parallel processing and the modularity.

We spread the computational processing stream over a cluster of PCs with multiple CPUs and GPUs using a construction of software nodes which are responsible for the functionality. The architecture is modular and expandable both in hard- and software, so that it can cope with multi-sensory integrations. Using the enhanced object recognition system on the architecture we show that our approach achieves better performance in recognition and speed compared to existing models.



Figure 1

Figure 2

Acknowledgements

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$\left[T\ 55\right]$ Synthesis of Distributed Cognitive Systems: Interacting Maps for Sensor Fusion

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Environmental interaction is an important aspect in the life of every physical entity, which impacts its internal state and allows the acquisition of new behaviors. A prerequisite for such interaction is multimodal sensory fusion with the goal of providing a consistent internal representation of the external world. In technical systems, such a representation is obtained by fusing noisy data from various available sensors, which combined generate a richer representation compared to individual use. State-of-the-art technologies apply probabilistic methods for combining prior and observed information, but these techniques are computationally inefficient for a large number of sensors.

In our project we propose extending an existing initial model of interacting maps for sensory interpretation with the focus on multimodal sensory fusion. The core aspect here is to design and implement a neuro-biologically inspired method for real-time distributed interpretation of sensory stimuli in a mobile robotic setting: a distributed graphical computing system with inter-merged information storage and processing that allows efficient parallel reasoning. This network architecture consists of interconnected heterogeneous software units, each encoding and processing a different feature about the environment that is represented in a local map. A map here is defined as a pixel based representation of some perceived or inferred aspect of the current environment, in which each entry contains a value of a certain type (e.g. a scalar of image brightness or a 2D vector of local optic flow). Such extracted pieces of environmental knowledge interact by mutual influence to ensure overall system coherence: the values represented in each map slowly drift in the direction that minimizes disagreement between the two sides of an assumed inter-map relationship through mutual influence. Although by system design each map specializes in representing a certain feature of the environment, the required relations between maps for such influence are established through a learning process: the true relations between maps are a priori unknown, but exist hidden within the observed real-world data. Therefore, our system needs to infer those relations over time from correlated sensory signals.

Starting from the proposed distributed processing architecture, our main research investigates self-constructing and adapting internal relations between maps (structural plasticity) that reflect the underlying relations between multimodal sensory information streams. We investigate optimized network distributions on available computing resources without an explicit a priori network topology provided by a systems designer. This new architecture reflects distributed information processing as known to occur in brains, and ensures a fast, robust and scalable computational architecture appropriate for real-time real-world robotic applications.

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[T 56] Human category learning is consistent with Bayesian generative but not discriminative classification strategies

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Since an early age, humans have adopted the ability to group visual entities into categories. Mechanisms that correspond to categorization processes, are typically investigated at both neuronal (Freedman, 2011) and behavioural contexts. Here we step back and design tests with the aim of realising which computational process is used by our brain for forming categories (i.e. classification). In machine learning and pattern recognition two types of classification algorithms are known: 1. Generative and 2. Discriminative approaches. Generative approaches solve the categorization problem by building a probabilistic model of how each category was formed and infer category labels. In contrast, the discriminative approach learns a direct mapping between input and category labels. Recent work (Hsu and Griffiths, 2010) shows human classification is consistent with discriminative and generative classification depending on task 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 of visual objects in two different tasks (two Persian-characters and 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 two 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. Similar to the generative classifier, subjects were strongly influenced by knowledge of the distribution associated with alternative categories as classification boundaries shifted towards B for both tasks across all subjects. Our results indicate that categorization in both tasks is consistent only with generative and not discriminative classification. Our experimental design is directly amenable for neurophysiological studies to investigate the neuronal substrates of generative classification in the brain.



Figure 1

Figure 2

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$[T\ 57]$ Decision time and uncertainty: evidence for a sampling-based representation in human vision

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There is increasing psychophysical evidence supporting the view of human perception as probabilistic inference that relies on representations of uncertainty about sensory stimuli and that is appropriate for statistically optimal decision making and learning. A recent proposal concerning the neural bases of these representations posits that instantaneous neural activity corresponds to samples from the probability distribution it represents. Since samples are drawn sequentially, a crucial implication of such sampling-based representations is that the number of samples drawn, and consequently the precision of representing uncertainty, will depend on the time available. To test this implication we created an orientation-matching task in which we measured both subjects' performance and their level of uncertainty. In each trial, we showed 2-10 differently oriented line segments spaced evenly on a circle extending 2° of visual angle. After the stimulus disappeared, subjects were instructed to match the orientation of the target line and then indicate their confidence about the response. We varied the available response time (but not the stimulus time) trial-to-trial to influence the number of samples available before making a decision. We found that subjects' performance and uncertainty judgment were correlated and that this correlation was independent of the number of line segments presented in the trial. Importantly, with decreasing the response time this correlation decreased significantly while the performance levels did not change. Thus, limiting the available time specifically influences the reliability of uncertainty representation, in agreement with sampling-based representations of uncertainty in the cortex.

[T 58] Dynamic Bayesian Networks for Cue Integration

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If we want to understand how humans use contextual cues to solve tasks such as estimating distances from optic flow during path integration, our models need to represent the available information and formally describe how these representations are processed. In particular the temporal dynamics need to be incorporated, since it has been shown that humans exploit short-term experience gained in previous trials (Petzschner und Glasauer, 2011). Existing studies often use a Bayesian approach to model optimal integration of cues (Ernst und Banks,

2002) or trial-to-trial learning of priors (Berniker et al., 2010). However, less common is an explicit theoretical treatment of the causal probabilistic structure over time of such computational problems.

In the present theoretical work we reformulate existing models for a simple magnitude estimation task in terms of dynamic Bayesian networks (Kjaerulff, 1992), thereby making explicit assumptions about temporal-causal relationships. We developed these existing models for a different type of study that tested how humans exploit contextual cues in a distance estimation task within a virtual reality (VR). Humans had to produce and subsequently reproduce a distance and indicated via button press when they thought they had reached the same displacement during reproduction that they experienced in the production phase. In one experimental condition an additional symbolic cue was displayed at the beginning of each trial that indicated whether the upcoming distance would be "short" or "long".

The existing models use a simplified notion to explain the effect of the symbolic cue on human performance. They separate between a static estimation part and a dynamic learning part. The estimation part combines symbolic cue, sensory information and prior experience based on assumptions about how they might be probabilistically related. The dynamic part uses Kalman filters for the trial-to-trial update of certain quantities, for example the prior mean. It is based on assumptions about the probabilistic relations in time for each updated quantity separately.

By reformulating these models under a new framework we capture not only the probabilistic causal relations in the two parts separately but also those relations spanning both parts. Thereby we achieve a deeper understanding of the dynamic processing of contextual cues over time.

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[T 59] Contextual Encoding of Saccadic Scene Changes in the Retina

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Fast, sudden eye movements ("saccades") form an essential feature of visual behavior. The visual signals on the retina are thus segmented into brief image fixations, separated by global motion signals. It has been shown that the activity of retinal ganglion cells is strongly affected by saccade-like image shifts. This suggests that there may be a specific representation of saccades by the retina, either by way of short bursts of spikes or by suppression of spiking activity (e.g., Noda & Adey 1974, Roska & Werblin 2003). Little is known, however, about how the responses to the motion signal interact with the encoding of the image content at the subsequent fixation. Here, we address this question by analyzing ganglion cell activity in the isolated mouse retina, recorded with multi-electrode arrays, in response to simulated saccades.

For about half of the recorded cells, we found strong spiking activity during the saccade. This supports the idea that the retina actively encodes the saccade and may signal the abrupt scene change to downstream brain areas. Furthermore, we characterized the responses to the newly fixated image. While there appears to be only little influence of the preceding motion signal itself on these responses, the responses depended strongly on the image content during the fixation period prior to the saccade. Thus, saccadic vision may provide 'context' to each fixation, and ganglion cells encode image transitions rather than currently fixated image. Based on this perspective, we classified retinal ganglion cells into five response types, suggesting that the retina encodes at least five parallel channels of information under saccadic visual stimulation.

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[T 60] Spike-Triggered Analysis of Contrast Adaptation in the Retina

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Retinal ganglion cells have to encode the visual world under different viewing conditions. When contrast changes, they show a fast dynamical change in sensitivity and temporal filtering characteristics. However, ganglion cells are often better described by multiple filter components in parallel. Here, we therefore ask whether they adapt independently or whether their relative importance for the ganglion cell response changes. We thus study the temporal features represented by ganglion cells by recording responses from isolated axolotl retinas using a multielectrode array. We apply spike-triggered average (STA) and spike-triggered covariance (STC) analysis to determine the set of features represented by each ganglion cells under different contrast conditions. Following a switch from a low-contrast condition to one of high contrast, we found for pure OFF cells that the stimulus feature encoded by the STA under low contrast is preserved as the most significant feature detected by the STC analysis under high contrast. However, a second stimulus features emerges as an additional filter component under high contrast. For ON-OFF cells with contributions from both ON and OFF pathways, on the other hand, this scheme does not hold. Rather, ON and OFF inputs are found to adapt independently. Together, these results suggest that contrast adaption of dynamic stimuli occurs separately in ON and OFF pathways in retina and that adaptation within a single pathway can be described by changing contributions from multiple parallel filtering processes.

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$[T\ 61]$ Spatial integration in the receptive field surround of retinal ganglion cells

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How a sensory neuron spatially integrates signals over its receptive field is one of the determinants of the neuron's function. In retinal ganglion cells, for example, it has long been known that signals are linearly integrated in some cells, whereas nonlinear integration occurs in others [1]. Although this difference in spatial integration is thought to give rise to different functional roles in visual processing, a detailed quantification of the integration is still lacking.

Here we aim at quantifying how signals are integrated in the receptive field in the amphibian retina, using closed-loop experiments. Closed-loop measurements allow us to determine the center and surround of the receptive field during the experiment. We then divide the receptive field and present different contrast step stimuli to each subfield. To identify potential nonlinearities in spatial stimulus integration, we perform iso-response measurements, where combinations of different contrasts that lead to the same pre-specified response are determined. A recent study which employed this approach has revealed a threshold-quadratic nonlinearity in the receptive field center [2]. Based on this result, we investigate how signals are integrated in the receptive field surround.

We use multi-electrode arrays to record extracellular spiking activity from isolated amphibian retinas. While the receptive field center is stimulated with a fixed contrast, two distinct surround regions are stimulated with combinations of different contrast values. Iso-response curves are determined for the firing rate and latency. The shapes of these curves reveal the signal integration characteristics in the receptive field surround.

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$\left[T\ 62\right]$ Integration of visual and electrosensory information in a discrimination task

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Weakly electric fish (Apteronotus albifrons) possess an electric sense that is employed to guide their behavior under low visibility conditions. The animals produce and electric organ discharge (EOD) which leads to an electric field surrounding the fish. With cutaneous electroreceptors distributed all over their body which are tuned to the own electric field they can sense distortions of the self-generated field and use this information. Any object having a conductivity different from the surrounding medium (water) will distort the field. Strongly conductive objects locally increase the field intensity and less conductive objects locally reduce the electric field amplitude. While animals of this species are a widely used model system for studies on sensory processing. These, however, have been concentrated on the processing of electrosensory information, their visual sense has been largely neglected.

Here we set out to establish a behavioral paradigm to assess learning and the integration of visual and electrosensory information. In a two-alternative-forced-choice discrimination task animals were trained to certain combinations of electrosensory and visual cues. In test experiments these cues were set into conflict. Our results show that fish of this species are well able to learn such a discrimination task yielding discrimination performances of 100% correct choices. They further can discriminate objects using visual or electrosensory information alone. In conflict situations the animals show decreased discrimination performance indicating that both senses contribute in approximately equal shares.

We thus have established a behavioral paradigm that will in the future allow us to relate physiological findings back to behavior and vice versa.

$\left[T\;63\right]$ The neural representation of time: An information-theoretical perspective

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Accurate representations of time are crucial for a wide range of brain functions such as speech recognition and the planning and execution of coordinated movements. While the neural basis of these representations remains debated, there is a large body of psychological studies probing the capabilities and limits of time perception. A prominent finding in these experiments is Weber's law (also called the "scalar property"), the linear scaling of timing errors with duration of the interval that needs to be estimated. The ability to reproduce this scaling has been taken as a criterion for the validity of neurocomputational models of time perception. However, the origin of Weber's law remains unknown, and currently only a few models generically reproduce it.

Here, we use an information-theoretical framework to investigate the statistical origin of Weber's law in time perception, as well as the frequently observed deviations from this law [1]. We employ general Gaussian random processes as an abstract model for the neural representations of time, with temporal changes in the mean, the variance and the covariance, and use Fisher information to compute the theoretical lower bound of timing errors. Under the assumption that the brain is able to compute optimal estimates of time in this sense, we find that Weber's law only holds exactly if the estimate is based on temporal changes in the variance of the process. In contrast, the timing errors scale sublinearly with interval duration if the systematic changes in the mean of a process are used for estimation, as is the case in the majority of time perception models. Estimates based on temporal correlations even result in a superlinear scaling, as we exemplify for power-law exponentially decaying correlations. We also relate these three types of estimators to more concrete neurocomputational models of time perception and show that this pattern is consistent with the scaling behaviors that are found in these models. Furthermore, we extend the framework to the case that multiple processes are available for estimation. We address two case studies that illustrate specific issues that arise in the presence of multiple processes. First, we evaluate a previous covariance-based model [2] and show that the minimal timing error it produces scales exponentially and Weber's law is approximated only for relatively short intervals. Second, we show how a neurocomputational model can be formulated as a stochastic process using the example of the synfire chain model [3].Within this framework, we confirm that time perception based on optimal selection of multiple synfire chains also results in a statistical optimal estimate of time, and also approximates Weber's law for somewhat longer intervals.

The information-theoretical framework highlights the possibility to estimate time intervals from various sources, including systematic changes of states in the brain, but also the decay of such neuronal signals or signal correlations over time. While most temporal information can be captured when only the systematic changes in the processes are used, psychophysical studies which report Weber's law to hold provide evidence for the notion that information may be conveyed by the variance alone. As neocortical cells have been shown to provide a population rate code with high temporal resolution when working in a variance-driven regime [4], our results suggest that this processing mode is relevant for the perception of time.

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[T 64] Modeling fruit fly olfactory receptor neuron-responses

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Olfaction is critical for fundamental survival skills such as finding food, mate and shelter. Insect olfactory systems are ideally suited to study the neural basis of olfaction since they follow the same design principles and fulfill the same behavioral functions as mammalian olfactory systems but consist of much fewer neurons. In addition, mathematical models of these relatively simple neural systems can be readily implemented in technical devices.

Here, we present a mathematical model to describe the response properties of fruit fly olfactory receptor neurons (ORNs). These first-order olfactory neurons have been repeatedly modeled in the past. However, all previous models ignored the influence of odor concentration, despite its pronounced effect on the "meaning" of an odor as well as its importance in tracking odor trails. To fill this gap, our model includes both odor-identity and odorconcentration. Hallem and Carlson (2006) have characterized the responses of 24 fruit fly ORN types to 19 odors across four concentrations. We take these data to fit a sigmoidal odor concentration-ORN response curve for each odor-ORN pair. Based on the parameter distribution of these sample odor-ORN pairs, we then implement a larger model consisting of 24 ORNs and 110 odors. We directly compare the predictions of this model to the corresponding large dataset of Hallem and Carlson (2006) at the single odor concentration they used. The model captures salient features of the data in terms of ORN odor tuning-widths and perceptive distances between the odors. Furthermore, we find the combinatorial odor codes to be expanding with increasing odor concentration, mimicking functional imaging data (e.g.,Root et al. 2007). In addition to fitting well with experimental data and successfully encoding odor-concentration as well as odor-identity, the model is described by only few parameters. It can thus serve as a realistic, reliable and simple input layer to models of the insect olfactory pathway attempting to explain, e.g., learning of odor-identity and -concentration or effects of odor mixtures.

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[T 65] Learning and Recognizing Human Speech using Dynamical, Hierarchical Bayesian Inference

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Even the most sophisticated speech recognition algorithms today are not at the level of human performance when it comes to tasks such as recognition in noisy environments, adaptation to speed fluctuations and generalization to different speakers and accents. Therefore, it is important to understand the mechanisms of human speech recognition and develop neurobiologically plausible models that can replicate some of these capabilities. In this project, we use dynamical systems theory and a Bayesian inference scheme [1] to propose a hierarchical speech learning and recognition model. This hierarchical approach is inspired by the song recognition system of birds [2] which shares anatomical and functional similarities with the human speech recognition system [3]. By using a cochlea model as the lowest level of the hierarchical model [4], we obtain a mechanism that can recognize words or sentences from sound waves, in an online fashion. We expose the model to a benchmark speech recognition task and show that the model can learn words rapidly and recognize accurately and robustly, even under adverse conditions, from different speakers.

Furthermore, we used the model to provide computational explanations what may cause differences between people in (i) adapting to new accents, and (ii) learning a second language. In the first application, we show that adaptation from a British to a New Zealand accent depends on the strength of internal expectations about the speech sounds. In the second application, we qualitatively explain the results of a behavioral experiment [5] which measured the effects of noise on recognizing English words for native speakers vs. Italian immigrants to Canada, who started acquiring English at different ages in life. Here, we model differences in behavioral performance between groups as differences in the expected precision of the internal speech dynamics. Intuitively, the computational results show that the success of learning a second language critically depends on being able to expect deviations in the already learned internal dynamics (i.e. the representation of the first language).

In summary, inspired by the song recognition mechanism of birds, we propose a hierarchical Bayesian model for learning and online recognition of human speech. The model is shown to be robust under adverse conditions and it has the potential to explain some of the neural mechanisms underlying the behavioral results of accent adaptation and second language learning.

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[T 66] A Normative Model of Neuronal Dynamics for Visual Feature Binding Based on Phase-Synchrony and Natural Image Statistics

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Normative models of sensory processing in neural networks were recently very successful in visual feature extraction for object recognition. The biological motivation for these models is based on neuronal rate coding of visual features while neglecting the temporal dynamics on fast time scales. Here these rate coding feature extraction models are extended with a second network variable representing the relative phase of oscillating activity of different neurons. These phase variables allow modeling synchronization phenomena of active neurons and thereby to bind visual features belonging to the same stimulus.

Receptive fields based on retinal and LGN processing mechanisms are used and applied to images resulting in the neuronal activity levels for a layer corresponding to the primary visual cortex. The synchronizing and desynchronizing intralayer connection strengths in the network are set according to the cross-correlation of neuronal activities using second order statistics of natural images. To reduce the high demand on computational resources these intralayer connections are sparse with a connection probability decreasing with distance in visual space. The mathematical framework for the phase update rule is biologically motivated and based on coupled neural oscillators close to their limit cycle. Currently we are changing the feature templates to be learned unsupervised using non-negative sparse-coding.

In contrast to classical image segmentation algorithms, the phase tagging is not characterized by a fixed partitioning of the visual space. Instead the binding of a set of neurons is represented by the similarity of the phase variables, which biologically corresponds to synchronized activity. The results of the simulations are dynamic binding maps of the visual features. We show the network characteristics using artificial gray scale images and natural color images. In addition, the networks ability to bind features that are representing the same physical object is evaluated using a hand labeled dataset of images (LabelMe). Without noise the degree of synchronization increases continuously over time. We show that a peak in segmentation performance is achieved after around 20 network iterations. The binding performance is compared to a binding based on chromatic hue. The binding using hue is superior for larger segment sizes because the phase interaction is weak over larger distances in visual space. The results indicate that the phase segmentation outperforms hue segmentation for small to medium segment sizes.

This approach allows combining multi-scale image segmentation and object recognition into a unified hierarchical neuronal network model. This has the potential advantage that feature binding and feature extraction can be accomplished simultaneously at different scales of the hierarchy. Furthermore, top-down feedback can modulate feature binding while intralayer feature binding can modulate bottom-up feature extraction processes.

Acknowledgements SFB 936 Multi-Site Communication in the Brain

$\left[T\ 67\right]$ Undisturbed long-term monitoring of weakly electric fish in a small stream in Panama

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A prerequisite for the full understanding of sensory systems is knowledge about the natural context these systems evolved in. The electric sense of the gymnotiform electric fish Apteronotus leptorhynchus is a successful model system in research on the neural computations underlying behavior. These fish generate an electric organ discharge, which can be modulated in amplitude and frequency to create various communication signals. Much is known about the sensory system's anatomy and physiology as well as the fish's behavior and intraspecific communication signals. However, recent laboratory studies indicate that electrocommunication behavior depends strongly on the experimental situation. Further, the fish's behavior is subject to seasonal changes. Therefore a better knowledge about the fish's natural behavior in its natural habitat is desirable, in particular for interpreting electrophysiological data of the electrosensory systems. The present study targets just this question by providing and applying a novel method for undisturbed long-term monitoring of electric fish. Using an array of electrodes, which is spread out over the fish's habitat and continuously records the electric fields of the fish, allows for tracking of individual fish's motion, communication signals, and conspecific interactions. We discuss the underlying principles, prospects and limits of our method and present recent data from our study-site in Panama, where we monitored Apteronotus rostratus, a close relative of A. leptorhynchus, during the transition from dry to rainy season.

$[\top \, 68]$ Stochastic generation of gamma-band activity in primary visual cortex of awake and anesthetized monkeys

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Oscillatory neural activity within the gamma band (25-90 Hz) is generally thought to be able to provide a timing signal for harmonizing neural computations across different brain regions. Using time-frequency analyses of the dynamics of gamma-band activity in the local field potentials recorded from monkey primary visual cortex, we found identical temporal characteristics of gamma activity in both awake and anesthetized brain states, including large variability of peak frequency, brief oscillatory epochs, and stochastic statistics of the incidence and duration of oscillatory events. These findings indicate that gamma-band activity is temporally unstructured and is in its nature a noisy signal generated by neural networks. This idea was corroborated further by our neural-network simulations. Our results suggest that gamma-band activity is too random to serve as a timing signal for synchronizing neuronal responses, but that it can be used as a measure of the general state of the cortical network.

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$\left[T\ 69\right]$ Predictable visual stimuli are perceived earlier than unpredictable events

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How is it possible that we timely react to visual events despite the significant processing delays within the visual system? This delay is estimated to be already about 100ms in higher visual areas, a delay which is relevant if one needs to initiate fast reactions, such as catching a ball in flight or initiating escape. To compensate delays the brain employs predictive mechanisms. An example is the internal forward model which allows the motor system to predict an upcoming sensory state and thus to react even before sensory feedback is available. It is quite likely that - apart from this and other predictive mechanisms on the motor level - purely perceptual predictions could also contribute to delay compensation. Yet, to our knowledge, there is no compelling evidence for delay compensation on a strictly perceptual level. Hence, we asked whether predictability of a visual stimulus affects the time of perceived stimulus onset. Specifically, we hypothesized that predictable visual stimuli have an earlier perceived onset compared to non-predictable stimuli.

We tested our hypothesis in a psychophysical experiment, in which we initially screened 23 subjects in a dual task that engaged temporal interval judgements. In the middle of a black screen streams of individual letters were presented. Each letter was presented for 300ms with a 1000ms default interval between letters. The sequence of letters was either in alphabetic order and thus predictable or, alternatively, the last letter of a sequence was chosen at random and thus not predictable. In each trial subjects had to indicate whether or not the last letter

agreed with the alphabetic order. Moreover, subjects had to estimate whether the duration of the last interval, which was of varying length, was either longer or shorter as compared to the preceding intervals of 1000ms duration. Varying the length of the last interval allowed us to estimate the point of subjective equivalence (PSE) between intervals. As we expected predictable letters to be perceived earlier, the PSE should be larger in predictable sequences than the PSE in non-predictable ones. Since our experiment required precise timing we applied rather strict exclusion criteria to both trials and subjects. For the six subjects that survived these criteria there was a significant shift of the PSE towards larger values for predictable sequences (median shift: 54.99 ms; p=0.0313). Hence, our findings show that predictable visual stimuli are in fact perceived earlier than non-predictable ones. This suggests that even the perceptual system is compensating for delays in sensory information processing, allowing us to establish a timely percept of our environment.

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[T 70] Detection of linear ego-acceleration from optic flow

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Human observers are able to estimate various ego-motion parameters from optic flow, including rotation, translational heading, time to collision (TTC), time to passage (TTP), etc. The perception of linear ego-acceleration or deceleration, i.e. changes of translational velocity, is less well understood. While time-to-passage experiments indicate that ego-acceleration is neglected, subjects are able to keep their (perceived) speed constant under changing conditions, indicating that some sense of ego-acceleration or velocity change must be present. In this paper, we analyze the ego-acceleration perception and its relation to geometrical parameters of the environment using simulated flights through cylindrical and conic (narrowing or widening) corridors. Theoretical analysis shows that a logarithmic ego-acceleration parameter, called the acceleration rate rho, can be calculated from retinal acceleration measurements. This parameter is independent of the geometrical layout of the scene; if veridical ego-motion is known at some instant in time, acceleration rate allows to update ego-motion without further depth-velocity calibration. Results indicate, however, that subjects systematically confuse ego-acceleration with corridor narrowing and ego-deceleration with corridor widening, while veridically judging ego-acceleration in straight corridors. We conclude that judgments of ego-acceleration are based on first order retinal flow, and do not make use of acceleration rate or retinal acceleration.

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[T 71] A single psychotomimetic dose of ketamine disrupts corticothalamic dynamics

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Sensory and cognitive deficits are common in schizophrenia. The underlying anatomo-functional mechanisms remain elusive. There is a growing body of literature indicating the involvement of dysfunctional thalamic networks in the pathophysiology of schizophrenia, including disturbances in function-related gamma frequency (30-80 Hz) oscillations. A postulated mechanism of these impairments is the reduced N-Methyl d-Aspartate receptor (NM-DAr) activation at glutamatergic synapses on GABAergic interneurons.

Ketamine is a non-competitive NMDAr antagonist that when administered at sub-anaesthetic doses in humans and rodents produces symptoms reminiscent of psychosis and also induces aberrant gamma oscillations in cortical and sub-cortical structures, including the thalamus. Corticothalamic and thalamocortical pathways are glutamatergic and work together during brain operations, including during cognition and sensory information processing. Corticothalamic pathways originate from layer VI and innervate simultaneously GABAergic thalamic reticular nucleus neurons and thalamocortical neurons of the dorsal thalamus.

The goal of the present study was to explore the spatiotemporal dynamics of the corticothalamic and thalamocortical pathways in the rat somatosensory system under physiological (vehicle) and pathological (ketamine) conditions. We conducted under light anesthesia (4) multisite cell-to-network recordings in the rat somatosensory thalamus. Its background activity was challenged by stimulation of the vibrissae. Sensory stimulation evoked a short-latency ($3.3 \pm 0.1 \text{ ms}$, n=30 from 3 animals) prethalamic response and a longer latency ($9.6 \pm 0.1 \text{ ms}$, n = 30 from 3 animals) corticothalamic response. A single injection of ketamine (2.5 mg/kg, sc) significantly increased the power of gamma oscillations (~240 % of vehicle, p < 0.001) and decreased the amplitude of the sensory-evoked corticothalamic response (vehicle condition: -0.35 \pm 0.02 mV; ketamine condition: -0.26 \pm 0.05 mV, p < 0.001, n = 20).

In conclusion, the present results support the hypothesis that the psychotomimetic effects of ketamine are characterized by a reduction of the sensory signal-to-gamma noise ratio in corticothalamic systems.

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$\left[T\ 72\right]$ Contrast invariant feature selectivity in balanced random networks

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Neurons in the primary visual cortex (V1) of mammals are highly selective for the orientation of a light bar [1, 2, 3], while they receive afferent connections from neurons in lateral geniculate nucleus (LGN) which are themselves not selective. The emergence of this property in cortex has been subject of debate since decades, and served as a paradigm to unravel the key mechanisms of information processing in the brain. We investigate the problem from a network point of view, by focusing on random recurrent networks with no specific pattern of connectivity.

By exploring a large-scale network model of spiking neurons through simulations and theoretical analysis, we show how a purely random network operating in the inhibition dominated regime contributes to feature selectivity. In particular, we demonstrate how tuning amplification can happen in these networks as a consequence of 'selective attenuation', a general mechanism which selectively suppresses the common mode. By systematically investigating the relevant parameter space, we pinpoint different regimes of orientation selectivity, which yields testable predictions for the biological cortex.

The 'selective attenuation' mechanism also yields contrast invariance [4, 3] of feature selectivity, which ensures feature detection for a wide range of input scales. Therefore, we suggest that the basic mechanism of contrast invariance is a consequence of intracortical interactions, and neither a single cell property, nor a purely feedforward mechanism. We argue in favor of 'tuning amplification' as the key process of the recurrent processing stage, for which no specific structure is needed. This mechanism could, in principle, also work for other sensory features and other sensory modalities as well, since the neural hardware necessary to achieve it is readily available in the cortex.

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[T 73] Temporal segregation of mitral and tufted cell activity – the role of glomerular and granule layer interneurons

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In olfaction, the sniff rhythm shapes activity across cell populations. We have previously shown that the two major types of output neurons of the mammalian olfactory bulb (OB), mitral and tufted cells (M / TC), lock to different phases of the sniff rhythm, and that this temporal segregation is caused by GABAergic inputs selectively delaying MC activation. Here we assess, using optogenetic manipulations of selective populations of OB interneurons, in combination with whole cell recordings from principal and interneurons in vivo, which inhibitory circuits underlie this separation.

We first tested the contribution from granule cells (GC). AAV carrying flexed ArchT and GFP were injected into the GC layer of mice that express cre under the control of Gad65 promoter. Intracellular recordings from GCs show that 42% (8/19 cells) of GCs were infected, hyperpolarizing by 10-30 mV in response to light presentations, at depth up to 0.8 mm. Despite the efficient silencing of GCs, there was no change in the physiology of MC or TC.

Next we turned to glomerular interneurons. Periglomerular cells (PG) comprise of heterogeneous populations, among others PGo, receiving direct olfactory sensory neuron (OSN) input, and PGe, whose dominant drive is generated by OB excitatory neurons, i.e. MC, TC and other excitatory cells. To functionally dissect the role of PGo and PGe, we expressed ChR2 in Gad65+ neurons in the GC layer. Then, optically driving such GCs resulted in strong hyperpolarisations of MCs and TCs, reducing the excitatory drive in PGe cells, while leaving PGo cells unaltered. Whole cell recordings from such identified PGo cells (n = 8 cells), revealed that their peak depolarization occurs 43 ms before the trough of MC membrane potential, but synchronized to TCs. This is consistent with the notion that TCs and PGo are both directly driven by OSN input, while MCs are selectively delayed by PGo input.

To test if PG cells, indeed, separate MC activation from TC activation, we directly assessed the role of Gad65+ neurons in the glomerular layer by optogenetic silencing with AAV carrying flexed ArchT. Our preliminary results indicate that, unlike with GC silencing, which consistently produced no observable alterations to MC or TC phase, silencing of glomerular layer Gad65+ neurons cause a wide range of effect, most notably changes in sniff-coupling of MCs.

Hence, our work suggests that feed-forward inhibitory circuits consisting of PGo cells delay sniff-coupled activities in MCs. The study also stresses the crucial, but complex nature of glomerular circuitry in OB processing.

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$[\top 74]$ A novel volumetric electroporation design permits reliable and quantitative neuronal network tracing

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Electroporation, the application of short electric field pulses to transiently permeabilize the plasma membrane in order to render cells susceptible to a variety of molecules has become a widespread technique in the neurosciences over the past decade. While glass microelectrode electroporation has mainly been used for single cell electroporation, it has also been proposed for network delineation. Especially in the emerging field of connectomics where physiological data and ultrastructural anatomy combine to provide a foundation for computational modelling, a way of delineating neurons participating in a network module of interest appears desirable.

However, approaches presented so far lack a quantitative assessment of the extent of their efficacy. Furthermore, several studies indicate a highly limited volume in which effective electroporation may occur.

Here we present a novel electroporation technique using glass micropipettes modified with nanofabrication techniques for volumetric electroporation. By "gating" fractions of the total applied current through multiple openings around the tip a more homogeneous electric field is created around the tip of the pipette when compared to standard glass microelectrodes.

We investigated and compared the properties of the electric fields of both techniques numerically by using the finite element method and experimentally in vivo. For an increase of effective electroporation volume, we find that it is not a feasible solution to simply increase the applied current with the common approach because i) very high peak potentials are generated in vicinity to the pipette tip and ii) we observe the formation of gas bubbles beyond a current density of approx. 12 $\mu A/\mu m^2$. Our new design allows for reduced peak current densities meaning that according to our simulations we can pass approx. double the total amount of current until the same peak potential which we set at 700 mV is reached. In turn, this results in an approx. 10-fold increase of the effective electroporation volume.

We tested our new technique in a glomerulus of the mouse main olfactory bulb. This structure of neuropil serves as a valuable model network because it is supposed to represent a distinct computational unit associated with a specific olfactory channel. To assess the reliability of our method, we performed two independent electroporation protocols with two differently coloured dextran dyes on the same glomerulus. Labelled cells were quantified separately for each of the dyes. Preliminary statistical results indicate that at least 80 % of covered cells by the second dye are also labelled by the first electroporation already; meaning that at most 20% of cells, almost exclusively small periglomerular cells, may be missed by the first attempt. Furthermore, cells extending their dendrites and axons to the glomerulus of interest but with cell bodies more than 600µm away could reliably be labelled.

Although still leaving space for further improvements we argue that our new approach expands the range of applications for electroporation and provides a reliable technique for small to medium sized network delineation.

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$\left[T\ 75\right]$ Band-pass properties of neurons in the early auditory system of the cricket

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In many communication systems information is encoded in the temporal pattern of signals. For rhythmic signals that carry information in specific frequency bands, a neuronal system may profit from tuning its filter properties towards a peak sensitivity in the relevant frequency range. Such tuning may be expressed in resonant peaks of the firing rate, located at the relevant stimulus frequencies. We explore this hypothesis by combining experiment and model in a study on single cells of the peripheral insect auditory system.

The cricket is a formidable model system for investigating the processing of temporally patterned signals: to attract mating partners, male crickets produce a rhythmic song composed of short, almost pure-tone sound pulses. The temporal pattern of these pulses is characteristic for a particular cricket species and is evaluated by females. The rhythmicity of signals suggests that resonant properties within the auditory pathway may contribute to information processing.

To verify whether resonant mechanisms are expressed in the peripheral auditory system of the cricket we first obtained extracellular recordings from three types of auditory neurons (AN1, AN2 and ON1). For acoustic stimulation we chose pure-tone signals with a swept-frequency sinusoidal envelope. The stimuli were designed to cover a wide range of envelope frequencies

which included the pulse frequency of the species' calling song (~25 Hz). Transfer functions extracted from spectrograms of the spike trains revealed that both AN2 and ON1 act as bandpass filters on the stimulus envelope. For AN1 no band-pass properties were observed. The best-frequencies of ON1 were close to the frequency of the species' calling song, for AN2 they were slightly higher.

Are these band-pass properties indicative of resonant mechanisms in the auditory pathway? We explored three simple models that were plausible candidates for reproducing the observed effects. These models utilize different, cell-intrinsic or network-based mechanisms to shape a filter: spike-triggered adaptation, sub-threshold resonance and interplay of excitation and inhibition. In fact, all three proposed mechanisms were able to reproduce the band-pass properties and are thus candidates for centering a small nervous system's limited coding capacity on behaviorally relevant signal components.

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$\left[T\ 76\right]$ Wave Propagation in the Human Cochlea with Cochlear Implant (CI) Electrodes

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The supply of profoundly hearing impaired patients with cochlear implants has become a standard with large success related to speech understanding without disturbing noise. As is known in noisy environments the additional transmission of the low frequency pitch of speech increases the sentence recognition rate. Therefore the surgeons try to preserve the low frequency abilities of patients by a conservative operation technique and short CI electrodes.

For a better understanding of the wave propagation in the cochlea with implanted electrodes human temporal bones were scanned by a μ -CT and three-dimensional reconstructions of the data set were created. With that the acoustic fluid-structure coupled system was evaluated by numerical methods.

The results show the displacements of the cochlear partition (cp) and the basilar membrane under varying conditions in three dimensions. Surprisingly even the increase of cp displacement with an implanted CI electrode was found. The small effect (some dB), which is also found in audiograms of CI patients, is attributed to the distribution of acoustic energy to those places which are not fixed by the CI electrode.

The numerical simulations give details to future implantation techniques and the design of better CI electrodes.

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$\left[T\ 77\right]$ Internally Coupled Ears (ICE): How Neuronal Processing Gets Restricted

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Lizards, frogs, most birds, and alligators have internally coupled ears (ICE) where the tympanic membranes connect through a large mouth or other cavity and influence each other. Here a new model of auditory information processing for internally coupled ears is presented. This model is analytically soluble. The mouth cavity is simplified as a cylinder so that the processing of the incoming sound waves can be described through the internally coupled tympanic membranes. We have applied the model to Hemidactylus frenatus, one of the smallest lizards on earth. For this animal, the model shows that the internal coupling of the ears enhances internal time differences by a factor of 3 up to about 3 kHz and creates internal amplitude differences in the tympanic membrane vibrations for frequencies beyond 3 kHz. These results are in very good agreement with experimental measurements up to a frequency of 5 kHz. Above this threshold, it has been found experimentally that the model systematically overestimates the amplitude of vibrations of the tympanic membrane. To test whether and how the actual shape of the mouth cavity may modify the results found for the simplified cylindrical geometry, the eigenmodes and eigenfrequencies for the reconstructed mouth cavity have been calculated numerically. The lowest eigenfrequency is found to be 5.1 kHz, allowing a simple explanation of how the directional response of the tympanic membrane is affected by resonance. Implications for lizards and other animals using the ICE technique are presented.

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[T 78] How retinal processing aids cortical invariance learning

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Many areas of visual cortex show invariant responses to certain stimulus features. Perhaps the best known example of this is the phase invariant response of so-called complex cells in V1, however several other such invariances can be found in cortical representations, such as gaze-invariant encoding of object positions. Several studies have proposed that such representations can be learned by exploiting differences in the temporal correlation structure of such features under natural viewing conditions (Michler et al, J Neurophysiol 2009; Teichmann et al, Neural Comp. 2012). In general, however, these studies use raw visual stimuli as input to cortical networks. This ignores the effects of spatio-temporal signal processing in the retina, as well as the division of retinal signals into magno-cellular and parvo-cellular streams. Here we investigate how such processing contributes to the learning of invariances in visual cortex, in particular the development of complex cell properties in V1, and image stabilization under fixational eye movements.

We present a model retina with different cell types that captures both the mostly linear behaviour of midget cells, as well as much of the non-linear behaviour of parasol cells observed in retinal recordings. We then use this model retina as an input layer to a cortical invariance learning network that exploits a self-organised topographical structure to learn selectivity to slowly varying features (Michler et al, J Neurophysiol 2009).

When stimulated using drifting natural images this model learns complex cell representations in it's output layer. We find that cells receiving parasol cell input display a higher degree of phase invariance than those trained on midget cell input, while remaining orientation selective. When trained on a combination of midget and parasol inputs, the complex units tune preferentially to parasol cells.

Furthermore, we investigate how parallel processing in magno-cellular and parvo-cellular pathways can contribute to image stabilisation. We demonstrate how, using a non-linear combination of midget and parasol inputs, a cortical network may learn to distinguish local and global image shifts, generating a gaze invariant representation.

Our results suggest that retinal non-linearities - such as those associated with parasol ganglion cells - facilitate the learning of complex cell properties and, together with the bifurcation of retinal inputs into parallel pathways, support image stabilisation under fixational eye movements.

Acknowledgements

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[T 79] Predicting Eye Movements in a Contour Detection Task

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An important task for the visual system is grouping local image elements into meaningful objects. One fundamental process for performing this task is contour integration, in which collinearly aligned local edges are merged into global contours. Models for contour integration often use iterative algorithms to explain how this cognitive process is performed in the brain. By employing an association field (AF) which quantifies how strongly two oriented edge elements are linked to be part of a contour, such a model integrates edge elements in a recurrent manner. This process generates saliency maps for contours of increasing lengths as time proceeds.

Recently, we developed a probabilistic model of contour integration which explains human contour detection behavior to a previously unprecedented degree [1]. Given this performance, we wondered whether the model might also explain the spatiotemporal dynamics of contour integration. Measuring eye movements can be a useful method to test the corresponding model predictions, hypothesizing that subsequent fixations of subjects preferentially visit 'hotspots' of neural activity which dynamically emerge during the integration process.

Here we compare model simulations with data from a recent experiment [3], in which eye movements were measured while observers were instructed to search for a 7-element contour embedded in a background of randomly oriented Gabor elements [2]. The experiment consisted of two tasks: for the first task observers were asked to indicate whether a global contour was on the left or right hemifield (left-right task), while the second task required observers to indicate presence or absence of a contour (present-absent task). The parameters of the model were first optimized for the left-right task, requiring it to reproduce both human performance and decisions as best as possible.

The optimal model was then used to predict potential locations for saccade targets which we compared to fixation trajectories of observers for stimuli from the second task, hereby excluding fixations near the target contour from our search. For edge elements near saccade targets, the model predicts a probability to belong to a contour which is two times higher than for other edge elements. On average, 70% +/- 6% of all fixations were predicted, which is significantly larger than for a model making random predictions (d'=0.63). Thus fixations are indeed not random, but are likely to occur on locations judged salient by the model. This result confirms both the validity of our model and the hypothesis that saccades on random Gabor fields preferentially visit locations with edge configurations similar to contours.

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$\left[T\ 80\right]$ Seeing in the dark: higher visual performance in nocturnal insects

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Even though humans see poorly at night, the majority of the world's animals – both on land and under water- are active in dim light conditions. Many of them actually use their visual sense to navigate in their environment. Despite possessing tiny eyes and brains, nocturnal insects can distinguish colour, avoid obstacles during flight and find their way home using learned visual landmarks. But how is this remarkable visual performance possible? What is the nature of the brain's nocturnal visual circuitry? How have the visual properties of this circuitry been optimised to maximize visual performance in dim light conditions?

In order to approach these questions, we study the visual motion processing circuitry in hovering hawkmoths – a group of fast-flying insects renowned for their impressive visual abilities, in which closely related species are active under completely different light conditions, ranging from bright sunlight to strictly nocturnal species. Wide field motion sensitive (HS-like) neurons in the lobula plate of two hawkmoth species, one day and one night active, have been shown to be tuned to their visual ecology.

We are quantifying these differences in spatial and temporal tuning at various light levels ranging from daylight to starlight using intracellular recording from wide field motion sensitive neurons in the lobula plate, together with a detailed anatomical comparison of the neuronal circuits. These results will allow us to determine the general neural strategies that nocturnal species use to optimise visual performance at night, principles that are likely to apply to all nocturnal animals.

$[T\ 81]$ Echolocation vs. echo suppression: influence of the precedence effect on the human-sonar localization of reflective surfaces

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Echolocation is an effective perception-action ability of humans, especially used by blind people. However, the precedence effect predicts a conflict of echo analysis and echo suppression: when localizing sound sources, the human auditory system suppresses spatial information of echoes, but just this information underlies effective echolocation.

A common approach to investigate the precedence effect is the arrangement of two sound sources that present a direct sound (lead) and a delayed copy (lag). Several experiments on lag-discrimination suppression have quantified the deterioration of spatial information of the lag produced by the lead.

This study investigates the interaction of echolocation and precedence effect in terms of discrimination suppression. Sighted subjects performed two versions of an azimuth-discrimination experiment in virtual acoustic space: In the 'listening' version, subjects had to discriminate between positions of a single sound source, the leading, or the lagging of two sources, respectively. In the 'echolocation' version, the sound sources were replaced by sound reflectors. Here, subjects evaluated the echoes generated in real time from self-produced vocalizations and thereby discriminated between positions of a single reflector, the leading, or the lagging of two reflectors, respectively.

Our results show that sighted subjects can be trained to discriminate reflective surfaces by echolocation with accuracy comparable to sound source localization. In the listening version, the presence of a lagging source impaired lead-discrimination only slightly by a factor of 1.6, while a leading source impaired lag-discrimination considerably by a factor of 8.8. The asymmetry between lead- and lag-discrimination shows a strong influence of the precedence effect, which facilitates localization of the lead at the expense of the lag. In the echolocation version, however, this asymmetry was significantly weaker: lead and lag discrimination deteriorated by a factor of 4.8 and 6.2, respectively. These data indicate that the precedence effect is weakened in an echolocation context.

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Motor control, movement, navigation

$\left[T \ 82 \right]$ Canceling actions involves a race between basal ganglia pathways

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Salient cues can prompt the rapid interruption and redirection of planned movements. It has been proposed that such action cancelation involves a specific pathway through the subthalamic nucleus (STN). Here we combine in-vivo electrophysiology in rats performing a stopsignal task with computational modelling and optogenetics to reveal the basal ganglia circuits involved in action cancelation.

First, we compared neural activity in different basal ganglia structures during action cancelation. STN neurons showed low latency responses to the Stop cue, irrespective of whether action suppression was successful or not. By contrast, neurons downstream in the substantia nigra pars reticulata (SNr) responded to the Stop cue only when actions were successfully suppressed. Consistent with "race" models, our results suggest that successful action cancelation requires Stop cue information to reach SNr via STN ahead of the increased striatal GABAergic input that promotes movement execution.

Based on this experimental data, we next developed a novel neurobiologically-grounded variant of the race model in an integrate-and-fire model of SNr. The model successfully reproduces basic features of the electrophysiological data. Exploration of different scenarios of striatal input patterns suggests the existence of a crucial time point after which STN excitation cannot overcome striatal inhibition anymore. This may correspond to a neural 'point of no return' and indicate that the go process has won the race against the stop process. Our neural race model predicts that blockade of the STN input to SNr shifts this 'point of no return' in favor of the striatal go process and impairs stopping performance. Finally, we test this prediction with selective, precisely-timed optogenetic suppression of the STN-SNr pathway.

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$[\top\ 83]$ How internal metabolic state changes motor coordination computations in reaching movements

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Optimal feedback control theory has been very successful in explaining human motor coordination data (Todorov & Jordan, 2002; Diedrichsen & Shadmehr, 2010). This theory of motor control derives control policies from the minimisation of cost functions. Several costs have been proposed, each which can explain the data, due to their common quadratic mathematical form. None of these costs have been demonstrated to be the one minimised by the nervous system. We take the view that many motor coordination tasks involve trade-offs between multiple conflicting and undesirable costs. During a motor task humans balance these costs in a characteristic manner yet very little is known about how this fits with optimal control theory. Here we ask whether the brain's computation strategies are sensitive to internal metabolic state and reflect an energetic control cost in reaching movements.

Mammalian muscle consists of a mixture of fast and slow muscle fibres, with characteristic activation regimes (Tansey et al. 1996) and metabolic efficiencies (Reggiani et al. 2000). Slow muscle fibres are predominantly activated at low total muscle force levels while the more metabolically costly fast fibres are activated only at higher force levels. Although the relationship between metabolic energy consumption in a single muscle fibre varies linearly with force production, modelling a population of muscle fibres allows a first biophysical principles derivation of a quadratic cost function. This cost function is dependent on the ratio of fast to slow muscle fibres which crucially varies over a muscular system in independently to the size of motor pools (thought to be the main predictor of signal dependent noise; Hamilton et al. 2004), suggesting signal-dependent noise and metabolic efficiency derived cost functions will produce different optimal behaviours. We model the human arm as a 6-muscle 2-joint system operating under optimal feedback control (Todorov & Li, 2005) and we model the control cost as the sum of a signal-dependent motor noise cost (Harris & Wolpert, 1998) and metabolic cost based upon our muscle fibre model. By comparing the optimal control strategies under each cost function and human behaviour in different metabolic regimes we produce a quantitative description of the cost function underlying human motor coordination acting in two different metabolic regimes.

Our experimental data is based on a dynamic centre-out reaching task and a static force production task. In the dynamic task, subjects perform frictionless reaching movements from the centre of the workspace to a target in one of 8 directions. In the static task, subjects produce a number of target forces as accurately as possible for 10 seconds. The force supplied by the subject is defined as the sum of forces acting upon two perpendicular force sensors: one at the wrist and one just below the elbow. We produce two distinct internal metabolic states by performing each task during the morning on two separate days where the subject either follows their normal eating/drinking routine or fasts from 8pm the evening before the session. Two groups of subjects perform the tasks following both metabolic regimes in a counterbalanced manner.

Our results show that motor coordination bias depends on metabolic state. The noise optimal strategy predicts a bias of -0.24 (more force from muscles acting over the shoulder joint) whereas the metabolic energy optimal strategy predicts a bias of +0.02 (slightly more force from muscles acting over the elbow joint). We use a bootstrapping technique to find the population (N=5) mean bias (with 95% confidence intervals) for the fasting group: -0.11 and the non-fasting group: -0.19. This is a statistically significant change in the direction predicted by metabolic state driving the trade-off from motor noise to metabolic efficiency. Our result suggests that after fasting humans value metabolic cost more than during their normal routine. Understanding these effects allows us a first glimpse at how the computational strategies in our brain depend on non-neuronal, physiological states.

Acknowledgements

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$[\top 84]$ What is the hierarchical representation of tasks involving objects with complex internal dynamics?

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Motor circuits, limb kinematics and many real-world tasks are organised hierarchically [1-2]. This prompts the question how the brain represents hierarchical task dependencies and how these are mapped onto the nervous system and control of movement. It was previously suggested that the CNS represents object manipulation tasks with regard to an intrinsic frame of reference centered on the body's actuators and sensors and/or an extrinsic frame of reference related to task context, environmental settings or properties of point-like objects [3-5]. Ultimately, these two reference frames have to be linked to support the completion of high-level tasks [1], such as pouring wine into a glass. Here, we examine how joint- and body-based reference frames are organised as parts of a hierarchical structure of task representation that underlies motor learning. Towards this end we focus on the manipulation of objects with naturalistic internal dynamic.

We test 3 possible hierarchical schemes of motor learning in object manipulation tasks: (a) In the first one task dynamics are principally learned and represented in intrinsic joint-based reference frames, on which the extrinsic reference frame of the object depends. This predicts, that humans generalise learned motor tasks over all joint space, but with regard to only one object orientation. (b) Conversely, in the second scheme, task dynamics are principally learned in an object-centered reference frame. This predicts generalisation across object orientations, but not across joint configurations. (c) In the third scheme both reference frames are learned independently.

In order to test which of the three candidate mechanisms underlies motor control we conducted a behavioural study. Human subjects were asked to perform a rotational task within a given accuracy inside a 3D virtual reality setup, using a bottle of complex or static internal dynamics. In 2 different experiments subjects learned a single training task and were subsequently instructed to complete multiple testing tasks, in which object or joint positioning varied (experiment 1 and 2 respectively). Their performance was estimated in terms of pivot point displacement and used to examine how learning is transferred from training to testing conditions. Our results revealed a significant increase of pivot point displacement from training to testing phases in both experiments and for both object types. (Wilcoxon test, p<0.0125). This increase demonstrates a poor generalization capability of learned task dynamics to novel task contexts. This observation provides supporting evidence that task representations are independently learned for both the body-centered and object-centered coordinate frames and ad-hoc combined during motor actions. Our results lead to further investigations of the frames' respective timescales, their potentially weighted contribution to motor learning, as well as the dependence of this weight on the nature of object dynamics.

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[T 85] Sensory predictions of intended movements in monkey posterior parietal and dorsal premotor cortices

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It is well-established that cross-modal integration of sensory information leads to reach goal representations in different spatial frames of reference in the posterior parietal cortex (PPC) and dorsal premotor cortex (PMd). Additionally, there is emerging consensus that this feed-forward integration needs to be accompanied by feedback mechanisms which allow updating of motor goals and movement corrections based on on-line state estimations and motor error signals. Yet, direct neurophysiological evidence for the representation of forward predictions during movement execution is difficult to provide due to confounding factors. Beyond immediate motor control, the encoding of anticipated sensory effects of an intended movement, prior to execution, has been postulated as a possible mechanism of action selection and planning. Here we directly test the existence of sensory prediction neurons in monkey PPC and PMd.

We used delayed and memory-guided reach tasks in which monkeys had to perform either pro or anti reaches under either normal or reversed vision through inverting prisms. This task double-dissociates the spatial information about the sensory instruction, the intended physical movement, and the predicted visual feedback about the movement. The pro vs. anti comparisons dissociated the visual memory of the cue from the movement intention, in both the normal viewing context and the prism viewing context. The prism vs. non-prism comparisons dissociated the physical intention from the visual prediction in the pro and anti contexts. Especially, the combined prism and anti-reach task created situations where the sensory cue and physical reach directions were identical, but the visual predictions were opposite.

About one fourth of the neurons in PPC and PMd which were movement related and directionally selective in the prism and no-prism condition encoded the direction of the anticipated visual feedback, rather than the intended physical arm movement direction. The remaining neurons encoded the physical direction of planned movement. Our results provide direct evidence for the notion that motor planning not only evokes neuronal representations linked to the planned action per se, but also to its anticipated perceivable sensory consequences. These predictive representations establish a role of forward model prediction in the fronto-parietal network, even before a motor command is issued, as an integral part of the planning and probably also selection process for actions. This concept tightly relates to the ecological approach of perception, motor awareness, the mirror-neuron system, and modern concepts of neural adaptive motor control. This work was supported by the Federal Ministry for Education and Research (BMBF, Germany, grants, 01GQ0814 and 01GQ0951), the German Research Foundation (DFG, grant SFB-889), and the State of Lower Saxony (grant VWZN2563).

[T 86] A model of the optokinetic reflex system in larval Xenopus

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Vestibular and optokinetic reflexes are classically considered to be the major contributors for maintaining visual acuity during locomotion in vertebrates. Here, we present a computational model of the optokinetic reflex system, which helps to elucidate the functional organization and sensory-motor processing within the neural circuitry responsible for the visual image stabilizing system in Xenopus laevis. The optokinetic reflex performance was tested by various step and sinusoidal visual stimulus patterns, which were presented by rotation of a vertically striped drum in semi-intact preparations of larval Xenopus with a functional visual system. Eye movements were studied by computer analysis of videos recorded from the animals during optokinetic stimulation with a camera at 50 frames per second. The optokinetic response of larval Xenopus consisted of slow following phases, which were regularly interrupted by resetting fast phases. The horizontal ocular motor range was \sim 60° and the maximal gain was 0.63 ± 0.03 at 2°/s constant rotation. Miniature oscillations with a frequency of 2.78 ± 0.39 Hz could be observed during the slow phases independent of stimulation velocity. Simultaneous motion recordings of one eye and multiple-unit recordings of the contralateral lateral rectus nerve during optokinetic stimulation revealed the presence of distinct motoneuronal subgroups that were differentially active during slow and fast phases, respectively. Based on these data a computational model of the optokinetic reflex circuitry was established, simulating the interaction of the separate neuronal subgroups involved in generating the optokinetic responses on a systems level with integrating structures responsible for both slow and fast phases. The individual subsystems were approximated by gain elements and their dominant time constants, omitting further temporal characteristics. This allowed studying the dynamic behavior of the interaction between the optokinetic subsystems. Besides allowing simulations of new stimulation patterns that can be tested experimentally, the model also supports a potential task-dependent activation of separate motoneuronal subgroups for slow and fast phases, converging at the mechanical properties of the eyeball. The experimentally measured miniature oscillations emerged as an intrinsic property of the underlying model structure incorporating visual feedback pathways and uncompensated propagation delays, suggesting that the observed oscillations most likely originate from delays in the sensory transduction process. Extension of the computational model will provide further understanding about the nature of neuronal projections and adaptive changes of the optokinetic system during ontogeny. Moreover, it allows formalizing hypotheses on oculomotor behavior and eco-physiological plasticity that can be tested by experimental manipulations.

$[T\ 87]$ How to Pass People - A Dynamic Navigation Model Using Repulsive Potentials

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When walking through a shopping center, pedestrians cross path with dozens of other people, but do not collide with them. In order to do so, they need to adapt their motion to avoid collisions and pass people at respectful distance. There are infinite possibilities to avoid collisions with other pedestrians. However, it has been shown that such movements follow stereotypical trajectories. This indicates that pedestrians use specific strategies to avoid obstacles while moving to their desired location. Furthermore there is evidence that human can predict future states of the environment. Such future state predictions can be taken into account for the planning of trajectories. Here, we present a model that is able to qualitatively describe collision avoidance trajectories of a subject, when an interferer is crossing the path of the subject.

In our model, Newton's law of motion is used to describe the dynamics of the subject. To simulate the goal directed movement of the subject we added a minimum-jerk controller (Hoff & Arbib 1993) that generates a force pointing to the desired goal. The interferer was represented by a repulsive potential field. To take into account the subject's ability to predict future states, the potential field was modeled to be dependent on the velocity of the interferer. The potential field consisted of two components: one along the movement direction of the interferer and the second perpendicular to this direction. The potential field along the movement direction was based on the equation of the Maxwell-Boltzmann distribution with the 'temperature' corresponding to the velocity of the interferer. The maximum of the distribution was set to the position of the interferer. This had the effect that for higher velocities the potential field spread towards the moving direction. In the perpendicular direction, the potential was modeled by a Gaussian distribution centered at the interferer's actual position.

To validate the model, we simulated the model behavior when an interferer and a subject walk from a predefined starting position to a fixed goal position and compared it with experimental data. The starting angle between the two intended paths was 45°, 90°, 135°, and 180°. In the experiment the interferer was instructed not to consider the subject while approaching his goal position. The comparison of the simulated results with the experimental results showed that our model was able to predict the key features of the measured trajectories and the velocities profiles: a) the subject passed behind the interferer, b) in the 90° case, the subject adjusted their walking speed rather than their path. Our navigation and obstacle-avoidance model can be implemented in mobile robots to achieve a better predictability of robotic behavior.

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$\left[T\ 88\right]$ Finite Size Effects in Grid-Cell Attractor Models for Spatial Navigation

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Rodents feature an internal representation of space that resides in the medial entorhinal cortex, a cortical region one synapse up-stream of the hippocampus. Grid cells have been implicated to be the building blocks for this internal map and fire in multiple locations that form a regular pattern, which resembles a hexagonal lattice [Hafting et al, 2005]. Although the mechanism that underlies the grid cell firing has not been discovered yet, different types of models have been proposed. Here, we focus on continuous attractor networks, a class of model that has been successfully used to describe a broad range of neural and cognitive phenomena. Due to their continuous set of stable states, these models can perform accurate path integration [Knierem & Zhang, 2012]. They are robust against noise, do not need external cues for the pattern formation, and can reliably integrate internal signals. This corresponds well to experimental observations that rats can navigate using path integration and that grid-cell patterns are stable even in complete darkness over a timescale of minutes [Etienne & Jeffery, 2004, Hafting et al, 2005].

We base our investigation on the model of Burak & Fiete [2009]. We find that the properties of these neural networks strongly depend on the strength and range of synaptic weights, which we varied systematically. We investigated regularity and path integration capability of the network subject to finite size effects, such as rotations and distortion of the activity pattern.

$\left[T\ 89\right]$ Spatial behavior of mongolian gerbils in complex virtual environments

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Virtual reality (VR) environments are increasingly used to study spatial behavior in rodents. In many approaches so far the design of the environments did not go beyond simple open fields or linear tracks. How to make rodents learn to navigate in more complex virtual environments is hardly investigated. We use a VR setup with a spherical treadmill that is surrounded by a 360° toroidal screen onto which the virtual environment is projected. This design permits a fixation of the animal such that it can freely rotate around its vertical body axis. We trained gerbils (Meriones unguiculatus) to perform spatial tasks in virtual mazes of different complexity. First the animals learned to run back and forth between the two ends of a virtual linear track. At the ends they received a food reward. They had to learn to orient with only visual information, not to collide with the virtual walls and optimize the path from one reward to the next. Performance increased within about ten training sessions to almost optimal values: The animals avoided virtual walls and ran straight paths from one track end to the other. Running speed was consistent with what is typically observed in real environments. When afterwards presenting more complex mazes such as U- or 8-shaped arenas the animals were able to transfer their previously acquired skills to the new tasks after only a few trials. We furthermore implemented two-alternative choice tasks using a virtual y-maze were animals were required to run to the end of one arm depending on their decision.

[T 90] Adaptive Neural Oscillator with Synaptic Plasticity Enabling Adaptive Hexapod Locomotion

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There is strong evidence and it is widely accepted that the rhythmic neural activity necessary for animal locomotion is basically produced by central pattern generators (CPGs). They can generate periodic patterns without requiring periodic input or sensory feedback. However, sensory feedback still plays an important role when it comes to coordination of multiple joints or limps and adaptation to changing environments.

Recently, we developed an adaptive neural oscillator with synaptic plasticity that is able to adapt to and memorize an external frequency quite fast and works within a wide frequency range [1]. It is based on a discrete-time two neuron SO(2)- network and inspired by a general oscillator adaptation rule. A third neuron with additional plastic synapses is introduced to accelerate the adaptation process.

We use this mechanism as a CPG to control the joints of a simulated hexapod robot. The sine shaped output of the CPG is fed into a modular feed-forward post-processing network that generates appropriate motor commands to control the limbs of the robot with the given frequency. Due to the limited torque of the motor a delay between the angle set point and the actual motor position is observed. The signals of the forward-backward joints' angle sensors are used as a feedback signal to the adaptive CPG. By trying to make the feedback signal and the CPG output coincident, the adaptation mechanism maintains a given phase delay between the motor command and the actual angle sensor value.

The phase delay between the motor command and the angle sensor signal depends on the motor power, the current workload and the frequency at which the motor is driven. For higher frequencies, lower motor power or higher workload the phase delay increases. As a consequence the CPG converts to a lower frequency. The same holds for the opposite case. If the robot reaches e. g. an upwards slope, the workload increases and so does the phase delay. Therefore, the CPG frequency decreases until the original phase delay is recovered. If the robot reaches a negative slope the opposite effect can be observed. This behavior is reasonable as only a lower frequency enables the robot to climb upwards efficiently. In contrast, a higher walking frequency can be used when walking downwards without wasting energy.

As a further finding we observe that blocking the robot's movement, e. g. by applying a large downwards force, effectively results in a huge phase delay as the motors nearly cannot follow motor commands at all. This leads to a reduction of the oscillation frequency towards zero which is a useful behavior to prevent motor damage.

The application of the recently developed neural oscillator with synaptic plasticity as a CPG for a simulated hexapod robot results in autonomous and meaningful adaptation of the robot's walking speed when confronted with terrains with different slopes.

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[T 91] Reactive Neural Climbing Control for Hexapod Robots

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Insects, e.g. cockroaches, have found fascinating solutions for the problem of locomotion, in particular climbing over a large variety of obstacles. Neuroethological study has identified key behavioral patterns of these animals necessary for climbing: body flexion [1], center of mass (CoM) elevation [2], and local leg reflexes [3]. For example, when cockroaches start to climb over an obstacle they extend their middle legs to push the front body from the ground (CoM elevation). Afterwards, they tilt the prothorax down (i.e., body flexion) to support their locomotion and keep balance during climbing. In other situations, like locomotion through complex landscapes, there is a high probability for legs to get stuck. Searching and elevator reflexes tend to solve such problems leading to effective locomotion including climbing over obstacles.

Inspired by this finding, we develop reactive climbing control for our hexapod robot AMOS II. The controller is composed of three main neural circuits: neural locomotion control, neural reactive backbone joint control, and neural local leg reflex control. The locomotion control generates basic walking behavior including omnidirectional walking and different gaits of the robot. The reactive backbone joint control supports the climbing behavior of the robot by emulating the body flexion observed in cockroaches. The local leg reflex control activates searching and elevator reflexes as well as CoM elevation.

The controller was developed and successfully tested using our modular robot control environment, allowing physical simulation and simple transferring to AMOS II. Experimental results show that the developed reactive climbing control allows the robot to surmount obstacles with a maximum height of 13 cm which equals 75% of its leg length (see supplementary video at http://www.manoonpong.com/BCCN2012/ReactiveClimbing.wmv). As a comparison, a quadruped robot presented in [4] successfully negotiated obstacles up to 40% of its leg length while the hexapod Gregor I [5] and the octopod Scorpion IV [6] achieved a height of 65% and 55% of its leg length, respectively. In addition, AMOS II displays the three key behavior patterns found in neuroethological studies. Therefore, the experiments not only show that AMOS II exhibits outstanding climbing capabilities, but its control system also generates climbing behavior similar to the behavior observed in insects.

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[T 92] Motor equivalence reveals coarticulation in arm movement sequences involving obstacle avoidance

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We study movement sequences involving obstacle avoidance in naturalistic 3D arm movements in humans looking for coarticulation. We use the concept of the uncontrolled manifold (Scholz & Schoener, 1999) to uncover motor equivalent solutions when movements in one segment are preceded by different movements in the preceding segment.

In the experiment, participants moved an object with their hand along a horizontal path from one target to the next while avoiding obstacles placed between the targets. Each of four segments began with tapping the object on a target, then moving over an obstacle and tapping on the next target, which started the following segment. The obstacles varied in height, higher obstacles being placed in the second and third segments of the movement. We looked for coarticulation, that is, for influences of these higher obstacles on the first and last segments.

Avoiding lower obstacles immediately after avoiding higher obstacles resulted in adaption of the spatial path of the transported object (post-coarticulation). This adaption increased with increasing height of the preceding obstacle.

At the joint level we decomposed the variance of joint configurations into components that leave the spatial position of the transported object invariant (UCM) and the orthogonal complement (ORT). We found higher variance within the UCM than within ORT across the entire movement sequence.

Coarticulation was addressed at the joint level by decomposing the difference between joint configurations in different conditions into a UCM and an ORT component. The UCM component is motor equivalent because it leaves the task variable invariant. The difference between joint configurations in a given segment, when different obstacle conditions were experienced in the preceding segment, lay largely in the UCM. Such motor equivalence is evidence for coarticulation at the level of the joint angles. Anticipatory coarticulation was not found consistently across all participants.

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[T 93] Modular Robot Control Environment – Testing Neural Control on Simulated and Real Robots

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To develop new control approaches for robotic devices and evaluate their results it is important to be able to efficiently test them not only in simulated but also real environments. This means switching between simulated and real systems should be easily possible using the same controller code (without reprogramming). Furthermore, the development process should be able to continuously increase robot functionality in order to solve more complex tasks. This can be achieved based on modularity. A modular structure is considered as a major advantage, compared to many other approaches due to the following aspects: 1) It is flexible, allowing to simply rearrange, add, and/or remove modules for controlling different types of robots. 2) Each module is typically independent of other modules in its functioning and does not influence or become influenced by other modules.

Taking this into account, here we present a modular robot control environment relying on the C++ programming language and providing an artificial neural network library. It is used to develop neurocontrollers for different robots. The very same controller code can now be tested in simulation and on real hardware, which allows speeding up the development process. The modular robot control environment also allows to exchange robots and controller in a plug-and-play manner where parameters of the simulation and real robot can be observed and changed online.

We have applied the modular robot control environment to develop neural control of hexapod walking robots AMOSII. They are biologically inspired hardware platforms developed in collaboration with the Fraunhofer Institute for Intelligent Analysis and Information Systems IAIS. They are used to study the coordination of many degrees of freedom, to perform experiments with neural control, memory, and learning. The robots were modeled using LPZRobots [1], a physically realistic simulation toolkit (freely available under GNU General Public License).

Employing iterated development cycles, including progression of a neural controller and tests on the simulated and real hexapod platform, a variety of biologically inspired walking gaits as well as orienting, taxis and their combinations have been successfully achieved. By recently developing another module for adaptive climbing behavior, the hexapod can now overcome obstacles of various heights (e.g., ~75% of its leg length, which is higher than those that other comparable legged robots have achieved so far). The presented modular robot control environment can also be applied to different types of robotic systems, like wheeled robots and manipulators (e.g., integration of the E-puck mobile robot and the KUKA-DLR Lightweight Robot arm in preparation). Figure 1: Modular Robot Control Environment: The developed neural controllers can easily be transferred to and tested on real and simulated hardware platforms. Here a neural control for hexapod locomotion is depicted.



Figure 1

Acknowledgements

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Learning, plasticity, memory

$\left[T\ 94\right]$ Biologically-inspired neural controller based on adaptive reward learning

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Human learns tasks from their own experiences by self-exploration and observation of others' actions. The evaluation of the achieved task is driven by rewards. Human can improve their skills in order to gain more rewards (e.g. Happiness, Food, Money, and etc...). By observing its cortical activities, neurobiological studies suggest that the orbitofrontal cortex (OFC) is related to reward dealing in the human brain [1]. Neurons of OFC are the key reward structure of the brain, where reward is coded in an adaptive and flexible way [2]. Studies of the Anterior Cingulate Cortex (ACC) suggest that it is responsible to avoid repeating mistakes [3]. This cortical area acts as an early warning system (EWS) that adjusts the behavior to avoid dangerous situations. It responds not only to the sources of errors (external error feedback), but also to earliest sources of error information available (internal error detection) [4]. EWS has shown to be affected by the tolerant to risks, psychological studies provide further evidences of people's strategies into two classes as in taking or aversion risks [5].

"NeuroRobotics" research draw on human learning methods in order to improve the autonomy and the robustness of robots for their dealing with environment changes. In connection with these neurological studies, we proposed a learning method based on human learning from experiences (ACC) and inspired by the way the human brain code rewards (OFC), in order to allow a humanoid robot to learn a walking task. With the vigilance threshold concept that represents the tolerance to risk, the method guaranteed the balance between exploration and exploitation, unlike other searching methods (e.g. Q-learning, Monte Carlo...). Furthermore, it is able to converge into multiple learning targets.

Most task learning methods based on reward use predefined parameters in their reward function [6], which cannot be obtained without previous experiences to achieve the desired task. Learning based adaptive reward don't require any previous information about the reward, it is able to build the experience only based on the reward available information after starting from scratch.

Our approach has been implemented on the NAO humanoid robot, controlled by a bioinspired neural controller based on a central pattern generator (CPG). The learning system adapts the oscillation frequency and the motor neuron gain in pitch and roll in order to walk on flat and sloped terrain, and to switch between them.

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[T 95] Linking Geometry-Dependent Nonlinear Current Conduction Characteristics to Synaptic Efficacy

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Protruding from the dendrites of several neuronal types are subcellular compartments known as spines, which are targeted by synapses. The morphology of spines is highly dynamic, likely affecting the strength of the synapse — a key aspect of neuronal plasticity. 3D spine reconstructions at nanometer resolution reveal a dense assembly of supra-molecular structures that create a spatially intricate network of intracellular components. Actin filaments, microtubuli, endoplasmic reticulum, spine apparati, and the cellular membrane have polar surfaces that contact the aqueous phase. Within this tight ultrastructural mesh, slits measuring less than 100 nm are not uncommon, thus favoring the emergence of nonlinear current conduction characteristics. In order to appreciate how the geometry affects current conduction within highly confined spaces, the Poisson-Nernst-Planck system needs to be solved for spatial complex geometries. Here we describe how different functional and computational properties of synapses can arise from current conduction characteristics induced by specific geometrical constraints and compare these to engineering applications in nanofluidics.

$\left[T \; 96\right] \;$ A model of basal ganglia for automaticity in categorization tasks

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Dividing objects into categories is one of the remarkable human abilities, but its neuronal basis (Seger & Miller, 2010) and its impressive fast execution is still little understood. After several repetitions of the same categorization task, the speed of the decision process increases. This mechanism is called automaticity (Ashby et al., 2010). The neuronal foundations for categorization are the Basal Ganglia (BG) and the prefrontal cortex (PFC) which are connected via thalamocortical loops (Seger & Miller, 2010). The associate loop, which contains the most category specific cells, is formed by prefrontal cortex, caudate nucleus (CN), globus pallidus internal segment (GPi) and thalamus (Thal) and it is driven by visual cells in inferior temporal cortex (IT). We will present a model which simulates the shift of the neuronal activation patterns during automaticity as observed by Antzoulatos & Miller (2012) in a prototypedistortion categorization task (Seger & Miller, 2010). Initially (pre-automatic phase), primarily the neurons of caudate nucleus react to specific categories. But after many repetitions (automatic phase), neurons in the caudate nucleus show no longer category specific responses, instead the cells in the prefrontal cortex become category specific (Antzoulatos & Miller, 2012; Ashby et al., 2010). We propose that after the emergence of these category-specific cells in prefrontal cortex, cortical-cortical connections will be developed between prefrontal and premotor cortex (PM) due to Hebbian learning. This induces the profitable decrease of reaction times, because the information processing chain is shifted from IT->PFC->CN->GPi->Thal->PM (pre-automatic phase) to the shorter and hence faster inter-cortical chain IT->PFC->PM (automatic phase). Therefore, our model simulates these inter-cortical connections, the substantia nigra pars compacta (SNc), Dopamine releases and the direct pathways of the associate and of the motor loop. In summary, the model, which is an advancement of our earlier work (Schroll et al., 2012), clarifies the neuronal activation pattern in the Basal Ganglia and the cortex during a prototype-distortion categorization task and its shift during automaticity.

Acknowledgements

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[T 97] Impact of recurrent connectivity on off-line memory reprocessing in a hierarchical neural network formed by unsupervised learning

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Multiple experimental studies provide evidence for memory performance improvement following off-line regimes like restful waking or states of sleep, where brain is not actively involved in processing of external stimuli. It has been hypothesized that this improvement is due to off-line reprocessing and consolidation of initially labile memory traces formed during active waking. Although it is obvious that such improvement requires beneficial modifications to be done in the memory network during off-line regime, not much is known about what kind of changes are indeed induced in the memory network during off-line reprocessing.

In our study we examine off-line memory reprocessing in a hierarchical recurrent neural network model that is able to self-generate ongoing sparse activity even in absence of external stimulation due to self-excitable but competitive neural dynamics that shapes winner-take-all like behavior of network units. In this regime, the network reactivates memory traces established during preceding on-line learning, where it has been exposed to natural face images of different persons in unsupervised fashion [1]. Remarkably, this off-line memory replay turns out to be highly beneficial for the network recognition performance [2, 3]. To our surprise, the positive effect was independent of synapse-specific plasticity, relying completely on a synapse-unspecific local mechanism of homeostatic activity regulation that equalizes unit excitabilities within network layers during off-line reprocessing. Moreover, fully recurrent network gets a much stronger performance boost after off-line reprocessing as compared to its purely feed-forward version.

To clarify the contribution of different network connectivity types to the positive effect observed after the off-line reprocessing, we conducted experiments where a specific kind of long-range recurrent connectivity, lateral or top-down, was disabled following off-line regime. Disabling either lateral or top-down connectivity in the recognition test phase results in decrease of the performance boost achieved through preceding off-line reprocessing. Loss of top-down connectivity impairs network performance stronger than loss of lateral connectivity. Interestingly, even if both top-down and lateral connectivity are disabled, there is still a significant advantage over performance of a purely feed-forward network that employed neither lateral nor top-down connectivity during learning. This indicates that off-line reprocessing in the fully recurrent network is able to boost recognition performance even if the network has to rely on its established feed-forward structure only. These findings suggest that while long-range recurrent connectivity is crucial during on-line learning and may help to further enhance the performance boost following off-line reprocessing, it is not necessary for maintaining the major benefit obtained after the off-line regime.

Acknowledgements

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[T 98] Modelling the effects of slow wave sleep on synaptic plasticity

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Multiple studies have shown the importance of slow wave sleep for the development of memories. Furthermore slow oscillatory activity can be modulated by non-invasive stimulation, which leads to an enhancement of memory consolidation. However the exact mechanisms remain unknown. Here we combine a biophysical model of up/down state generation proposed by Compte et al. with a Ca2+-dependent plasticity rule Bhalla et al. as the first step towards developing a model for long-term plasticity during slow wave sleep. We show that the synaptic efficacy is indeed elevated after one up/down cycle and keeps increasing with every further cycle, approaching the stable potentiated state. However the number of up/down states needed to push the synapse in the strong state is far from the one seen in natural slow wave sleep. As the plasticity model focuses solely on single synapses we investigate the effect of additional downstream plasticity related proteins and kinases e.g. MAPK, which are know to play a crucial role in LTP and link the cell wide activation by the up/down states to the plasticity of the individual synapses.

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Upinder S Bhalla.

$\left[T \ 99\right]$ Neuronal activity during sleep and memory formation in the Honey bee

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Human beings spend almost one third of their life sleeping, and the consequences of sleep deprivation have been widely reported. Despite the increasing insight into the mechanisms of sleep generation, the function of sleep still remains unclear. Several hypothesis have been proposed, one of which claims that sleep periods are favorable for brain plasticity and for learning and memory (1). In this framework, sleep would be involved in the processing of the memory traces that would then be incorporated into long-term memory.

At the behavioral level, it has been reported that the honey bee Apis mellifera displays distinct sleep phases which can be monitored by tracking the bee's antennal movements, and that these sleep phases are associated with memory consolidation (2). But so far there is no evidence of the implications of the neuronal activity during sleep in memory formation. In this work, long term extracellular activity of multiple feedback neurons of the protocerebral-calycal tract (PCT) was recorded during a combined visual and olfactory learning paradigm, and during sleep phases as well. PCT neurons respond to a variety of sensory modalities (3) and are a potential candidate for multi-sensory learning and memory formation in the bee brain. By recording the activity of these neurons we were able to monitor the overall changes in multi-unit activity pattern during training and testing sessions with the pattern observed during sleep for these units. Our goal is to relate neural activity during the sleep phases with the animal's performance during memory retention tests.

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[T 100] Recruitment of hippocampo-neocortical networks during a virtual reality version of the radial arm maze task in humans

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Hippocampal-prefrontal interactions are essential for spatial navigation and memory, and disturbed in patients with schizophrenia and subjects at genetic risk (Meyer-Lindenberg et al., 2005; Esslinger et al., 2009). In an effort to develop translational tasks that aid in investigating this system, we have established a virtual reality version of the radial arm maze, a reward-based spatial working memory task that is widely used in rodents. During the acquisition of fMRI blood oxygenation level dependent (BOLD) data subjects navigated through a

virtual park surrounded by various landmarks to find hidden gold coins at the end of 12 alleys. The paradigm was completely self-paced and consisted of three task (training/encoding, delay, test/retrieval) and matched control phases, respectively, in each trial. The task design enforced the use of a spatial, landmark-based strategy.

Analysis of the pilot data recorded from a group of healthy subjects showed a strong recruitment of a network associated with spatial working memory and navigation. In the blocked design, we observed activations of the dorsolateral prefrontal cortex, parietal and midbrain areas (Adcock et al., 2006) during both training and test phases. While activation of (para-)hippocampal areas was specific to the training phase, activation of the ventral striatum was only observed during the test period. Behavioral data was analyzed to determine when subjects encoded and retrieved information about the location of hidden rewards during the training and test phase respectively. Event-related analysis revealed that hippocampal areas are selectively recruited during encoding, while activation of parietal areas was weak. During retrieval, strong activations were found in parietal and prefrontal areas as well as the ventral striatum. Furthermore, we employed a set of multivariate statistical methods to characterize task stage-specific activation patterns (see poster by Demanuele et al.).

Our analyses suggest a contribution of neural signals for salience related to dopamine function to the navigation task we employed, further strengthening the usefulness of this approach as a translational method to examine disorders such as schizophrenia.

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$[T\ 101]$ Encoding short-term episodic memory: vectors of association in models of word-list free recall.

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Neural memory, the acquisition and storage of new information in biological substrates, is axiomatic to the operation of brains as we conceive them. However, much in our theories of memory remain undetermined. We examine behavioural data from human short-term recall experiments to constrain theories of human memory, using simulations at varying levels of biological detail, including spiking neuron networks as well as simplified algorithmic models. We assess the need for a separate short-term memory storage as proposed by dual-store 'buffer models' (eg Davelaar et. al. 2006), considering in particular the retrograde effects of noise-masked words on the recall of preceding unmasked ones, as studied in the Wingfield lab at Brandeis. We propose a generalised buffer, and neural substrates to support it, to account for these effects, which can also capture temporal context information as per the TCM framework of Howard and Kahana (2002).

Acknowledgements

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[T 102] Electric field modulation of long-term plastic effects

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Transcranial electrical stimulation in humans can lead to electric fields of at most 1V/m on the cortical surface. This may polarize cell membranes by a fraction of a milivolt. While these intensities seem very small, there are a number of in vitro experiments explaining the basic mechanisms by which such low-amplitude electric fields may nevertheless acutely alter neuronal activity, both at the single cell and at the network level . However, the long-term plastic effects which have been repeatedly observed clinically are less understood.

Here we are particularly interested in the effects of slow-oscillating stimulation during sleep which were shown to boost the consolidation of hippocampus-dependent declarative memory. How synaptic connections are modified resulting in a memory improvement is still unknown. Currently, two main complementary hypotheses exist regarding consolidation of memory during sleep. The synaptic homeostasis hypothesis conjunctures that consolidation is in part a result of synaptic downscaling that improves the signal-to-noise ratio for all synapses that were potentiated during prior waking experiences. The active system consolidation hypothesis proposes an active consolidation process where learning-specific synaptic connections are strengthened by means of increased plasticity-related immediate early gene transcription and induction of LTP.

Slow-oscillating stimulation might be improving memory consolidation by means of modulating synaptic downscaling and/or learning-specific synaptic connections. Current results of our group show that this low-amplitude fields induced an effect on the homeostatic downscaling of endogenous slow-waves during sleep. However, the modulation LTP processes related to the potentiation of learning related synapses has not yet been studied for such fields. Previous studies show that electrical stimulation coupled with ongoing activity in the brain induces plasticity, here we will focus on the modulation of LTP processes while applying acutely several low-amplitude field configurations. Thus linking the long-term behavioral effects with acute electrical stimulation.

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[T 103] Control of Learning Using Theta Susceptibility of Synaptic Plasticity Dynamics

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Synaptic plasticity is the neural basis for learning and memory formation. Given its importance, the exact rules that govern synaptic change depending on neural activity are not sufficiently well understood. The simplistic spike timing dependent plasticity rule in response to single pre- and postsynaptic spike does not generalize to more complex spike pattern, which show an intricate combination of suppressing and fascilitating effects in multiple spike interactions. This neccessitates a dynamical formulation of synaptic plasticity. For this purpose, we developed the contribution dynamics (CD) model that captures many of the effects found in experimental data of synaptic change in response to complex spike pattern. When subjected to constant poissonian firing, the model synapse exhibits a BCM like characteristic of weight change depending on the mean firing rates of both neurons, plus an additional conversion of long term potentiation to long term depression for very high firing rates, thus preventing excessivly high synaptic weights. For time dependent periodic firing, the synapse is susceptible to rate modulation in the theta range (around 7Hz). Here, we investigate the effects of this susceptibility when CD synapses are implemented in neural networks. We show that application of a global theta modulation during activation of a particular set of neurons effectivly acts as a reward signal, selectivly strengthening the connections between coactivated neurons. This provides a possible explanation for the known importance of theta oscillations for learning.

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[T 104] Cellular and Nuclear Morphology...and Calcium Signaling: Revealing the Interplay between Structure and Function

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Calcium plays a pivotal role in relaying electrical signals of the cell to subcellular compartments, such as the nucleus. Since this one ion type is used by the cell for many processes a neuron needs to establish finely tuned calcium pathways in order to be able to differentiate multiple tasks, [1, 2, 3].

While it is known that neurons can actively change their shape upon neuronal activity, [4, 5, 6, 7], we here present novel findings of activity-regulated nuclear morphology, [8, 9]. With the help of an experimental and computational modeling approach, we show that hippocampal neurons can change the previously spherical shape of their nuclei to complex and infolded morphologies. This morphology regulation is demonstrated to be regulated by NMDA-receptor gated calcium, while synaptic and extra-synaptic NMDA-receptors elicit opposing effects on nuclear morphology, [8].

The structural alterations of the cell nucleus have significant effects on nuclear calcium dynamics. Compartmentalization of the nucleus, due to membrane infoldings, changes calcium frequencies, amplitudes and spatial distributions, [8, 10]. Since these parameters have been shown to control downstream events towards gene transcription, [11, 12], the results elucidate the cellular control of nuclear function with the help of morphology modulation. With respect to processes downstream of calcium, we show that histone H3 phosphorylation is closely linked to nuclear morphology. Investigating the nuclear morphologies of hippocampal neurons, two major classes were identified [9, 10]. One class contains non-infolded nuclei that have the function of calcium signal integrators, while the other class contains highly infolded nuclei, which function as frequency detectors of nuclear calcium, [10].

Extending this interdisciplinary approach of investigating structure/function relationships in neurons, the effects of cellular morphology – as well as the morphology of the endoplasmic reticulum and other organelles – on neuronal calcium signals is currently being investigated. This endeavor makes use of highly detailed, three-dimensional models of neuronal calcium dynamics, including the three-dimensional morphology of the cell and its organelles.

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[T 105] Multimodal map formation without visual teacher: A dynamical model for the blind Mexican cavefish Astyanax Mexicanus.

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About fifty percent of all vertebrates are fish. Since fish live in water where quite often light (and therefore vision) is not a useful signal they should rely on other sensory inputs. One of them is water motion that they can detect through their lateral-line system. The mechanosensory lateral line, unique to aquatic vertebrates, is divided into two subsystems, viz., superficial (SN) and canal neuromasts (CN) that both exhibit different response properties to hydrodynamic stimuli. Previous studies have shown that SNs encode water velocity, CNs respond to its first derivative, namely, water acceleration.

From previous work we also know the spatiotemporal distribution of firing rates for SNs and CNs based on the hydrodynamics of a sphere moving along the fish's lateral-line system. The key question we now investigate is how fish can use CN and SN input modalities to build an internal representation of a moving object positioned at a certain position and distance. We show that a simple two-layer network is capable to extract the position information with high precision not only from ideal sensory input, but also for very noisy input and signals

with different offset and amplitude. The integration of both SN and CN signals within a multimodal map on the one hand further stabilizes the localization, but it is also crucial to the learning process. Particularly, animals such as the blind Mexican cavefish (Astyanax Mexicanus), which lack visual input as a distinctive teacher, need to strongly exploit correlations between different modalities of the rather blurred lateral-line input and the feedback coming from higher brain area to still be able to learn a precise map. By applying stability analysis to the dynamic we describe the actual map formation and derive a suitable Hebbian learning rule. Finally, we study the associated stable manifold to get possible initial conditions that enable multimodal integration in a neuronal system such as the lateral-line system of fish.

*The contribution of the first two authors is equal.

[T 106] Novel self-organizing rules for retinotopic remapping

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Retinotopic maps in the primary visual cortex are plastic even in the mature brain. Particularly after permanent changes in external input, i.e. after focal retinal lesions, maps in the cortex adapt so that neurons deprived of input (lesion projection zone, LPZ) become responsive to adjacent input representations. This 'filling-in' process is currently explained by STDP. However, STDP is a fast process while the time course of reorganization continues over weeks until one year [1]. Recent data indicates that structural plasticity (forming new synapses, breaking old ones) is involved in this reorganization [2,3] and acts very much on the same time scale. Therefore, we propose the first model investigating structural plasticity in application to cortical remapping. The model implements local activity-dependent rules for changes in the morphology of the neuron. In accordance with experimental findings, model neurons aim to maintain their electrical activity on average at a certain pre-defined set-point [4] by adapting the number of contact sites (axonal and dendritic elements). New (vacant) synaptic elements are offered to the network and connect to form synapses. The probability for synapse formation between two neurons depends on the amounts of vacant synaptic elements offered and the Euclidean distance between the two neurons. Network rewiring is therefore a reciprocal process between activity and network structure: Activity levels inside the LPZ (low) and outside the LPZ (high) locally induce the formation of axonal and dendritic elements, respectively, that in turn form synapses in a cooperative and compensatory manner leading to increasing activities in the LPZ again. The consequence of transporting activities via new synapses from the outside of the LPZ into the LPZ is an enlargement of input representation from intact areas and a sequential filling-in of the LPZ (Fig. 1)-by contrast not obtained in self-organizing maps. The novelty of the model is to generate predictions how local cellular responses lead to rewiring and remapping on an anatomical network level.

Caption Figure 1: Cortical remapping emerges from new horizontal connections formed from intact areas into the LPZ. A) Colors indicate spatial input representations. White dashed circle indicates LPZ. B) New connections impinging on cells in the LPZ (white dots). Connections originating in the peri-LPZ (green), LPZ border (orange), LPZ center (blue). Horizontal and vertical bars indicate the relative position of the areas to the entire network.





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[T 107] Interactions 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 (van Vreeswijk & Sompolinsky, 1996) and because it shapes cortical responses to sensory stimuli (Monier et al., 2008). 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 (Vogels et al., 2011).

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 for different excitatory learning rules and show that the interaction of excitatory and inhibitory plasticity can lead to non-trivial effects.

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[T 108] Modelling the interaction of structural and synaptic plasticity

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Recently it has been shown that learning is associated with structural changes in neural tissue. The underlying mechanism, named structural plasticity, drives the formation of new synapses and the removal of existing ones on a timescale of days and weeks. This enlarges the potential for information storage in neuronal networks and is thus important for understanding long-term memory formation. On shorter timescales (minutes to hours) another process, named synaptic plasticity, which influences the transmission efficiencies (weights) of a synapse, also contributes to information storage.

We investigate the interaction between these two processes – still widely unknown – in the following rather simple model: We use rate based neurons with the total transmission efficiency between two neurons being just the sum of weights of all synapses connecting these two neurons. Thus, the number of synapses as well as their weights influence the same quantity and we can investigate the effects arising from structural and synaptic plasticity competing on different timescales. Synaptic plasticity is modeled by Hebbian learning with weight dependent synaptic scaling. For structural plasticity we propose a model, consisting of three processes: First, we have an activity dependent outgrowth and retraction of dendritic arbors. The growth process determines the number of potential synaptic sites. Second, the formation of a synapse at each of these potential synaptic sites happens at random with a fixed formation probability. Third, the removal of existing synapses also happens randomly, but with a weight-dependent probability.

Although both processes are quite complex, we can show that the system converges to a stable state. In this state the activity determines the probability distribution of number and strength of the synapses between neurons. The combined mechanisms could also serve to form highly interconnected clusters, which are candidates for memory representation.

Acknowledgements

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Attention, reward, decision making

[T 109] Non-multiplicative attentional modulation patterns in area MT: modeling the possible role of functional interactions with area V1

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We analyzed single unit recordings in area MT from macaque monkeys performing an attentional task. They were presented a complex composite stimulus made out of moving randomdot-patterns (RDP) at two distinct locations within the receptive field of the recorded MT cell. Attention was directed to a fixation spot or to only one of the two RDPs. The angle between the two RDPs was kept fixed at 120 degrees so that covarying the motion directions provided tuning curves with two peaks. We found that the positions of the response peaks were different from what the single-motion orientation-preferences of the cell predicted. Furthermore they depended on the attentional condition, showing strong signatures of non-linear interactions during the integration of the two stimuli by MT neurons. In particular, repulsion between the response peaks was observed in the attend-fix condition, while in the attend-in condition, the peak associated to the response to the non-attended RDP was attracted back toward the peak associated to the response to the attended RDP.

By using a mean-field ring model of the local circuit of area MT, we could easily reproduce the repulsion effect in the attend-fix condition, assuming local functional interactions described by a kernel with a negative Gaussian like shape. However reproducing qualitatively the complete set of observed non-linear modulations in both the attend-fix and attend-in condition was possible only through an extremely fine tuning of all the parameters.

This raises the question whether additional circuitry is needed to explain robustly and simultaneously all the observed effects. We explore therefore multi-areal network models with multiple coupled rings, in which functional interactions between hypercolumns of area V1 and MT are also taken into account. In this enlarged modeling setting we systematically explore sets of multi-areal functional mechanisms that might underlie non-linear patters of attentional modulation, commenting on their plausibility.

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[T 110] Modulation of dopaminergic activity by the expectation of reward: a computational neural model.

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In classical conditioning experiments, dopaminergic neurons in the ventral tegmental area (VTA) exhibit a reward-prediction error pattern by producing phasic bursts for unexpected rewards (US) and reward-predicting stimuli (CS), and making a pause in firing at reward omission [1]. The pathways subserving time estimation of rewards are not fully determined yet, but the lateral habenula (LHb) has been shown to be excited by small or absent rewards and to selectively inhibit VTA cells. Additionally, cells in the striatum are considered as co-incidence detectors able to respond for particular cortical patterns, what can be used for time estimation when cortical oscillations at various frequencies are deterministic [2].

Using mean-firing rate neurons and homeostatic covariance-based learning rules (as in [3]), we propose here a computational model of the interactions during conditioning between the ventromedial prefrontal cortex (vmPFC), the ventral basal ganglia (vBG, including the shell part of the nucleus accumbens NAcc and the ventral pallidum VP), LHb, the amygdala, the lateral hypothalamus (LH) as well as VTA. The basolateral amygdala learns to represent the emotional valence of a rewarding or punishing US with respect to the organism's homeostasis signaled by LH, as well as to associate this valence to the predicting CS. The centromedial amygdala elicits dopaminergic bursts in VTA for both CS and US. The emotional valence of a predicting cue is further transmitted to the shell of NAcc, which opens a recurring loop with vmPFC through VP and the mediodorsal thalamus, allowing vmPFC neurons to exhibit oscillating patterns at various frequencies, but synchronized at CS onset. When the learned delay between the CS and US has passed, the shell detects the corresponding pattern in vmPFC and inhibits VTA, either directly to cancel VTA activation for expected rewards, or indirectly through VP and LHb to pause dopaminergic activation through activation of the inhibitory interneurons of VTA.

This model proposes a functional explanation of dopaminergic activation during conditioning with respect to the known anatomy and explains behavioural data such as extinction or the scalar property of time estimation. It points out the importance of homeostasis in the valuation of rewards and the formation of preferences. It forms a first step towards the comprehension of ventral BG functioning in the learning of incentive values and ultimately decisionmaking.

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[T 111] Processing of competing stimuli in the chicken midbrain slice

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The midbrain is an important processing area for sensory information in vertebrates. The optic tectum (TeO) and its mammalian counterpart, the superior colliculus, receive multimodal, topological information and contain a sensory space map which plays a role in spatial attention and in orientation movements. This saliency map allows shifting the focus of attention to most relevant information (Itti and Koch, 2001; Marin et al., 2007; Mysore et al., 2010).

In birds, a complex feedback circuitry is formed by neurons of the 15 layers of the optic tectum and modulatory midbrain areas, e.g. the nuclei isthmi (NI). This presumably accounts for the accentuation of evolutionary relevant visual information and for suppression of less important information (Wang et al., 2006). To date, knowledge on this network is derived from tracing studies and extracellular recordings. Here, we use an optical imaging approach with voltage sensitive dyes in a slice preparation, which allows us to explore neuronal population responses with respect to the general cytoarchitecture of the TeO.

We have analyzed how a dual stimulation paradigm of the retinorecipient layers affects the spatio-temporal response pattern in the tectal network. We systematically varied parameters such as distance, temporal delay and pattern of the stimuli and analysed the interlaminar and intralaminar population response. In this approach, a second stimulus of equal strength did not influence the control response, whereas a stronger concurrent stimulus such as a burst reduced the amplitude in specific layers while not affecting the overall spatio-temporal pattern. Severing the connections to the NI abolished this effect. We will discuss our findings with respect to models described in literature.

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[T 112] Inferring human intrinsic rewards through inverse reinforcement learning

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In a large variety of situations one would like to have an expressive and accurate model of observed behavior. Here we show the advantage of expressing behavior as a combination of concurrent goals in the context of optimal control, which has the distinct advantage of expressing behavioral goals as reward functions. We show that, in such a setting, a specific formulation of inverse reinforcement learning can be derived that allows the recovery of reward weights, which quantify how much individual component tasks contribute to the overall behavior. By parameterizing the contributions of individual modules through their respective Q-functions one does not require explicit transition functions for the recovery of the reward weights. We show how to recover the component reward weights for individual tasks and demonstrate through simulations that good estimates can be obtained already with minimal amounts of observation.

We apply this framework to a sequence of experiments involving human participants in a multiple objective navigation task in a virtual environment. Participants were given different task specifications leading do different walking behavior. It is shown that the recovered intrinsic reward weights reflect the given instructions on a trial by trial and individual subject's basis, but that subjects have systematic biases that lead them to assign rewards to tasks that they were not instructed to do. Furthermore, we show how the modular framework predicts behavior in novel configurations and novel task combinations.

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$[T\ 113]$ The role of reinforcement learning models to assess decision-making in the Iowa Gambling Task under the influence of alcohol

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The Iowa Gambling Task (IGT) [1] is one of the most widely used laboratory tests to study decision making. In this task, participants attempt to maximize gains by selecting cards from four different decks, each of which is characterized by a specific frequency and magnitude schedule of rewards and punishments. Two of the decks are advantageous because they possess a positive average net payoff, whereas the other two have negative average net payoff, thus considered disadvantageous. A previous study [2] indicates that alcohol tends to improve performance in the task, that is, participants hit more often the advantageous than the disadvantageous decks after alcohol intake, but this effect was observed in combination with MDMA (amphetamines). Therefore, it remains an open issue to determine the specific decision making deficits elicited by alcohol consumption while completing the IGT. Moreover, the nature of the IGT (basically a four-armed bandit problem) makes reinforcement learning models suitable to assess such deficits.

We conducted a study where 77 healthy participants performed the IGT, once sober and once alcoholized, following a randomized cross-over design. We fitted two reinforcement learning models to the data, namely, the Expectancy-Valence (EV) model and the Prospect-Decay-Independent (PDI) model (for more details on these models we refer the reader to [3]). We confirm the findings in [3] in the sense that PDI provides an overall better fit to the data compared to EV. Furthermore, we assess the role of alcohol intake in IGT performance by completing regression analyses where the alcohol concentration of the participant acts as an explanatory variable for the difference between the estimated values of the model parameters across sessions.

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Brain disease, network dysfunction and intervention

[T 114] Novel bursting mode leads to seizure termination

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Many types of seizure manifest themselves in stereotype patterns of electrical activity characterized by alternations of the spike/polyspike and wave (SW/PSW) EEG discharges and fast runs of EEG spikes. This includes absence seizures (typical and atypical), absence status epilepticus, Lennox Gastault syndrome, West syndrome, and posttraumatic epilepsy [Niedermeyer, 2005]. However, the dynamics and the mechanisms of transitions between fast spiking (tonic activity) and SW/PSW complexes (bursting) in cortical networks during epileptic seizures are still poorly understood. In our previous modeling studies [Fröhlich et al., 2006, 2010] we showed that coexistence of tonic spiking and bursting states for a range of elevated extracellular K+ concentrations is critical for the maintenance of seizure-like activity in cortical networks. Since, the extracellular K+ concentration increases during tonic spiking and decreases during bursting, the bistability between tonic spiking and bursting allows the network activity to smoothly switch between the two modes, leading to sustained seizure. In a recent study, we showed that a shift in the system dynamics associated with progressive build up of intracellular Na+ concentration causes the disappearance of bistability between tonic spiking and bursting and may lead to a quick termination of seizure [Krishnan & Bazhenov 2011].

In this new study we report that reducing Na+ spiking currents in pyramidal cell dendrites rids of bistability as well. To reveal underlying dynamics we constructed α -parametric manifolds of the fast subsystem comprised of equilibria and periodic orbits [Shilnikov 2011]. We found that the mechanism underlying the smooth transition is due to a safe bifurcation of a homoclinic orbit of a saddle-node equilibrium state terminating the quiescence period of bursting (Figure 1). We revealed a new topology of bursting earlier unknown in computational neuroscience where the system dynamics smoothly evolve between four specific bifurcations stages, local and not. We hypothesize that a similar topology of quiescence and tonic spiking manifold in a phase space of other high-order models guarantees an absence of sustainable seizure-like activity. In the cortical network model including populations of excitatory pyramidal cells and inhibitory interneurons, reduction of the dendritic Na+ spiking currents prevented sustained epileptiform activity and promoted fast termination of paroxysmal bursting.

Our study predicts that pharmacological manipulations of the dendritic Na conductances will increase seizure initiation threshold and may even prevent epileptic seizures. These results may likely have implications onto drug development and deepen our understanding of the origin of seizure.



Figure 1: State trajectory (blue line) in 3D projection of the phase space. Green surface - manifold of fast motion. Red line - equilibrium states of fast subsystem.

Figure 1

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[T 115] Firing-phase coupling is preserved in the hippocampus of epileptic mice

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Structural changes in the hippocampal network associated with mesial temporal lobe epilepsy (MTLE) very likely contribute to seizure susceptibility. These changes should not only be reflected in epileptic seizures but also affect ongoing brain activity.

Recent findings in mice suggest that the theta and gamma rhythms in ongoing activity are indeed altered in the epileptic hippocampus. In particular, the cross-structural coupling of theta activity between the dentate gyrus and the medial entorhinal cortex as well as the cross-frequency coupling between theta and gamma rhythms within the dentate gyrus has been shown to be shifted [1]. The mechanisms underlying these shifts, however, are unknown, as are their possible contributions to the generation of epileptic activity.

Importantly, theta and gamma band activity of the local field potentials (LFPs) are associated with preferential phase-coupled firing of single cells but it is unclear whether this coupling is preserved in epileptic animals.

To address this, we investigated the firing of hippocampal neurons with respect to theta and gamma rhythms using the intrahippocampal kainate mouse model, which reproduces key

features of MTLE. We implanted custom-made multi-site silicon probes [2] to record simultaneously single-unit activity and LFPs at several positions in the hippocampal formation.

We find that the phase-coupled firing of single cells to theta and gamma band activity is preserved in hippocampal and parahippocampal areas in epileptic mice. Since theta band activity is shifted between entorhinal cortex and hippocampus [1], these data indicate that this is associated with a shift of single cell firing.

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[T 116] Impaired cross-frequency coupling in temporal lobe epilepsy

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The hippocampal formation is involved in mesial temporal lobe epilepsy. In many cases, this syndrome is accompanied by histological changes in different hippocampal subfields. While epileptiform activity (EA) is a transient phenomenon, these changes should be reflected in activity between EA because they are persistent. Moreover, investigation of this 'EA-free' ongoing activity could provide information on how seizures are generated in the first place.

We recently found that, in fact, during EA-free epochs, theta band activity is shifted between the medial entorhinal cortex and the dentate gyrus in the intrahippocampal kainate mouse model in vivo (Froriep et al., 2011).

Following these findings, we tested whether cross-frequency coupling between theta (4-8 Hz) and gamma (30-150 Hz) oscillations within these structures is shifted as well. While no phase shifts in theta-gamma coupling were found in the entorhinal cortex, we found an inversion of theta-gamma coupling in the dentate gyrus of epileptic mice. Because gamma activity is correlated with activity from single neurons, these findings suggest different spike timings with respect to the theta rhythm under epileptic as compared to healthy conditions.

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[T 117] **ZNF804A** polymorphism effects on hippocampus-prefrontal cortex connectivity during a working memory task: An fMRI wavelet transform coherence analysis

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Even though it is known that a substantial part of the risk for developing psychiatric disorders is inheritable, the genetic and neural mechanisms underlying this heritability are only partially understood yet. The single nucleotide polymorphism (SNP) rs1344706 of the ZNF804A gene was one of the first risk polymorphisms for schizophrenia and bipolar disorder supported by genome-wide association studies. Although the molecular function of ZNF804A still needs to be fully resolved, it could be shown by human functional magnetic resonance imaging (fMRI) that rs1344706 influences functional connectivity between brain regions. In particular, functional connectivity between dorsolateral prefrontal cortex (DLPFC) and hippocampus (HC) was found to be increased during the time course of a working memory experiment in healthy risk allele carriers, resembling findings in schizophrenic subjects.

However, it remains elusive whether the effect of the genotype is stable over the time course of the experiment or manifests only at specific time points. To test for nonstationary effects of rs1344706 we reanalyzed n-back fMRI data of N=120 healthy subjects, mostly also included in the aforementioned study, with continuous wavelet transformation, a method well suited for analyzing time-frequency properties of time series and identifying temporally and spectrally restricted processes. We then calculated the wavelet transform coherence between regions of interest in the DLPFC and HC and tested for genetic effects with general linear models. rs1344706 effects were found to be temporally much more restricted and of higher frequency than the time course of the experiment, showing that methods using stationarity assumptions like correlations over the whole time course might miss potentially important effects that can be pinpointed in time-frequency space.

$[T\ 118]$ Functional brain networks are affected by tobacco abstinence in humans: implications for tobacco addiction

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Tobacco addiction is a major public health concern in the world. Current anti-tobacco therapies are far from satisfactory, mainly due to the lack of knowledge on the circuits mediating tobacco addiction and how these circuits are modified by acute and long term nicotine use. To address this question, we imaged the brain of smokers during the resting state for 5 minutes. Subjects were instructed to stay as still as possible in the scanner (eyes open or closed), while a fixation "x" was presented in the field of view.

The Resting State Functional Connectivity (RSFC) is a relatively new technique to study human brain function in which the functional connectivity among different brain areas is studied. RSFC has shown striking coincidence with networks necessary for certain types of behaviors. Besides a hierarchical, whole brain data-driven RSFC, we measured expired CO (a measure of tobacco use in the previous few hours) and assessed responses to a series of questionnaires such as the Fagerström Test for Nicotine Dependence. We have analyzed a sample of 43 smokers in both sated and abstinent conditions (as well as 43 matched controls) and found that the percentage of representation of anatomical brain regions in functional brain networks is affected by abstinence. Several cortical areas are affected, which suggests that when habitual smokers abstain from smoking, several areas of the brain change their connectivity properties, presumably to accommodate to withdrawal of nicotine. We have also included RSFC analysis of 16 subjects who appeared twice, so that we could assess the stability of our methods.

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Data analysis, machine learning, neuroinformatics

$[T\ 119]$ A method for unbiased estimates of cross-correlations in stationarity-segmented spike train data

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Correlations among neurons are supposed to play an important part in neural computation and information coding [1]. Pairwise cross-correlation functions remain the most popular tool for investigating functional interactions between neurons in experimental data. Many applications of correlation functions, however, implicitly tend to assume that the underlying processes are stationary. This assumption will usually fail for neurons recorded in vivo since their activity during awake states and behavioral tasks is heavily influenced by stimulus-, movement-, or cognition-related processes, as well as by more general processes like slow oscillations or changes in states of alertness [2]. To address the problem of non-stationarity, we introduce a statistical method which detects violations of weak-sense stationarity in spike trains, and then "slices" spike trains into stationary segments according to the detected nonstationarities. Pairwise Pearson cross-correlations (PCC) are computed on these stationary segments, and then further corrected by removing any remaining co-modulation that may occur across segments. We probe these methods on both simulated data sets and on in-vivo recordings from cortical neurons in behaving animals.

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[T 120] Independent components of reconstructed current sources reflect activity of individual cell populations

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Local field potential (LFP) – the low-frequency part of the potential recorded extracellularly in the brain – reflects neural activity at the population level. The interpretation of LFP is complicated because it can mix activity from remote cells, on the order of millimeters from the electrode. To understand better the connection between the recordings and the local cell activity we expanded the thalamocortical model of Traub et al. (2005)[1] to compute simultaneous LFP [2], transmembrane currents and spiking activity.

We used this model to study the information contained in independent components obtained from the reconstructed Current Source Density (CSD) [3], which smooths transmembrane currents, decomposed with Independent Component Analysis (ICA) [4]. We found out that three components obtained reliably matched well the activity of two dominating cell populations: superior pyramidal cells in layer 2/3 (rhythmic spiking) and tufted pyramids from layer 5 (intrinsically bursting). Interestingly, the pyramidal population from layer 2/3 could not be well described as a product of spatial profile and temporal activation, but was matched well by a sum of two such products which we recovered in two of the ICA components in our analysis, which seem to reflect different inputs on dendritic trees within the population.



Figure 1

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[T 121] Digitization of Complex 3D Structure by Fast Automatically Structural Tracing Algorithm (FASTA)

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In recent years, numerous three-dimensional digital images were taken from confocal laser scanning microscope, X-ray and other imaging techniques for complex structures like neurons, blood vessel, collagen, fibers, etc... However, how to analyze these complex structures to obtain useful information is very challenging. One particular problem, e.g. the tracking of neuron fibers, is essential for quantitative analysis of neurons. Therefore, a very efficient tracing algorithm is crucial and very desirable. At present there are methods and commercial software packages for this function. But it requires a viewer to use his/her vision and judgment to connect or trace the fibers. Not only the task is very labor intensive but the result is susceptible to errors and is usually lack of objectivity. Here we report a new method developed by us which can automatically trace the image data of tree-like or network-like structures, such as neurons and blood vessels, without depending on the human intervention. All image voxels were encoded based on the idea of Huygens principle and traced via these codelets with some stopping criterions. With this method, some characteristic quantity of fibers can be found, for example, the center line, the branch points, the end points, the cross section area, and the branch angles etc...

$\left[T \ 122\right]$ 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 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.

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[T 123] Do Morphologically Distinct Projection Neurons in the Honey Bee Antennal Lobe Spike Differently?

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It is widely acknowledged that a neurons function is reflected in both, its morphology and its electro-physiological properties. However it is very difficult to conclude from either of these two characteristics to the other one. In a previous study [1] we employed semi-supervised hierarchical clustering to explore spiking properties which most effectively describe differences between local neurons (LNs) and projection neurons (PNs) in the honey bee antennal lobe (AL). Here we used the same approach to explore differences between two types of PNs. These morphologically similar neuron families leave the AL via different tracts, the lateral (l-APT PNs) and the medial Antenno Protocerebral Tract (m-APT PNs). The existence of these two separated pathways suggests functional differences between its neurons. But is this assumption supported by systematic differences in electrophysiological features? And if so, which features are most helpful to separate m-APT PNs from l-APT PNs?

We analyzed data from 122 extracellularly recorded AL units which, based on electrode placement were unambiguously identified as belonging to the m- or the l-APT [2]. For each unit well established measures of electrophysiological activity were estimated. We explored clustering of units based on the principal components (PCs) of every possible combination of these measures. Using hierarchical clustering with wards-linkage we determined which combination of measures performed best in separating l-APT units and m-APT units from each other. We repeated the same clustering routine on the original data, without prior principal component analysis.

We find that clustering of l-APT units and m-APT units by means of electrophysiological features performs rather poor (~36% above chance level) as compared to cluster results between .LNs and PNs (~81 above chance level). The properties which contributed most to the separation of units from different tracts were the mean evoked rate within a response window, Fano-factor, and a units lifetime sparseness (reflecting odour tuning). Repetition of the analysis without PC-transformation of physiological measures led to the same result, albeit with a reduced classification performance (34% above chance level without vs. 39% with PCA

Electrophysiological properties of units from the l-APT and the m-APT appear far more similar than those of LNs and PNs as a whole. In agreement with our results, many recent experimental findings have repeatedly indicated difficulties to differentiate physiological properties of l-PNs and m-PNs [2, 3, 4]. What has been described often a times phenomenologicaly, are differences in odour tuning, firing frequency and sometimes rate profiles. These phenomena are well captured in those features that were identified as best separators: life time sparseness, Fano-factor and evoked Rate. Taken together, our quantitative results seem to confirm the qualitative experience.

Acknowledgements

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$\left[T\ 124\right]$ Determination of firing frequencies from multiple spike train record

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When monitoring neuronal activity with single extracellular electrode the action potentials from different neurons are commonly recorded and the individual spike trains have to be separated, (Kim and McNames, 2007; Berdondini et al., 2009; Hill et al., 2011; Roxin et al., 2011). If the separation is difficult or fails (Pawlas and Lansky, 2011), then as a minimal result of the experiment, the individual firing rates are of interest. Proposed method solves

the problem of their identification. This is possible only under the condition that the recorded neurons are independent in their activities. The analysis of the superposed record is based on the presence of the refractory period in neuronal firing, and it gives partial knowledge about the probability distribution of specific clusters of spikes.

An approach for solution was given by (Meunier et al., 2003) for two superposed spike trains. We propose two methods for determination of the firing rates, which extend the original result. They can be applied for any number of simultaneously recorded neurons and an estimation of the refractory period is sufficient for the inferrence (not necessarily the accurate value). In addition, the method can be used for inferring about the refractory period itself.

Fig. 1. Averages of three estimated firing rates as functions of the hypothetical refractory period, t. The result is bases on one thousand simulation trials of superpostion of activity of three independently spiking neurons. The samples were generated in accordance with gamma distribution with shape parameter 0.5, the true firing rates were equal to 5, 10 and 15 spikes/s and the true refractory period was equal to 5 ms. Note the turn in the dependencies when the hypothetical refractory period, t, exceeds the true value 5 ms.



Figure 1

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[T 125] Building common high-dimensional models of neural representational spaces

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Multivariate pattern (MVP) analysis of fMRI data can decode patterns of neural responses within cortical fields, such as primary visual (V1) or ventral temporal cortex (VT), to identify the stimuli that evoked those patterns. MVP analysis can detect fine distinctions among stimuli based on pattern differences that have a fine spatial scale. Because functional cortical topographies are difficult to align across brains at a fine spatial scale, MVP analysis generally is done by building a new classifier model for each brain. Consequently, common models have not been developed that capture the fine-scale structure of representational spaces and are valid across brains. It is unknown whether brains have a common set of response functions that afford MVP decoding or whether each brain develops its own set that is sufficient but idiosyncratic.

Previously, we have developed an algorithm for building common models of representational spaces within cortical fields by aligning data across brains in a high-dimensional space rather than in an anatomical space (Haxby et al., 2011). This algorithm is called 'hyperalignment'. This method bases inter-subject alignment on functional responses to a complex, natural stimulus to achieve general validity across a wide spectrum of stimuli or representational states. Hyperalignment uses the procrustean transformation to rotate the voxel spaces of individual brains into a single high-dimensional space in which each dimension is a response tuning function – a profile of differential responses to stimuli – that is common across brains.

This method is a radical departure from previous methods for aligning functional data across brains that are based on anatomy, both in terms of computational power and because it reflect a reconceptualization of brain functional organization. Anatomy-based methods afford only coarse alignment of functional cortical topographies. By contrast, preliminary results using the first algorithm indicate that hyperalignment affords between-subject MVP classification of complex visual stimuli with accuracies that equal or exceed within-subject classification and far exceed between-subject classification of anatomically-aligned data. More importantly, our methods capture the organization of representational spaces in terms of a set of basis functions that are topographic patterns associated with distinct response profiles and functional connectivities. Previous methods conceive of cortical areas as containing a function or set of functions that activate the area, rather than as a high-dimensional representational space that encodes information in population responses, and conceive of functional connectivity as co-activation of areas rather than as shared high-dimensional information. We are currently working on extending our alignment technique to the domain of functional connectivity of brain regions. The idea behind functional connectivity hyperalignment is to rotate data into a common space in which the patterns of connectivities with other brain locations are in optimal alignment. Functional connectivity alignment promises a further increment in power and utility by 1) making it possible to align representational spaces for brain areas that do not show a consistent response to external stimuli across subjects, e.g. the default system, and 2) making it possible to use cognitive paradigms that are not time-locked, e.g. devising and

executing plans.

In this presentation we review the performance of the hyperalignment algorithm on a number of datasets, as well as present preliminary evidence showing the general feasibility of connectivity-based hyperalignment of high-dimensional representational spaces.

Software for our algorithms and demo fMRI datasets are available on the PyMVPA website (http://www.pymvpa.org).

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[T 126] Neuronal data storage using document oriented databases

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The modern neurosciences produce increasingly large amounts of data - both from experiments and large scale simulations. While sharing of scientific data is common in other areas of biological sciences, the neurosciences are faced with barriers in data sharing. Furthermore, the information about how the data was acquired (the so called "metadata") has the tendency to vanish with time. Often, it is the difficulty of finding and accessing the necessary information about the data, i.e., the metadata, that limits data sharing. Only well annotated data can be easily reused later. We present the NEuRonal Database (NERD), a project aiming to provide a database solution to the challenges of storing, retrieving, annotating and sharing of neuronal data. It smoothly integrates with the the data management framework of the German Neuroinformatics Node (G-Node, www.g-node.org) and is designed as an optional server side backend for the G-Node Data API. Instead of a standard relational database approach, NERD uses a document oriented data model and is intended to facilitate storage of large amounts of time series data, integrating and indexing corresponding meta information in the odML format [1]. In order to achieve quick searching on all levels of data annotation, NERD uses a bimodal approach towards data storage. The actual data are separated from the description of data structure and metadata, and both are stored differentially while keeping them tightly interlinked. By exploiting the main features of document oriented databases and combining them with the power of the HDF5 file format and distributed file systems, we provide a neat and scalable solution to the challenges of data management. Furthermore, the system accounts for the important requirement of versioning. NERD's "give me my figures back" functionality keeps track of the history of changes to the data and enables going back to any previous version. Here we present a detailed sketch of the NERD architecture and give usage examples on how to store data with NERD using the G-Node-API. Furthermore, we present benchmark results demonstrating NERDs performance under various conditions.

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Grewe J, Wachtler T, Benda J (2011) A bottom-up approach to data annotation in neurophysiology. Frontiers in Neuroinformatics 5:16.

[T 127] Novel method for closed-loop electroretinogram measurement of sensitivity in Drosophila

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In the compound eye of Drosophila, the six outer photoreceptors (R1-R6) of each ommatidium express rhodopsin 1 as their light sensing pigment. The inner photoreceptors R7 and R8 express one of four opsins (rhodopsin 3,4,5, and 6) with different spectral sensitivities and show different response dynamics. Spectral sensitivity of these rhodopsins has been determined in electroretinogram measurements (ERG) using the closed-loop voltage clamp technique [1]. In this technique, the intensity of a light source, flickering at around 10Hz, is adjusted such that the receptor response matches a predefined criterion level. However, since direct measurement of the receptor response amplitude under these conditions is unreliable, the standard deviation of the response during the stimulation period is typically taken as the target signal [2]. This protocol was established for electroretinogram (ERG) recordings from flies with functional outer photoreceptors R1-R6. Using flies lacking functional outer receptors, we recorded signals from inner photoreceptors R7 and/or R8. Because of the smaller signal size, a drift in baseline and the differences in response dynamics in these receptors compared to the outer receptors, we found this protocol to be inadequate for these measurements. Here we present a novel ERG protocol - Interleaved Reference Electroretinogram (INTER ERG) - that is able to reliably estimate the receptor potential amplitude directly. This method makes use of a reference light stimulus, which is activated in alternation with the test stimulus in an interleaved stimulus-reference design. The test stimulus light intensity is adjusted such that the ERG amplitude matches that evoked by the reference light. This protocol circumvents the problem of a drifting baseline [2] and furthermore yields reliable and comparable sensitivities independent of individual response differences. We show detailed data on the working range of the technique and furthermore present an ERG Plugin for RELACS [3,4] - a framework for closed loop electrophysiological experiments - developed to support standard ERG recordings as well as INTER ERG.

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$\left[T\ 128\right]\$ service.3dbar.org – online reconstruction of three-dimensional brain structures

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The knowledge of brain anatomy has been one of the foundations of neuroscience since its beginning. Traditionally the reference for brain structures has been provided by printed brain atlases containing at least one series of planar parallel brain sections containing a map of the intersected structures. However, the brain structure is three-dimensional and it is much more convenient to use three-dimensional brain atlases if possible.

In order to make precious anatomical information from two-dimensional atlases available in 3D, we have developed 3D Brain Atlas Reconstructor (3dBAR) software – a free, open source solution for performing automatic reconstruction of brain structure models from twodimensional atlases. The 3dBAR consists of a reconstructor software, a set of tools to perform conversion of existing atlases to Common Atlas Format (CAF) and a Python module for reconstructing structures from CAF data.

As 3dBAR is a complex offline package we provide some of its functionality as an online service. First, we provide a repository of free atlases (derived mainly from Scalable Brain Atlas – http://scalablebrainatlas.incf.org and Waxholm Space atlases) in CAF format, available to download and use with our software with no further conversion necessary. One can also download already reconstructed models of basic structures of different quality and format. It is also possible to request customized reconstructions (e.g. processed with non-standard pipeline or generating result in an additional file format) using on-line reconstruction wizard.

The service facilities are available to the user via a browser based interface. We also provide an interface for communication with external services and third-party applications. The mechanism provided is so flexible that the user web interface can be realized as a javascript-based client application and so is compatible with most of modern web browsers.

Currently, Scalable Brain Atlas contains a plugin using our service to visualize particular structures and download their reconstructions. The service functionality is also shared with WaxML services developed by the INCF DAI. Our plans include also combining the service facilities with neurosimulation software.

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$\left[T \ 129\right]$ A combination model of ICA and sparsity prior with respect to fMRI signal analysis

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The blood oxygen level dependent (BOLD) functional magnetic resonance imaging (fMRI) data effective analysis is a challenging task because of the complexity of neuron activity in human brain. Independent component analysis (ICA) has been widely used to investigate the functional connectivity of fMRI data, which assumes that the sources of functional regions are independent statistically. However, in the method, the spatial sparsity feature has usually been ignored, which is intrinsic property of the fMRI sources. In 2001, Alexander et al. demonstrated that the optimal sparse representation could significantly benefit the de-noising

of fMRI time courses [1]. Recently, Daubechies et al. also demonstrated that the sparsity was more general, intuitive and promising assumption for BOLD fMRI signals [2], whose sources were highly clustering and centering located. In this study, a combination model of FastICA and sparsity prior with respect to fMRI signal analysis, named SFICA, is presented. In this model, the sparse decomposition is performed on the fMRI signal using the wavelet packet decomposition, which yields wavelet tree nodes with different degree of sparsity [3]. Based on these wavelet tree nodes, a common fuzzy C-means clustering is applied to form the optimal sparse representation set of fMRI signal, which can be as an input of FastICA. Compared with FastICA, hybrid data experiment in our study demonstrated this combination model had better spatial source recovery performance on the ground of receiver operating characteristic (ROC) analysis (shown in Fig.1A). For task-related and resting state experimental tests, according to the skewness analysis and correlation variance analysis, almost all the functional networks discovered by this combination model were more symmetric with less skewness values in spatial domain and more consistent in temporal domain than the ones by FastICA. For simplicity, the partial experimental results corresponding to task-related experimental tests were showed in the Fig.1B.

Fig. 1: (A) Hybrid data experimental results: ROC curves of simulated signals S1 and S2 corresponding to anterior regions and the more posterior regions respectively, where the z-score ranges from 0.5 to 2.0; (B) Task-related data experimental results: the visual networks of one subject detected by the FastICA and SFICA methods corresponding to the task-related visual stimulus. The corresponding skewness values are labeled and the spatial differences of the visual networks corresponding to the two method are marked by circle shapes with distinct colors in this figure.



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Poster Session - Friday

Neurons, networks, dynamical systems

[F 1] Computational investigations of small-worlds networks in neuronal populations

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The study of the brain as neuronal network allows gaining insights to the analysis of information processing [1]. Network interactions can play a crucial role in this scenario. In fact many studies identify in the modality of neuronal interaction the key of the problem, but limitations in neuronal recordings makes the clear mechanisms elusive [2-4].

In this perspective, we investigated the functional organization of neuronal networks hypothesizing that they work as small-world networks [5]. We developed two different computational approaches: in the first, we asked whether neuronal populations actually express small-world properties during a learning task. To this purpose we developed the Inductive Conceptual Network (ICN), a hierarchical bio-inspired spiking network, able to learn invariant patterns by Variable-order Markov Models implemented in its nodes [6]. We found that the ICN model expressed small-word networks during learning. As control, we exerted the ICN with random binary inputs, where no patterns can be learnt, and we obtained no smallworld network functional organization among nodes. Conjecturing that the expression of small-world networks is not only related to learning, in the second part, we built the de facto network assuming that every information process in brain occurs exhibiting functionally a small-world network. In the de facto network the functional dependencies of the small-world networks, were reflected by synchronous spikes. From the analysis of spiking activity, versus the null hypothesis where small-world networks were replaced by random networks, we detected mainly three functional characteristics, observed in biological networks: timing and rate codes, conventional coding strategies [7], and the neuronal avalanches, cascades of bursting activities distributed as a power-law distribution [8]. Interestingly, rate and timing codes are thus allowed to coexist in the same network model yet in nodes at different hierarchical positions.

Our results suggest that small-word functional configurations represent a milestone of brain information processing at the level of neurons. In conclusion, accordingly with other theoretical and experimental works, short path length and sparse connectivity may promote simultaneous performance of information segregation (information retention) and integration (generalization) within neuronal systems.

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[F 2] Microscopic recruitment of network spikes in recurrent networks with synaptic short-term plasticity

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Recurrent networks with synaptic short-term plasticity show intermittent states of high activity in which virtually all neurons fire simultaneously ("network spikes"). A subpopulation of neurons with low to intermediate activity is instrumental in triggering such network spikes (Tsodykz, Uziel, Markram, 2000, J Neurosci 20 RC50(1-5)), in that they fire reliably before the network spike and in that their suppression eliminates most network spikes. Here we investigate the rank order of spikes among these 'early firing' neurons in simulated networks of excitatory and inhibitory neurons. Our simulations show that, given sparse random connectivity, this rank order is highly preserved and typically divided into several distinct cohorts of 'earl firing' neurons, which are recruited in quasi-deterministic order. In each case, activity propagates to the next cohort only after the last member of the preceding cohort has fired. These quasi-deterministic "microscopic recruitment paths" match experimental observations from mature cortical neuron cultures (Shahaf et al., 2008, PloS Computational Biology, 4(11) e1000228). We surmise that this "order-based representation" reflects the variability of connectivity and, furthermore, that it tightly constrains the effective connectivity of cortical neuron cultures.

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[F 3] Comparing visual and motor cortex: representational coding versus dynamical systems

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Systems neuroscience often employs models that explain neural responses in terms of represented stimulus features or movement parameters. These models can be powerful, but do not apply equally well to all circuits. For example, the activity of a central pattern generator is best captured by its intrinsic dynamics. Here, we examine the population response in a number of cortical areas, and ask whether responses appear stimulus driven (i.e. are better described as a function of external parameters) or internally generated (i.e. are better described by a dynamical system). We analyzed datasets (44 - 218 single and/or multi-unit isolations) from visual areas V1 and MT (recorded during the presentation of visual stimuli) and from primary motor and premotor cortex (recorded during a delayed reach task). Our analyses did not fit particular representational or dynamical models, but instead asked whether basic features of the data tended to obey or violate the expectations of a dynamical system. The principal expectation is, for a k-dimensional dynamical system, the number of temporal patterns (modes) present in the data should tend to be $\leq k$. This can be shown analytically for linear, time-varying dynamical systems. Conversely, stimulus-driven responses can display an arbitrary variety of temporal patterns, as determined by the stimuli. We therefore compared the number of temporal patterns in the data with the overall dimensionality of the system. We considered data of the form r(n,c,t), the rate of neuron n for condition c and time t. To determine the overall dimensionality, we applied PCA considering neurons as 'variables' and conditions and times as 'observations'. To determine the number of temporal patterns that the system displayed, we applied PCA again considering conditions as 'variables' and neurons and times as 'observations'. For each of these two applications of PCA we found the number of dimensions required to reconstruct the data to 90% precision. We then took the ratio (overall dimensionality divided by number of temporal patterns). For simulated data from stimulus-driven models, ratios were < 1. For simulated data from dynamical systems models, ratios were > 1. For the neural data from visual areas (2 datasets) the ratio lay close to the stimulus-driven prediction (ratios = 0.8, 1.1), while the population response from the motor areas (4 datasets) appeared more dynamical (ratios = 1.6, 1.8, 1.8, 2.4). These results indicate that, in visual areas the overall structure of the data is consistent with responses being largely a function of stimulus parameters. In contrast, in motor areas the structure of the data argues that responses are more strongly dominated by internal dynamics.

[F 4] Effects of hippocampal sharp wave ripple oscillations on medial entorhinal cortex layer V neurons in vitro

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The mammalian hippocampus displays a variety of state-dependent network oscillations which are believed to organize neuronal activity and synaptic plasticity during memory formation. The peculiar pattern of sharp wave-ripple complexes (SPW-R) entrains neurons into coactive neuronal assemblies within very fast oscillations at ~200 Hz. SPW-R emerge in hippocampal area CA3 and then propagate along the hippocampal "output loop" via CA1 to the entorhinal cortex (EC). The cellular effects of SPW-R in this downstream area are, however, unknown. We therefore investigated the activity of layer V (LV) principal neurons of the medial EC (mEC) during SPW-R oscillations in horizontal mouse brain slices. Intracellular recordings in the mEC were combined with extracellular monitoring of propagating network activity. Ongoing spontaneous SPW-R in CA1 were regularly followed by negative field potential deflections in deep layers of the mEC (5-10 ms delay; ~65 µV amplitude). Entorhinal events carried superimposed fast oscillations which were clearly slower than the original ripples in CA1. Intracellular recordings from mEC LV neurons revealed SPW-R-associated depolarizing synaptic potentials which reached ~2.5 mV and remained sub-threshold at resting potential (-72 \pm 5 mV). Amplitude of synaptic potentials correlated positively with amplitude of SPW-R in CA1 while delay time was short for large network events. Synaptic potentials were regularly superimposed by rhythmic activity with leading frequencies below the ripple band in CA1. Conductance analysis revealed that network-associated synaptic input was mostly excitatory. Upon subthreshold membrane depolarization, SPW-R in CA1 regularly triggered spikes in LV neurons. Cross-correlations between entorhinal spikes and field SPW-R in CA1 revealed strong coupling between spikes and sharp waves (delay 10 - 30 ms) but only weak correlation with ripple cycles in CA1. We have recently shown that waveform patterns of SPW-R contain specific signatures of the underlying multicellular assemblies (Reichinnek et al., 2010). We therefore analyzed the correlation between stably recurring SPW-R waveforms in CA1 and corresponding depolarizing synaptic potentials in mEC neurons. Indeed, these downstream synaptic waveform patterns were significantly correlated with the preceding SPW-R, as shown by analysis of information and sparsity of waveform distributions. These correlations were, however, strongly biased by the amplitude of the corresponding SPW-R, indicating dominant effects of convergent synaptic innervation.

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[F 5] Clustered connectivity promotes synchronous burst initiation in vitro

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Synchronous bursting events (SBE) are widely observed in developing neuronal systems suggesting that the capability to spontaneously initiate these dynamics reflects a crucial intermediate feature of forming networks. Consistently, SBE dynamics similarly and robustly also emerge as the predominant type of activity in networks of cultured neurons in vitro. We speculate that this might hint towards general neuronal mechanisms guiding network selforganization with the aim to establish these dynamics. Interestingly, theoretical models have shown that hierarchical network structures embedding clusters of strongly inter-connected neurons are optimal for initiating and sustaining spontaneous activity (Kaiser 2010) and clustered network structure typically emerges in networks forming in vitro (Kriegstein 1983). We hypothesize that activity-dependent structural plasticity, being a principle driving force of network self-organization, establishes clustered network structures and thereby promotes spontaneous activity levels. Previous studies showed that protein kinase C (PKC) inhibition promotes dendritic outgrowth and arborization (Metzger 2000), and impairs pruning (Kano 1995), linking this protein closely to structural plasticity. To test our hypothesis we thus inhibited PKC in developing networks of cortical neurons in vitro.

We show that developmental inhibition of PKC in cortical cell cultures increased dendritic outgrowth, impaired neurite fasciculation and clustering, and abolished network pruning. This resulted in more homogeneous and potentially better connected networks. Consistently, SBEs propagated faster and in more regular wave fronts. Yet, following our hypothesis, SBEs were triggered from fewer sites and at lower rates suggesting that these homogeneous networks embedded fewer SBE initiation zones. We tested if the homogeneous networks were able to support higher SBE rates providing additional input by electrical stimulation. Interestingly, homogeneous networks achieved comparable rates when electrically stimulated compared to the more clustered control networks. This data suggests that activity-dependent structural plasticity promotes network clustering and thereby spontaneous SBE levels during development. Based on recent evidence for a reciprocal scaling between synaptic strength and number of neuronal partners in vitro (Wilson 2007), we propose that locally more confined synaptic targeting within neuronal clusters promotes stronger and more recurrent coupling of neurons. The resulting connectivity structure could thereby more easily amplify spontaneous excitation locally beyond a critical threshold necessary for SBE initiation. In summary, our results indicate that activity-dependent structural plasticity promotes neuronal clustering and thereby the ability of in vitro networks to spontaneously initiate SBEs. We propose that this might reflect a general strategy pursued by neuronal networks to establish this crucial activity pattern during development.

Acknowledgements

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[F 6] Can power laws in macroscopic and microscopic neural recordings be explained by the cable properties of neurons?

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Power-law $(\sim 1/f^{\alpha})$ spectra are observed for both macroscopic (EEG, MEG [1,2]) and microscopic neuronal signals (membrane voltage and transmembrane currents in neuronal somas [3-7]) over a significant range of frequencies f. The power-law exponents α depend on the signal type: For the EEG, typical α 's have been observed to be between 1 and 2.5 [1,2], while the sub-threshold soma membrane potential typically have been found to have larger high-frequency signal attenuation with α 's ranging between 2 and 3 [3-7]. While apparently robust across species and brain regions, the origin of these power laws is not yet known.

In this biophysical modeling study we find that these microscopic and macroscopic power laws may have a common neural origin. If the neuron is bombarded with input currents with a homogeneous area density across its membrane, both simulations of a pyramidal neuron and analytical investigations of a simplified ball and stick neuron reveal high-frequency power laws in the soma potential, soma current, and the single-neuron contribution to EEG (transmembrane current dipole moment). The power-law coefficients α are seen to be systematically different for these three measurements, however, with the soma potential having the largest, and the soma current the smallest value of α .

The derived PSDs are based on transfer functions which are general with respect to the frequency characteristics of the input noise, whether it stems from synaptic inputs or intrinsic channel activity. However, within the frequency range typically studied in experiments, i.e., up to a few hundred hertz, the PSDs are found to express quasi power laws with exponents a in agreement with experimental results only if the input currents are (A) uncorrelated and (B) have approximately a 1/f spectrum. Exponential synapses express a $1/f^2$ spectrum for high frequencies. Thus, if synaptic noise is the main contributor to the power laws, a compensatory high-pass filter must exist, either stemming from processes within the neuronal membrane itself [7] or from the spiking network dynamics [8]. A and B, however, support the proposition that the origin of the observed power laws in neural recordings is intrinsic channel choice from ion channels with a 1/f spectrum. We speculate whether these 1/fcurrents may originate from potassium channels, more specifically the BK channel.

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[F 7] On the impact of oscillatory synchrony on directed functional connectivity metrics: a network-model-based study

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Perception, cognition and behavior require flexible communication and coordination between brain circuits. Experimental and theoretical evidence (Womelsdorf et al. 2007; Battaglia et al., 2012) show that phase locking between the oscillatory activity of different brain areas or local circuits may underlie the self-organized instantiation of effective communication channels. From a data analysis perspective, causal influences between different neuronal populations are often inferred from time series of neural activity obtained through electrophysiological recordings or imaging techniques using methods like Granger Causality or Transfer Entropy. However, the depiction of inter-areal interactions provided by such indirect "blackbox" approaches is difficult to interpret, because the underlying network dynamics associated to the recorded signals is known only partially or is completely hidden. Furthermore different metrics are not guaranteed but in special conditions to infer matching causal connectivities (aka directed functional connectivities). We consider here the dynamics of a toy system of two coupled (unidirectionally or bidirectionally) neural populations, described as large networks of spiking excitatory and inhibitory neurons with realistic heterogeneous parameters. By varying systematically the degree of synchronization of the resulting network activity and the strength of inter-population coupling, we explore the performance in different dynamical regimes of different causality metrics in inferring the underlying inter-population coupling from semi-realistic synthetic spike trains, LFPs and other imaging signals with different spatial and temporal resolutions. More specifically, we identify under which conditions linear techniques fail in providing a correct inference of the ongoing population interaction and we comment on possible practical strategies to overcome their limitations.

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[F 8] Spatio-temporal structure of network oscillations in the prefrontal cortex of neonatal and pre-juvenile rat

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The interactions between the prefrontal cortex (PFC) and hippocampus are critical for attentional and mnemonic abilities, yet their maturation is poorly understood. We previously showed that the neonatal PFC displays discontinuous oscillatory patterns that with ongoing maturation are replaced by continuous rhythms (Brockmann et al., 2011). The generation of these prefrontal oscillations is driven by hippocampal theta bursts. The intricate spatiotemporal relationship of slow and fast oscillatory components during various stages of development may reveal changes in the flow of activity within and between different brain structures.

We performed extracellular recordings of the local field potential (LFP) and multiple unit activity in postnatal day 7-15 rats in vivo using four-shank 32-channel Michigan electrodes. The recording sites were separated by 200 μ m in horizontal and 50 or 100 μ m in vertical direction. In our experiments, electrodes were inserted in parallel to the cortical surface, giving us access to neuronal activity at different cortical locations at 4 different depths. Here, we investigate in detail the spontaneous activity patterns (i) across and (ii) within cortical layers of the PFC.

We applied a clustering technique based on amplitude and frequency of the LFP to differentiate between two initial patterns of discontinuous oscillatory activity that are present at the end of the first postnatal week – spindle bursts (SBs) and nested gamma spindle bursts (NGs). In the following, we analyze and compare the features exhibited by neuronal recordings belonging to these two classes of oscillatory events, which are commonly separated by longer periods of quiescent activity. While both patterns exhibit spectral peaks at 4-12 Hz and 16-40 Hz, only NGs in upper layers are accompanied by phase locked spikes and display an additional frequency component above 100 Hz. We calculate the coherence within vs. across layers for the slower rhythms. The maximal coherence is observed within layers for the 4-12 Hz rhythm of SBs, and across layers for the 16-40 Hz rhythm of NGs. NGs show a stronger phase shift across layers. The direction of the shift is opposite for the two rhythms. Moreover, the amplitude of the fast rhythm (>100 Hz) appears strongly phase-coupled to the slower oscillations during NGs.

Towards the end of the second postnatal week the PFC switches to continuous oscillatory activity. At this age the signals are more coherent over the whole PFC and the phase shift of slower rhythms across layers diminishes. The power of fast rhythm (>100 Hz) decreases, whereas firing rates increase. The age- and layer-dependent differences may mirror the functional maturation of the PFC under the influence of hippocampal inputs.

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[F 9] Towards tracking homeostatic changes on high-density multielectrode arrays

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Homeostatic plasticity is one of the key mechanisms ensuring the remarkable adaptive abilities of the brain. However, this is still a relatively scantly explored branch of both experimental and computational neuroscience - in particular on a large, multi-neuronal scale. With recent advance in recording techniques, the lack of experimental data can be easily overcome - novel multielectrode arrays allow for high-density recordings from in vitro cultures consisting of thousands of neurons. What is needed to complement this rich data is analysis techniques that would be able to shed some light on the mechanism of the underlying process - in contrast to most conventional analysis techniques, such as firing rates, correlations or inter-burst intervals, which provide little more than descriptive information. In search for measures able to capture more complex phenomena, over the last decade a new approach has been developed - pairwise maximum entropy modelling (MaxEnt). It is a statistical model that fits two sets of parameters to explain the probability of spiking patterns in the network: individual neuron parameters that could be interpreted as excitability; and pairwise interaction parameters that could be interpreted as the functional connection strength between neurons. Successful application of this model to a variety of recordings has helped reevaluate the importance of neuronal interactions in shaping network activity (Schneidman et al., 2006; Shlens et al., 2006). Additionally, the shortcomings of MaxEnt in certain cases can serve as an indicator of higher-order interactions between neurons (Ohiorhenuan et al., 2010).

In present work we examine the extent to which the statistics of MaxEnd model fits and parameters can assist in understanding different modes of activity of a neuronal culture – specifically, along the duration of a homeostatic experiment. Neural activity from primary neuron cultures was recorded with the 4096 channel Active Pixel Sensor (APS) MEA, allowing for reliable isolation of single unit activity at near-cellular resolution (Berdondini et al., 2009). 20-minute datasets were obtained at different stages of homeostatic compensation during and after long-term CNQX application. For the datasets with a stationary activity state, large numbers of four-unit MaxEnt models were constructed for randomly chosen neurons on two spatial scales.

Comparison of the statistics of the fits and parameters across the scales and across conditions indicates that different activity modes exhibit different profiles of local clustering and higher-order interactions.

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[F 10] Spikelets in Hippocampal CA1 Pyramidal Neurons: Possible Origins and Functional Implications

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Spikelets are brief spike-like depolarizations of small amplitude, measured in the soma of a neuron. Due to their all-or-none appearance, spikelets are considered to represent full action potentials (APs) generated in an electrotonically distinct compartment. Recently, prominent spikelet activity was demonstrated in hippocampal CA1 pyramidal neurons in awake behaving animals (Epsztein et al., 2010). However, the basic mechanisms underlying the generation of spikelets in these neurons are unknown.

In previous approaches, spikelets were described mainly in pairs of inhibitory neurons in the context of electrotonic coupling via dendritic or somatic gap junctions. However, these so-called coupling potentials exhibit substantially slower dynamics than the fast spikelets recorded from excitatory pyramidal neurons. In hippocampal pyramidal neurons, axo-axonic electrotonic coupling was instead suggested as a candidate mechanism for spikelet generation, although direct experimental evidence is rather scarce.

Analyzing computational models, we found that fast somatic spikelets can be generated in a single pyramidal neuron. Such spikelets are shaped by axial (longitudinal) currents from a spike elicited at the axon initial segment (AIS) that fails to backpropagate to the soma. The backpropagation failure might occur under conditions of increased electrotonic distance between the soma and the AIS and low input resistance of a neuron, as for example, during in-vivo bursting activity.

Therefore, somatic spikelets generated within a single neuron might represent APs that are only propagated forward, i.e., they are not backpropagated into dendrites and thus might not influence dendrites. As a result, this mechanism would enable pyramidal neurons in vivo to switch off dendritic plasticity without affecting the computations generating output spikes of the neuron. In this case, spikelets save energy since the large soma does not get (fully) activated during spikelet firing.

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[F 11] Membrane potential statistics reveal detailed correlation structure

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Much focus has been placed on determining the causes and functional roles of pairwisecorrelations that are observed amongst neurons (Cohen and Kohn, 2011). In the pursuit of an understanding of the impact of correlations on network activity, an important division amongst them can be made, that of 'within' versus 'between'. These types of correlations are structurally defined, with 'within' (W) referring to the amount of correlated activity within the pre-synaptic pool of neurons projecting to a given neuron, and 'between' (B) referring to the amount of correlation between two pre-synaptic pools, each projecting to a different post-synaptic cell. This distinction is important because these two types of correlations have different functional consequences: the later can serve to propagate existing correlations while the former influences firing rates (see Bujan et al. 2012).

Here we studied these two types of correlations in recurrent networks of excitatory and inhibitory spiking neurons. We find that in random homogeneous networks the W and B are comparable. Interestingly, in inhomogeneous random networks W and B greatly differ depending on the details of the network structure. Biological neural networks can be highly heterogeneous and thus we expect that even in vivo there will be difference in the values of W and B. Despite recent advances in the labeling of pre- or post-synaptic contacts of a neuron, it may not be possible to get enough details about network connectivity to reveal the differences between W and B experimentally.Fortunately, as our simulations show, statistics (variance and correlations) of the intracellular membrane potential could provide a good estimate of the W and B. Thus, in principle, the statistics of intracellular membrane potential could provide crucial information about the structure of the network.

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[F 12] Adaptation enhances a population code for gaps

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It is believed that the inferior colliculus (IC) functions as a central processing unit that converts the temporal code of the upstream pathways into the rate code of the thalamus and the cortex. Yet how the IC is able to encode the rich array of temporal structures of our natural acoustic environment remains poorly understood. Here we present a computational study that investigates how a recurrent network discriminates amplitude-modulated sound stimuli through the diverse response behaviors of its constituent neurons.

In our model, amplitude-modulated Poisson inputs are fed into a recurrent network. The network consists of a mixture of excitatory and inhibitory integrate-and-fire neurons, and its output is feed-forwardly connected to a linear read-out unit to perform canonical classification tasks. The analysis is then conducted as a function of neuronal parameters (adaptation, parameter value variance, etc.) to investigate the functionality of experimentally observed heterogeneity.

It is found that adaptation enhances the network's ability in gap-detection. The effect is most pronounced when the adaptive hyperpolarization time constant is on the scale of the gap size to be detected. This implies that the IC should contain a wide range of adaptive behavior in response to the natural environment, as is experimentally found.

[F 13] Intrinsically generated phase precession of grid cells in a network model

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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 oscillations of the local field potential (LFP) in the theta band (4-12 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 original hippocampus model, the core idea is that a population oscillation, i.e. LFP, is a little slower than the individual neuronal oscillators, when the latter have firing fields of limited spatial extent and are sequentially activated. The individual neurons hence phase precess with respect to the LFP. Extending the original model 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 that governs the transformation of the rate place code to spike timing. The compression parameter, however, has an 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 this phase coordination. The compression of the place code from rates to spike timing follows as a natural consequence of the self organization of firing phases. The model also explains phase precession for changes in the running speed of the animal and variable grid-spacing.

[F 14] Electrosensory Synapses with Ultra-Fast Synaptic Dynamics

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Electric fishes can generate electric fields around their bodies (electrogenic) and also detect electric fields (electroreceptive). The physics of electrolocation and electroreception is a very interesting subject in biophysics. This electrosensory system is a very useful model to study the dynamic of fast synapses like auditory system in human brain [1]. Synaptic depression is a form of short-term plasticity exhibited by many synapses. Short-term depression (STD) is also observed at many synapses of the Central Nervous System (CNS) and is important for diverse computations.

We have discovered a form of fast STD (FSTD) in the synaptic responses of pyramidal cells evoked by stimulation of their electrosensory afferent fibers (P-units). The dynamics of the

FSTD are matched to the mean and variance of natural P-unit discharge. FSTD exhibits switch-like behavior in that it is immediately activated with stimulus intervals near the mean interspike interval (ISI) of P-units (~5 ms) and recovers immediately after stimulation with the slightly longer intervals (>7.5 ms) that also occur during P-unit natural and evoked discharge patterns. Remarkably, the magnitude of evoked excitatory postsynaptic potentials appears to depend only on the duration of the previous ISI. Our theoretical analysis suggests that FSTD can serve as a mechanism for noise reduction. Because the kinetics of depression are as fast as the natural spike statistics, this role is distinct from previously ascribed functional roles of STD in gain modulation, synchrony detection or as a temporal filter [2].

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[F 15] Multiplexing of theta-nested gamma oscillations and grid firing fields in an attractor network model of layer II of the medial entorhinal cortex

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Grid cells in the medial entorhinal cortex (MEC) encode location through firing fields that form grid-like maps of the environment. At the same time network activity in the MEC is dominated by oscillations in the theta (4-12 Hz) and gamma (30-100 Hz) bands. The relationship between oscillatory activity and grid firing is not known. Our recent experimental data established that feedback inhibition between excitatory stellate cells and inhibitory fast spiking interneurons dominates the synaptic connectivity in layer II of the MEC. To determine if this circuit is sufficient to explain both the network oscillations and grid firing fields, we constructed a network of model stellate cells and interneurons. In this model, stellate cells connect exclusively to interneurons, while interneurons contact only stellate cells. We show that external excitatory conductances can drive the network into an attractor state. Feedback inhibition onto the model stellate cells has a synchronizing effect. Synaptic input to both populations of neurons is synchronized in the gamma frequency range (30 - 100 Hz). When coupled with a theta modulated external drive (8 Hz), we observed network synchronization during the trough of the theta signal only. When the borders of the network are connected with a twisted torus topology (Guanella et al. 2007) and velocity modulated inputs are applied to the circuit, excitatory neurons in the circuit generate grid-like firing fields. Due to limited stability of the attractor, the grid fields were blurred. However, it was possible to obtain stable grid fields by including a place cell resetting mechanism as an additional input to the network (Guanella et al. 2007). These results demonstrated that the same local circuit architecture feedback inhibition - supports emergence of attractor states and nested gamma oscillations. This has implications for mechanisms of both formation of grid-like receptive fields as well as population coding and information transmission between brain areas.

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[F 16] Effects of spike-timing dependent plasticity on network dynamics in a primary visual cortex model

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In higher mammals response properties of neurons in primary visual cortex (V1) change systematically with the location on the orientation map. Recordings from cat V1 revealed that orientation tuning characteristics of neurons in iso-orientation domains differ from those near pinwheel centers. For example, the membrane potential of neurons in iso-orientation domains is tuned more sharply compared to neurons close to pinwheel centers, however the firing rate is highly selective in both regions. In a previous modeling study [1] these features were shown to constrain the operating regime of a V1 network, defined by the strengths of recurrent excitatory and inhibitory synapses, relative to the afferent synaptic strengths. The most likely regime was characterized by a balance of recurrent excitation and inhibition, dominating the afferent input. Such a balance of synaptic inputs can be mediated by spiketiming dependent plasticity (STDP) which is well established as a learning rule for excitatory synapses [2]. More recently STDP rules on inhibitory synapses were also proposed as a mechanism of detailed balance in recurrent networks [3].

Here we investigate the effects of STDP on the operating regime and neuronal orientation tuning properties in a V1 network model. We simulate a model consisting of an excitatory and an inhibitory population of spiking neurons with structured recurrent connectivity and an orientation selective afferent input. We show that a recurrent operating regime emerges for a wide range of recurrent conductivities due to STDP. It prevents "runaway excitation" which has been observed to occur for parameter regions close to the operating regime with the strongest physiological evidence [1]. Accordingly, in our model STDP promotes parameter robustness. We further characterize how different classes of excitatory and inhibitory STDP learning rules affect the tuning properties of iso-domain and pinwheel neurons. We identify the parameterizations which provide the closest correspondence to their physiological tuning characteristics.

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[F 17] Effects of nonlocal coupling on the dynamics of neural systems

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Understanding the dynamics on networks is at the heart of modern nonlinear science and has a wide applicability to neuroscience. The interplay of network topology and local dynamics opens a variety of dynamical phenomena such as synchronization, clustering, waves, kinks, complex patterns, and chaos. Here we study the spatio-temporal dynamics of coupled neural oscillators with nonlocal interactions. In the considered configuration each element is coupled to its nearest neighbors within a finite range. Depending upon the control parameters chosen as coupling strength and coupling radius, we investigate the cooperative dynamics in a generic model for type-II excitability given by FitzHugh-Nagumo equations. The individual systems are considered to operate above a Hopf bifurcation, that is, they operate in the oscillatory regime.

On the basis of previous results on nonlocally coupled discrete maps and chaotic systems, we demonstrate the universality of a transition from coherence to incoherence in such systems, giving rise to spatial chaos and so-called chimera states. The latter arise as hybrid spatial patterns in regular networks of identical oscillators and consist of parts with high spatial coherence and regions where spatial coherence is lost.

We analyze the regions of stability of various types of solutions in the parameter space of coupling strength and coupling radius: completely synchronous oscillations, wave-like profiles, cluster states as well as partially incoherent states. Furthermore, we study the robustness of the observed patterns in the presence of inhomogeneities of the local elements that are introduced via different threshold parameters in the FitzHugh-Nagumo system.

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[F 18] Self- organized criticality as a universal brain state from deep sleep to wakefulness - evidence from intracranial depth recordings in humans

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Neuronal activity differs between wake and sleep states, so does the cognitive state [Tononi & Koch, 2008]. In contrast, a single attractor state, described as self-organized critical (SOC), has been proposed to govern human brain dynamics because of its optimal information transmission, coding and processing capabilities. This raises the question whether the human brain always operates in the SOC state, from wakefulness to deep sleep, or whether the transitions between cognitive states are reflected in transitions away from the SOC state. In addition, previous evidence for SOC was based on activity *within* single brain areas [Beggs & Plenz

2003], however, it is not known how the interactions *between* brain areas are organized. Here we asked whether the interactions between brain areas are SOC.

We addressed these questions by characterizing neuronal avalanches – spatiotemporal waves of enhanced activity – from up to 61 local field potential (LFP) channels of intracranial depth recordings (5 human patients, 100 hours of recordings). The electrodes were distributed inside the entire brain. Neuronal avalanches were characterized for each sleep stage separately. Note that this number of electrodes is sufficient to avoid major subsampling effects: Subsampling in SOC models may lead to wrong classifications of the system [Priesemann etal. 2009]. We show that avalanche distributions closely follow a power law for each vigilance state, independent of the threshold and the temporal scale. For a temporal scale (bin size) which equals one average inter event interval, the slope of the power law is 1.5 (maximum likelihood estimation [Clauset et al. 2009]). This indicates first that the interaction between brain areas are SOC, and second that SOC governs all cognitive states, from wakefulness to deep

sleep. Minor differences between cognitive states are, however, reflected in the avalanche distributions: Slow wave sleep is characterized by larger neuronal avalanches than REM sleep or wakefulness (difference in size: ds=19%, ds=12%; p<10-7, p<10-5, respectively). Differences between wakefulness and REM are also significant (p<10-3). Our SOC model predicts that these changes may be caused by tiny variations in the effective synaptic strength by less than 0.2%.

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[F 19] Lotka-Volterra Models Describe Large-Scale Activity of Balanced Random Networks

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The large-scale dynamics of a balanced random network of excitatory and inhibitory integrateand-fire neurons is the focus of our study. Based on the dynamical equations of the model, a mean field approach was employed to reduce the dimensionality of the network dynamics [1,2]. We analyzed the joint activity dynamics of excitatory and inhibitory populations using a pair of mutually interacting differential equations. In absence of a voltage leak for individual neurons, and for negligible synaptic transmission delay, these equations take the form of Lotka-Volterra equations. These are known for describing predator-prey systems, which correspond to excitatory and inhibitory populations in our case. We tried to find optimal parameters for the non-autonomous differential equations given a dataset from a numerical simulations of a network. Moreover, we attempted to analytically infer the parameters and compare it with the statistical estimates. As a next step, we analyzed the stability of the network considering two bifurcation parameters: "g", the relative strength of recurrent inhibition, which controls the balance between excitation and inhibition in the network, and "eta", the intensity of external input to the network. We found out that for a value of "g" that keeps the exact balance between excitation and inhibition, a bifurcation from unstable to stable network dynamics takes place. This bifurcation separates Synchronous Regular (SR) from Asynchronous Irregular (AI) activity of the network, similar to what was found in a previous study on the same network using a Fokker-Planck approach [3].

It has been shown that Lotka-Volterra equations are capable of representing switching dynamics between different states of neural networks [4]. Our analysis represents a first step toward analyzing the dynamics of more complex "networks of networks" that are implicated in various cognitive abilities of the brain.

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[F 20] Markov Models of Neuronal Populations: a Reduction of Integrate-and-Fire Dynamics

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Neuronal populations are capable of responding to transient input much faster than single neurons can. Neuronal codes that exploit this fact are thought to be more robust than a code based on stationary firing rates. Here, we studied populations of unconnected leaky integrateand-fire (LIF) neurons in the fluctuation driven regime, and compared them to ensembles of Markov Point processes (MPP). In particular, we were interested in characterising the transient responses to input mean modulation vs. input variance modulation, and finding the correspondence between the two models. Markov Point Processes are very attractive for neuronal modelling because many aspects of them are analytically tractable.

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[F 21] Scanning for relations of neuronal spiking activity and network structure across multifractal network ensembles

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Relations between structural features and spiking activity of neuronal networks have recently raised a lot of interest. Current studies typically focus on specific network models and attempt to discover relations between properties of the underlying graph and the signals generated by its neurons [1-4]. Structural parameters often considered in this context are degree distribution, degree correlations, and spectral radius of the adjacency matrix. Parameters typically used to characterize activity dynamics are firing rate, synchrony, spike train regularity, and spike count correlations.

Models of networks generally constrain the statistics of network properties due to their specific construction procedure. Results of the above type can hence be strongly biased by correlations between different features of the specific network model under consideration. Here we employ the multifractal network generator [5] to address network models with a broad distribution of properties and, consequently, generate realizations of networks with much higher variability than usual [4]. This approach can therefore be used to infer and systematically test the validity of structure-dynamics relations in a general context.

We present results based on a large set of simulations of networks comprised of excitatory and inhibitory integrate-and-fire neurons. Biophysical parameters and overall connectivity were arranged such that they would induce an asynchronous irregular activity state in the case of a random network with homogeneous coupling [6]. Firstly, our results indicate that different non-random structures can induce a large variety of activity regimes. Secondly, we find significant correlations between activity parameters and certain structural properties that have so far not received much attention. Thus our data mining approach might eventually lead to the discovery of network characteristics, the functional significance of which was previously unknown.

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[F 22] Effects of inhibition on dendritic signal propagation

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Inhibitory interneurons are very abundant in cortical structures. Many different subtypes with specific intrinsic properties are known. Their most distinctive feature, however, is their target of innervation. While principal cells converge predominantly onto dendrites, interneurons target locations from the most distal dendrites to axonic sites. The target site is highly cell-type specific. Consequently, interneurons are good candidates for selective modulation of neural activity in various stages of computation. As they can dynamically alter the effective dendritic morphology, they can be assumed to allow for complex computations.

During development, an overall increase in inhibition has been measured, suggesting that inhibition might play an important role in learning, i.e. the modification of synaptic connections. Therefore, the effect of inhibition on computations in dendrites, which are the locus of synaptic integration and plasticity, might be even more complex than previously expected. We hence investigated how inhibitory inputs affect dendritic computation in the most abundant excitatory cell type: pyramidal neurons. Based on multi-compartmental conductance-based models we analyzed how location, timing and strength of inhibition affects bidirectional signal propagation in dendrites.

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[F 23] Ventral Striatal Pathway Determines Actions Employed: A Computational Model

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In the last decade, there have been complimentary works proposing that the ventral striatum, namely nucleus accumbens, influences the dorsal striatum through midbrain dopamine cells [1]. Nucleus accumbens, especially shell region, has an important function in determining reward value of tasks in goal-directed behavior and the error in expectation [1]. Various works demonstrate the effects of nucleus accumbens in delayed reinforcement on action-outcome learning [2] and there are works showing the nucleus accumbens related dopamine transmission involvement in effort-related decision making processes [3]. It is suggested that through the striato-nigro-striatal pathway, limbic regions have impact on the motor regions of the basal ganglia and also ventral pallidum acts as an integrator between nucleus accumbens and other parts of the brain [1,3]. The value of a stimulus is calculated by the ventral pathway according to its salience to produce an action and if dopamine release triggered by this stimulus is sufficient, then the output of the basal ganglia is modulated to permit a behavior to occur [4].

The computational model proposed in this work focuses on the modulatory effect of nucleus accumbens related dopamine secretion in the dorsal striatal pathway. In the model, both ventral and dorsal basal ganglia circuits are considered and each neural structure is modeled by Hodgkin-Huxley (HH) like conductance neuron models. While deriving model for each

structure, ion channel dynamics are integrated and HH neuron model is modified to show the dynamic behavior of the considered neural structure. The simulation results are obtained with in-house built MATLAB* codes where differential equations defining the neuron dynamics are solved.

The simulation results reveal that the model is capable of showing the controversial role of direct and indirect pathways and how the ventral striatal pathway supports the indirect pathway effecting the action selection through cortico-striatal thalamic loop. The proposed model captures not only the connectivity of neural substrates but also the modulatory effect of neuro-transmitters which have an important impact on behavior. According to the proposed model, if the dorsal and ventral pathway decisions are consistent, the output of the dorsal loop is amplified. Otherwise, ventral path suppresses the dorsal output. Therefore the model demonstrates that with the existence of dopaminergic ventral striatal pathway, even if an action's salience is not sufficient to be selected, it can be preferred based on its value calculated by the ventral striatal pathway.

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[F 24] Boosting Voluntary Actions: Modeling the Role of Indirect Pathway

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The thalamo-cortical loop through basal ganglia (BG) is known to be effecting action selection and initiation [1-4]. There are two pathways, one direct and one indirect, through the BG which cooperate in action selection. Both pathways start with sensory or associaton cortex and unite on the main BG output, globus pallidus interna/substantia nigra pars reticulate (GPi/SNr) complex. It is considered that the direct pathway is dominant in the selection of the rewarding or voluntary actions and indirect pathway is effective in suppressing the unwanted actions to prevent them competing with voluntary ones. The direct and indirect pathways diverge in the striatum (Str). Selection of different pathways is related to the dopamine (DA) secretion to the Str from the substantia nigra pars compacta (SNc). There are different types of DA receptors on the neurons. The most important of these are D1 and D2 type DA receptors. D2 type receptors are the most abundant DA receptors in the central nervous system. Stimulation of D1 type receptors causes the neuron to become excited along the direct pathway while the stimulation of D2 type receptors causes the neuron to become inhibited along the indirect pathway.

The indirect pathway starts with the cortical stimulation of the Str. A group of Str neurons have GABAergic projections to the globus pallidus externa (GPe), which turn has inhibitory

connections to the subthalamic nucleus (STN). STN has glutamatergic (excitatory) connections to the GPi/SNr. With the inhibition from Str, GPe activity reduces and there is less inhibition to the STN. This enables STN to be more active and STN can excite GPi/SNr. Stimulation of GPi/SNr results in suppression of unwanted movements.

Here, the intention is to reveal the role of indirect pathway in voluntary action selection. To perform this aim, the information flow from associative cortex (AC) to subthalamic nucleus (STN) on indirect pathway will be obtained by the mathematical model. The model consists of modified Hodgkin-Huxley neuron models obtained by adding ion channels to mimic the different dynamic behaviour as postinhibitory rebound spiking, bursting etc. of each neural structure taking part in the indirect pathway and the connection between the neurons in the same neural structure is modelled with connection dynamics.

The simulation results reveal that the model is capable of reflecting the different neuronal activities of AC to STN through STR D2 and GPe. Considering similar works in the literature [5-7], this model deals with more neural structures and can simulate the membrane potentials of neural structures in the indirect pathway of BG for action selection. The results obtained are of value in understanding the functional activity of indirect pathway which is especially important in neurodegenerative diseases.

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[F 25] Stability of travelling waves in stochastic Nagumo equations

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A new mathematical approach to the qualitative as well as the quantitative study of the stability properties of the action potential travelling along the nerve axon is introduced that allows also to take into account stochastic perturbations. Rigorous results are obtained for the cable equation with space dependent mulitiplicative noise, where the variance is proportional to the distance of the orbit of the travelling wave. The results will be illustrated with a number of numerical simulations also for spatially extended stochastic FithHugh-Nagumo systems.

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[F 26] T-Spline Representation of Neuronal Cell Membrane and Extracellular Environment for Local Field Potential Modelling

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Advances in our biophysical understanding of the neuron are pushing a trend towards increasingly complex models. The physical properties of the neuropil (in particular resistivity and permittivity) are such that the extracellular medium plays a significant role in the functional coupling between neurons. However, propagation of signals via the extracellular bulk is often neglected in multicompartmental simulations. The combined action of these current flows gives rise to meso-scale fields that can be picked up and perturbed by Multi-Electrode Arrays (MEA). Their strength can be expressed as a scalar quantity known as the Local Field Potential (LFP). Knowledge of this field allows us to calculate the electric and magnetic field distribution, both inside and outside the neuropil itself. Therefore, it is of considerable interest to have an adequate forward model that can explain the generation, reach and other characteristics of the LFP. The use of simple approximations is precluded by the strong inhomogeneity and anisotropy of the neuropil. Instead, the spatially explicit Finite Element Method (FEM) is necessary to explain salient characteristics of the LFP [1].

To obtain an accurate description of the complex geometry, we begin by defining the cellular membrane mesh of individual neurons. Common interchange formats for reconstructed morphology describe the cell in terms of a tree 'skeleton', containing nodes and edges. Each node is assigned a radius, and the edges form tapered compartments between nodes. Our objective is to extrude a 3D volumetric mesh from this skeleton description. A recent approach uses subdivision surfaces, but requires resampling of the skeleton to diminish smoothing artefacts, and iterative refinement to reach the desired spatial resolution [2]. We instead use an extension of NURBS (Non-Uniform Rational Basis Splines). NURBS have numerous benefits: they are mathematically precise, smooth (continuous) to any desired order and computationally efficient. NURBS are industry-standard and ubiquitously supported by GPU hardware, enabling interactive visualization. Their generalization to T-splines in addition enables us to create an unbroken (watertight) surface from a set of geometric primitives [3].

T-spline surfaces are sampled to construct the FEM equation matrix. So-called isogeometric FEM retains the geometrically exact description of T-spline surfaces during this process [4]. Parametric mapping allows boundary conditions such as transmembrane currents to be imposed with minimal discretization error. The versatility of T-splines permits extension to any conceivable neuronal feature, such as the automated insertion of dendritic spines. Taken together, our work demonstrates that T-splines provide a universal formalism for neuroscientific geometric modelling with applications including visualization, data exchange and FEM.

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[F 27] Response classes of spike sequence processing

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The response properties of single neurons to inputs is an essential feature underlying the dynamics of neural networks. Usually, a neuron's response properties are characterized with regard to continuous input currents determining the neuron's mean output frequency in dependence of the mean input. The resulting response curve is always monotonically increasing with the input. However, in neural networks the typical input arrives at a neuron in the form of distinct pulses. We have shown recently that the response of neurons to regular spike sequences can be very different from the response to continuous input-currents [1], in particular leading to non-monotonic input-output relations. Here, we provide a classification of the generic responses and find five dynamical classes. This may help understand the underlying network dynamics in systems exhibiting regular spike sequences such as e.g. central pattern generators.

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[F 28] Network Self-organization Explains the Distribution of Synaptic Efficacies in Neocortex

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Computations performed by cortical circuits depend on their detailed patterns of synaptic connection strengths. Interestingly, the distribution of synaptic efficacies in neocortex has an approximately lognormal shape. Many weak synaptic connections coexist with few very strong connections such that only 20% of synapses contribute 50% of total synaptic strength [1]. Furthermore, recent evidence shows that weak connections fluctuate strongly while the few strong connections are relatively stable, suggesting them as a physiological basis for long-lasting memories [2]. It remains unclear, however, through what mechanisms these properties of cortical networks arise.

Here we show that lognormal-like synaptic weight distributions and the characteristic pattern of synapse stability can be parsimoniously explained as a consequence of network selforganization. We have developed a self-organizing recurrent neural network model (SORN) composed of binary threshold units [3]. The network receives no external input but selforganizes its connectivity structure through different forms of plasticity: additive spike-timing-dependent plasticity (STDP), the formation of new synaptic connections via structural plasticity, inhibitory spike-timing dependent plasticity, homeostatic synaptic scaling, and intrinsic plasticity of neuron excitability. Across a wide range of parameters, the network produces lognormal-like synaptic weight distributions and faithfully reproduces experimental data on synapse stability as a function of synaptic efficacy. We show that the lognormal-like weight distribution arises from a rich-get-richer mechanism induced by STDP: the probability that a synapse gets strengthened due to STDP grows approximately linearly with its current efficacy, while homeostatic synaptic scaling induces competition between synapses. Our model also predicts a power law scaling of the life times of newly established synaptic connections. Overall, our results suggest that the fundamental structural and dynamic properties of cortical networks arise from the self-organizing forces induced by different forms of plasticity.

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[F 29] Reciprocal inhibition and slow calcium decay in perigeniculate interneurons explain changes of spontaneous firing of thalamic cells caused by cortical inactivation

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The role of cortical feedback in thalamocortical processing loop has been extensively investigated over the last decades. With exception of several cases, these searches focused on cortical feedback exerted onto thalamo-cortical relay (TCR) cells of the dorsal lateral geniculate nucleus (LGN). In a previous, physiological study we showed in the cat visual system that cessation of cortical input, despite decrease of spontaneous activity of TCR cells, increased spontaneous firing of their recurrent inhibitory interneurons located in the perigeniculate neucleus (PGN). To identify mechanisms underlying such functional changes we conducted a modeling study in NEURON on several networks of point neurons with varied model parameters, such as membrane properties, synaptic weights and axonal delays. We considered six network topologies of the retino- geniculo-cortical system. All models were robust against changes of axonal delays except for the delay between LGN feed-forward interneuron and TCR cell. Models were manually tuned to achieve results closest to the experimental ones and than conformance of the models' output was verified by systematic search in the parameter space. The best representation of physiological results was obtained with models containing reciprocally connected PGN cells driven by the cortex assuming relatively slow decay of intracellular calcium. This strongly indicates that the thalamic reticular nucleus plays an essential role in the cortical influence over thalamo-cortical relay cells while the thalamic feed-forward interneurons are not essential in this process. Further, we suggest that the dependence of the activity of PGN cells on the rate of calcium removal can be one of the key factors determining individual cell response to elimination of cortical input.





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[F 30] Dynamical entropy production in cortical circuits with different network topologies

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The prevailing explanation for the irregularity of spike sequences in the cerebral cortex is a dynamic balance of excitatory and inhibitory synaptic inputs [1].

While the statistical properties of the balanced state are well described by mean field theory, the dynamics of the balanced state is still not well understood. It depends strongly on the underlying dynamics of individual neurons. Inhibitory networks of leaky integrate-andfire neurons show stable chaos [2]. In contrast, in a random network of neurons with a dynamic spike generation mechanism [3], deterministic extensive chaos in the balanced state was shown [5]. Single spike perturbations in such networks lead to extremely strong chaos, characterized by infinite maximal Lyapunov exponents [6,7]. Given the strong dependence of the dynamics of the balanced state on the single neuron dynamics, does the dynamics have as strong dependence on the network topology?

Previous studies of the dynamics of the balanced state used random (Erdős-Rényi) networks. We extended this analysis to arbitrary network topologies and analyzed the entropy production in small world topologies and ring networks [6]. We derived an analytical expression for the single spike Jacobian containing elements of the coupling matrix, which enabled us to calculate the Lyapunov spectrum for any desired topology, including multi-layer networks and hierarchical networks. Using neurons with a dynamic spike generation mechanism [8] we simulated the dynamics in numerically exact event-based simulations and calculated spectra for a variety of connectivities.

Our findings corroborate qualitatively the results obtained in Erdős-Rényi networks: Dynamic spike initiation of neurons leads to extensive chaos irrespective of the network topology.

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[F 31] Vesicle release statistics at graded potential synapses: modeling study

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Signal transfer characteristics of chemical synapses are strongly shaped by the molecular organization of the presynaptic active zone. Graded potential synapses are ubiquitous among sensory receptor neurons such as auditory and vestibular hair cells, retinal photoreceptors, and electroreceptors [1]. Generally, these synapses feature high fidelity, precision, and broad dynamic range when encoding transient or prolonged stimuli [1]. Experimental data describing the fine molecular organization of these synapses is rapidly accumulating, e.g., [2,3].

Here, we study an idealized biophysical model of the active zone of a graded potential synapse to relate its topography and molecular kinetic properties to the vesicle release dynamics. The model includes N independent Ca2+ channels described by two state Markov models. These channels can be arbitrarily distributed within the active zone along with M arbitrarily distributed vesicle docking sites. Each docking site is modeled as a two state Markov chain, one state being empty and the other - ready to release a docked vesicle. Release occurs immediately after binding of a single Ca2+ ion to the vesicle's Ca2+ sensor. The rate of binding is proportional to the calcium concentration [Ca2+] at the release site. Because Ca2+ diffusion from a channel to the release sensor is fast compared to the channel open times, we approximate [Ca2+] changes as instantaneous upon Ca2+ channel opening and closing [4]. We describe the [Ca2+] profile by a linearized buffered Ca2+ diffusion approximation [4]. Replenishment of empty docking sites occurs at constant rate.

In order to characterize transient and sustained responses of this model active zone, we analyze first release event latency after a voltage step and stationary release inter-event interval distributions. We obtain analytical expressions for these quantities for various active zone topographies. By using our formalism, we examine the influence of Ca2+ channel number, positioning, and gating kinetics, vesicle docking site number and positioning, kinetics of the Ca2+ release sensor, and vesicle replenishment rate. We confirm the analytical results by direct numerical simulations.

We find that, in a wide range of situations, the mean and variance of [Ca2+], and population variance of how much each channel contributes to the total [Ca2+] on average largely determine the release dynamics for a given active zone topography. For all active zone topographies, increasing number of release slots shifts the release inter-event interval statistics towards Poissonian. Increasing vesicle docking site and accompanying Ca2+ channel numbers proportionally changes the first event latency in the same way as effectively scaling the channel number.

We hope that our insights on this analytically treatable model can help in analyzing how the active zone topography shapes information encoding at graded potential synapses in first approximation.

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Neural encoding and decoding

[F 32] Beyond GLMs: a generative mixture modeling approach to neural system identification

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One of the principle goals of sensory systems neuroscience is to characterize the relationship between external stimuli and neuronal responses. A popular choice for modeling the responses of neurons is the generalized linear model (GLM). However, due to its inherent linearity, choosing a set of nonlinear features is often crucial but can be difficult in practice if the stimulus dimensionality is high or if the stimulus-response dependencies are complex.

Here, we derive a more flexible neuron model which is able to automatically extract highly nonlinear stimulus-response relationships from the data. We start out by representing intuitive and well understood distributions such as the spike-triggered and inter-spike interval distributions using nonparametric models. For instance, we use mixtures of Gaussians to represent spike-triggered distributions which allows for complex stimulus dependencies such as those of cells with multiple preferred stimuli. A simple application of Bayes' rule allows us to turn these distributions into a model of the neuron's response, which we dub spike-triggered mixture model (STM).

We demonstrate the superior representational power of the STM by fitting it to data generated by a trained GLM and vice versa. While the STM is able to reproduce the behavior of the GLM, the opposite is not the case. We also apply our model to single-cell recordings of primary afferents of the rat's whisker system and find quantitatively and qualitatively that it is able to better reproduce the cells' behavior than the GLM. In particular, we obtain much higher estimates of the cells' mutual information rates.



Figure 1

[F 33] Explicit coding in the brain: data-driven semantic analysis of human fMRI BOLD responses with Formal Concept Analysis

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Understanding how semantic information is represented in the brain has been an important research focus of neuroscience in the past few years. We showed previously (Endres et al 2010) that Formal Concept Analysis (FCA, (Ganter and Wille 1999)) can reveal interpretable semantic information (e.g. specialization hierarchies, or feature-based representation) from electrophysiological data. Unlike other analysis methods (e.g. hierarchical clustering), FCA does not impose inappropriate structure on the data. FCA is a mathematical formalism compatible with the explicit coding hypothesis (Foldiak, 2009)

Here, we investigate whether similar findings can be obtained from fMRI BOLD responses recorded from human subjects. While the BOLD response provides only an indirect measure of neural activity on a much coarser spatio-temporal scale than electrophysiological recordings, it has the advantage that it can be recorded from humans, which can be questioned about their perceptions during the experiment, thereby obviating the need of interpreting animal behavioural responses. Furthermore, the BOLD signal can be recorded from the whole brain simultaneously.

In our experiment, a single human subject was scanned while viewing 72 grayscale pictures of animate and inanimate objects in a target detection task (Siemens Trio 3T scanner, GE-EPI, TE=40ms, 38 axial slices, TR=3.08s, 48 sessions, amounting to a total of 10,176 volume images). These pictures comprise the formal objects for FCA. We computed formal attributes by learning a hierarchical Bayesian classifier, which maps BOLD responses onto binary features, and these features onto object labels. The connectivity matrix between the binary features and the object labels can then serve as the formal context.

In line with previous reports, FCA revealed a clear dissociation between animate and inanimate objects in a high-level visual area (inferior temporal cortex, IT), with the inanimate category including plants. The inanimate category was subdivided into plants and non-plants when we increased the number of attributes extracted from the fMRI responses. FCA also highlighted organizational differences between the IT and the primary visual cortex, V1. We show that subjective familiarity and similarity ratings are strongly correlated with the attribute structure computed from the fMRI signal.

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[F 34] Integration of Subunits in Mouse Retinal Ganglion Cells

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Ganglion cells integrate and process information in the retina and send the output to the brain. For example, they combine input from the center and the surround of their receptive fields. The center of the receptive field can as well be described as an integration of subunits. The subunit character may arise from the anatomical organization of retina and the signal processing of the photoreceptors and interneurons. It has been shown that ganglion cells in salamander deploy different forms of integration of these central subunits. In more detail, two functionally different types of ganglion cells were found, showing subunit nonlinearities that could be described as threshold-quadratic or threshold-square root, respectively. In the present study, we used closed- loop as well as classical open-loop experiments to describe the integration of central subunits of mouse retinal ganglion cells. We found nonlinear integration of nonlinear subunits, similar to what had been described in salamander. In addition, unlike in the salamander retina, we also observed ganglion cells with linear integration of linear subunits were found as well. This raises interesting questions about the potential mechanistic basis and the functional consequences of the different forms of spatial integration.

[F 35] Sound Decoding from Auditory Nerve Activity

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In the inner ear sounds are converted to discrete action potentials and sent to the central nervous system. This transformation is non-linear and results in massive information loss. However, we still can hear and analyze sounds with high fidelity. This is because the crucial features of sounds are still present in the auditory nerve signals.

Here we present a method which decodes sounds from a large population of simulated auditory nerve fibers (ANFs). We also use the procedure to reconstruct sounds from a model of an impaired cochlea. This way we are able to mimic how hearing impaired subjects perceive sounds.

The problem of reconstructing stimuli from neural activity is usually only approached with relatively small numbers of spikes. Procedures usually rely on the optimization of a linear filter using the reverse correlation technique (Bialek et al. 1991). Our approach leverages responses of a large population of ANFs (close to the number present in the human ear) and non-linear reconstruction using an artificial neural network (ANN).

We used the biophysical auditory periphery model from Zilany et al. (2009) which we adapted to replicate the human hearing range and thresholds. The particular ANN used was a multilayer perceptron (MLP) with a single hidden layer. The input to the MLP was a 10 ms sliding window from multiple spike trains across 10 different characteristic frequencies. The output was a single value of the reconstructed signal. In this way we trained and tested the MLP with sounds below 2 kHz. Unfortunately, this approach did not work for frequencies above 2 kHz, because of the lacking phase information (phase locking) in spike trains. We therefore developed a two-stage algorithm to reconstruct high frequency signals. First, spike trains were converted to a spectrogram by MLPs. Second, the spectrogram was transformed to an acoustic signal using an iterative method (Decorsiere et al. 2011). In order to convert spike trains to a spectrogram we trained 51 MLPs. The input to each MLP was a sliding window of 5 ms from multiple spike trains and the output one of 51 frequency channels of a spectrogram. Characteristic frequencies of the input fibers corresponded to the frequency of the generated output channel.

The system was trained with pure tones and a few seconds of speech samples. After training we were able to generate sound files from trains of a large population of nerve action potentials. The reconstructed speech was clearly understandable and well perceived. In addition, we reconstructed sounds from an impaired cochlear model and demonstrated how perception is degraded by outer hair cell loss.

Our reconstruction is a valuable tool to evaluate how well speech is encoded in different models of the auditory system. We can also use it to illustrate acoustically the effects of hearing loss.

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[F 36] Ion-channel noise in phasic auditory brainstem neuron models can lead to slope-based suprathreshold stochastic resonance

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Stochastic variability in ion channel conductances, due to random transitions between ion channel states, can nontrivially affect neural behavior. However, whether this ion-channel noise gives rise to noise-enhanced neural processing is unclear, having received little attention compared with synaptic noise. A recent exception (Ashida and Kubo, 2010) is simulations of a population of Hodgkin-Huxley models, with a Markov-based model of stochastic ion channel noise, that exhibited a noise-enhancing effect called suprathreshold stochastic resonance (SSR).

We have therefore investigated whether other forms of noise enhanced processing, or 'stochastic facilitation' can be observed due to ion-channel noise models. Specifically, we replaced current noise with channel noise in a detailed Hodgkin-Huxley like model of phasically firing neurons in the auditory brainstem that exhibits a noise-enhancing effect called slope-based stochastic resonance (SBSR), i.e. noise enables firing in response to slowly varying inputs (Gai, Doiron and Rinzel 2010). We found that SBSR persists for a broad range of noise levels (determined by membrane patch areas), and that SSR and SBSR can be combined to form slope-based SSR. This suggests intrinsic channel noise might be exploited in-vivo to enable phasic population responses to robustly encode slowly varying signals.

Acknowledgements

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[F 37] Decoding of reach and grasp kinematics from primate premotor, motor, and parietal cortex

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The primate motor, premotor, and parietal cortex are crucially involved in the planning and execution of dexterous hand movements. Specifically, neurons in the ventral premotor cortex (area F5) and the anterior intraparietal area (AIP) have been shown to represent the grip type, wrist orientation, and grip aperture during movement planning and execution. However, it is unclear to what extent these higher-order planning areas represent not only intended hand shapes, but also continuous hand kinematics during grasping. Here we demonstrate the decoding of spatial hand position and individual finger angles from spiking activity in F5, AIP, and primary motor cortex (M1).

A rhesus monkey (Macaca mulatta) was trained to perform a delayed grasping task with ~50 objects of different shape, size, and orientation that were presented in pseudo-random order on a carrousel in front of the monkey. Hand kinematics were monitored with a sensor glove that allowed the continuous tracking of 27 degrees of freedom of all fingers, wrist, and arm angles in 3D space (Schaffelhofer 2012). Neural data was recorded using 192 chronically implanted microelectrodes (FMAs, Microprobe Inc.) that were distributed evenly in F5, AIP, and the hand area of M1. After offline spike sorting (WaveClus, Plexon Offline Sorter), we utilized a Kalman Filter to predict hand kinematics from the population activity of individual areas.

For each finger, we decoded the orientation of the fingertip (distal phalanx) relative to the hand dorsum, which served as a good indicator of the overall finger closure. As expected, neural signals from M1 predicted these kinematics best: for fingers 1-5 we found a correlation coefficient (CC) between predicted and real trajectory of 0.65, 0.56, 0.62, 0.57, and 0.55, respectively. Similar predictions from area F5 were somewhat worse, but still surprisingly accurate (CC: 0.52, 0.37, 0.43, 0.41, 0.43). In contrast, predictions from AIP were significantly less accurate (CC: 0.29, 0.25, 0.28, 0.27, 0.30).

Furthermore, we also decoded the continuous reach (hand) position in space, for which we obtained the following CCs between the real and predicted x-, y-, and z-position: M1: 0.87, 0.72, 0.70; F5: 0.81, 0.64, 0.56; AIP: 0.52, 0.51, 0.36.

These results indicate that spiking activity in M1 and F5 can both predict the continuous reach and grasp kinematics well, while AIP is significantly less suitable. These findings could be useful for the future design of hand prosthetics.

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[F 38] The shaping of the coherence function of resonate-and-fire neuron models

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It is known that integrate-and-fire neurons act as low-pass filters on information [1], i.e. they preferentially encode information at low frequencies. However, many neurons cannot be described by such integrators, even qualitatively. Experiments show that in several areas of the mammalian brain single neurons display a resonance property in their subthreshold voltage dynamics, see for example [2,3]. These neurons are more appropriately described by so called resonate-and-fire neurons [4]. Here, we study the information transmission of a current-based resonate-and-fire neuron model [5] by means of the spectral coherence function. We use a stochastic input current (the Ornstein-Uhlenbeck process from statistical physics) to model a complex dynamical stimulus. We show by numerical simulations that resonate-and-fire neurons encode time-dependent stimuli preferentially at moderate frequencies, including their resonance frequency, i.e. the coherence function of this model shows a clear maximum as a function of frequency. This is in marked contrast to the low-pass coherence that is found for the pure subthreshold dynamics (in the absence of spiking) in spite of resonant filter properties. We discuss dynamical mechanisms that lead to the band-pass filtering of information in the spiking resonate-and-fire model.

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[F 39] The 'neural code' from the intrinsic perspective: Quantifying causal power at different spatio-temporal scales

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Understanding the neural code is a difficult issue that is fraught with both theoretical and experimental problems. Usually coding strategies are evaluated in terms of quantities that are easily accessible to experimental observation. For example one may quantify the information conveyed by the firing patterns of neurons in response to an ensemble of stimuli. On the other hand, it seems clear that the only codes or information that matter for the brain itself are "differences that make a difference" from the intrinsic perspective of the system itself, irrespective of external observers. But how can one evaluate which differences matter most? The problem is compounded by the fact that multiple spatial and temporal scales are potentially relevant - from molecules to synapses, neurons, and groups of neurons and from microseconds to milliseconds, seconds, minutes and hours. An often unstated assumption is that the microscopic level of description is the one that has true causal power. By contrast, higher levels of organization would be just convenient ways of grouping observations together for ease of description and understanding. However, the determination of what level of organization in the brain or any other complex system holds maximum causal power should be based on a general, objective way of quantifying causes and effects from the intrinsic perspective of a system. Only then does it become possible to identify the particular temporal or spatial scale at which causal interactions reach a maximum for this particular system and causally "supersede" interactions at lower or higher levels.

A way of systematically evaluating causes and effects by adopting an information-theoretic formalism has been recently developed in the context of integrated information theory (Tononi, 2008; in press). Specifically, effective information measures how much a particular current state of the neural system reduces the uncertainty about its causes and effects compared to the repertoire of all possible states, the maximum entropy distribution. Importantly, effective information captures the specificity/reliability of causes and effects (causal information) with respect to the system itself (its 'intrinsic' perspective). Moreover, integrated information measures to what extent the effective information generated by a subset of elements is irreducible to the information generated by its parts. By quantifying interactions in this way, it becomes possible to assess, in a principled manner, the spatiotemporal grain at which a system generates maximal effective information / integrated information and thus exerts maximum causal power.

Using simplified neuronal models, we show that a neural state at a coarser spatial and/or temporal scale (macro-level) may under certain circumstances produce more effective information than at a finer scale (micro-level), despite the higher entropy (larger repertoire of possible states) available at the micro-level. This means that, depending on the precise organization of a system, the causal effects of a neural state onto the neural system itself can be higher at a macro- than at a micro-level of organization. So far, we have identified the following requirements for the emergence of higher causal power at higher levels of spatio-temporal organization: i) the presence of noise or indeterminism, which allows for smart grouping of noisy, causally equivalent microstates into more deterministic macro-states; ii) the assumption of maximum entropy, which redistributes system states uniformly at the macro-level, with the consequence that, after smart grouping, equivalent micro-states become less represented than more unique ones; iii) for temporal emergence, the existence of multiple time scales of interaction, where interactions within a macro-element can occur faster than among macro-elements.

In general, identifying what levels of interaction hold most causal power, properly defined, should lead to a better understanding of what actually constitutes the neural code - one of the central problems of modern neuroscience - from the perspective of the brain itself (Kumar et al. 2010).

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Sensory processing and perception

[F 40] The yellow of a gray banana - Decoding colors from fMRI signals in the absence of chromatic stimulation

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Some objects that we deal with on a daily basis are associated with an object-specific color – such as yellow for bananas, red for strawberries, green for lettuce, etc. Such objects are referred to as color-diagnostic and their associated color as their memory color (Hering, 1920). Psychophysical evidence shows that achromatic, i.e. grayscale, images of color-diagnostic objects elicit percepts that are differentially biased towards their memory color (Hansen et al., 2006; Olkkonen et al., 2008). This phenomenon suggests some form of learned and automatic association between colors and particular objects.

In the present study we tested whether neural responses to color-diagnostic objects convey color-specific information, even when the objects were presented achromatically to subjects who were naïve to the purpose of the study.

We first collected fMRI data while participants viewed grayscale images of 8 different colordiagnostic objects (4 colors, 2 per color). We then recorded responses to chromatic stimulation with red, green, blue, and yellow abstract color stimuli that contained no object information. All object and color stimuli were set to equiluminance for each subject individually. To analyze the data, we applied a whole-brain searchlight procedure by training linear support vector machine classifiers to distinguish between local voxel patterns associated with the four colors. They were then tested on patterns elicited by color-diagnostic achromatic objects to predict their correct memory colors.

At the group level, we found significant decoding accuracy in a large cluster covering foveal regions of early visual cortex. In some but not all individual subjects, smaller clusters were also evident in the fusiform gyrus.

Our results suggest that memory color and color signals evoked by chromatic stimulation share a common neural mechanism in early visual cortex. Retinotopic mapping in combination with classification techniques will be used to clarify the contribution of individual visual areas to this mechanism.

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[F 41] Heterogeneity improves the encoding of natural stimuli in a neuronal population

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Neurons often show remarkable heterogeneity in terms of their response properties even if they belong to the same cell type. This heterogeneity can result from biophysical, anatomical or input differences. Theoretical studies have shown that heterogeneity can decorrelate the activity in a neuronal population and thereby increase its ability to carry information about the stimulus. Experimental evidence about whether and how this effect is exploited in neural systems, remains scarce to date.

We investigate this question in our model system, the weakly electric fish that uses an actively generated electric field (the electric organ discharge, EOD) for navigation as well as communication purposes. Via specialized electroreceptors distributed all over their body they sense modulations of this field. The behaviorally relevant amplitude modulations (AMs) result in communication contexts from the interaction with other fish, or in hunting tasks from prey. AMs are encoded in the activity of electroreceptor afferents of the P-type. P-units respond phase-locked and probabilistically to each EOD cycle and show prominent negative serial correlations between successive interspike intervals. They show a high degree of heterogeneity in both their baseline firing rate as well as their sensitivity and are thus well suited for studying possible functional roles of this heterogeneity.

We here analyze data from intracellular recordings of P-units as well as from computational simulations of a novel P-unit model. Using the model we apply targeted variations of model parameter to identify possible sources of the observed heterogeneity. Further, we examine the impact the heterogeneity has on the encoding of AM signals originating from communication signals. For both, cells and model, we find resonances of the responses to AMs matching their baseline frequencies and its harmonics. These resonances are known to degrade the encoding of the AM stimuli. Because of the heterogeneity in their baseline firing rate each cell has its resonance peaks at different frequencies. Pooling over this heterogenous population averages these resonance peaks away and ensures that all frequencies are equally well represented in the population. Furthermore, the heterogeneity in the sensitivity of the cells ensures that communication signals can be well encoded at all possible stimulus intensities occurring under natural conditions. Our results demonstrate that the heterogeneity in the response properties of neuronal populations indeed improves the representation of sensory stimuli.
[F 42] How Sensitive Is the Human Visual System to the Local Statistics of Natural Images?

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A key hypothesis in sensory system neuroscience is that sensory representations are adapted to the statistical regularities in sensory signals and thereby incorporate knowledge about the outside world. Supporting this hypothesis, several probabilistic models of local natural image regularities have been proposed that reproduce neural response properties. Although many such physiological links have been made, these models have not been linked directly to visual sensitivity. Previous psychophysical studies focus on global perception of large images, so little is known about sensitivity to local regularities. We present a new paradigm for controlled psychophysical studies of local natural image regularities and use it to compare how well such models capture perceptually relevant image content. To produce image stimuli with precise statistics, we start with a set of patches cut from natural images and alter their content to generate a matched set of patches whose statistics are equally likely under a model's assumptions. Observers have the task of discriminating natural patches from model patches in a forced choice experiment. The results show that human observers are remarkably sensitive to local correlations in natural images and that no current model is perfect for patches as small as 5 by 5 pixels or larger. Furthermore, discrimination performance was accurately predicted by model likelihood, an information theoretic measure of model efficacy, which altogether suggests that the visual system possesses a surprisingly large knowledge of natural image higher-order correlations, much more so than current image models. We also perform three cue identification experiments where we measure visual sensitivity to selected natural image features. The results reveal several prominent features of local natural image regularities including contrast fluctuations and shape statistics.

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[F 43] Cooperative phenomena in motion binding

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Many aspects of visual perception are characterized by 'cooperative behavior' such as orderdisorder transitions, multi-stable states, and 'hysteresis' (Williams, Phillips & Sekuler, 1986), presumably reflecting recurrent excitation and inhibition within the underlying neural populations (Buckthought, Kim & Wilson, 2008). We have studied hysteresis in the transition between ordered and disordered percepts induced by random-dot-kinematograms (RDK). Our aim was to establish the probability and dynamics of order-disorder transitions and to characterize their dependence on the number of display elements (dots).

Six observers viewed continuous RDK for 5 s – during which the fraction of orderly dots varied unpredictably (low-pass-filtered random walk) – reporting their initial and final percepts (orderly/disorderly). Orderly dots produced a coherent motion flow (either clockwise or anticlockwise, converging or diverging spirals, with varying angular velocity). We obtained pronounced hysteresis for 'orderly fractions' from 0.4 to 0.6. Random walks terminating at 0.5 consistently yielded different percepts, revealing a significant influence of the orderly fraction up to 2 s prior to termination. Reverse correlation showed the characteristic time-constant to be approximately 0.4 s.

We introduce a novel method for characterizing the cooperative dynamics of order-disorder transitions in motion binding. These observations provide powerful constraints for abstract neural models based on discrete stochastic integration (Braun & Mattia, 2010).

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[F 44] Neural correlates of reversing illusory rotation or depth: an MEG study

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A cloud of dots in planar motion can induce the compelling illusion of a rotation in depth ("structure-from-motion"). Surprisingly, reversing the planar motion does not necessarily reverse the global illusory rotation. In fact, two perceptual outcomes are possible: the illusory rotation either reverses (while illusory depth is maintained) or remains constant (while illusory depth is inverted) (Pastukhov, Vonau, & Braun, 2012). Importantly, the latter outcome leaves the overall illusory shape unchanged (provided it is rotationally symmetric, e.g., a sphere, or cylinder), as only the local illusory depth of individual dots is affected.

Braun, J., & Mattia, M. (2010). Attractors and noise: twin drivers of decisions and multistability. NeuroImage, 52(3), 740-51.

Here we compare EEG/MEG activity associated with these alternative perceptual interpretations of physically identical events (reversals of planar motion): Eighteen observers viewed an ambiguously rotating sphere presented for 1500 ms with a reversal of planar motion occurring with at variable points in time. Observers reported whether the global illusory rotation had reversed (maintaining local illusory depth) or had remained constant (inverting local illusory depth). To ensure that both outcomes were equally probable, we adjusted the distance between opposing dots at the moment of reverals (Stonkute, Braun, & Pastukhov, 2012).

Reversals of global illusory rotation were associated with phasic activity in a medial-temporal area (presumptive hMT, ~180 ms) and, somewhat later, in an immediately adjacent superior region (~270 ms). In contrast, reversals of local illusory depth elicit phasic activity near the intraparietal sulcus (presumptive LIP) and in ventral extrastriate areas (~215 ms). The latter activity pattern is likely to reflect renewed "binding" between neural representations of local depth and of global rotation.

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[F 45] When correlation implies causation in multisensory integration

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Inferring which signals have a common underlying cause, and hence should be integrated, represents a primary challenge for a perceptual system dealing with multiple sensory inputs. This challenge is often referred to as the correspondence problem or causal inference. Previous research has demonstrated that spatiotemporal cues, along with prior knowledge, are exploited by the human brain to solve this problem. Here we explore the role of correlation between the fine temporal structure of auditory and visual signals in causal inference. Specifically, we investigated whether correlated signals are inferred to originate from the same distal event and hence are integrated optimally. In a localization task with visual, auditory, and combined audiovisual targets, the improvement in precision for combined relative to unimodal targets was statistically optimal only when audiovisual signals were correlated. This result demonstrates that humans use the similarity in the temporal structure of multisensory signals to solve the correspondence problem, hence inferring causation from correlation.

[F 46] The Impact of Data Transmission Rate on Human Tracking Task with Electrocutaneous Feedback

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In electrocutaneous stimulation (ELCUS), low level electrical current pulses are delivered to the skin to activate sensory nerve fibers and stimulate the sense of touch. Tactile stimulation is one of the methods for sensory substitution [1]. For example, ELCUS can provide sensory feedback to an amputee about the current state of the hand prosthesis, thereby closing the control loop [2]. Importantly, ELCUS is a discrete communication channel delivering information in the form of pulses with quantized intensity. The goal of this study was to test how the data transmission rate (DTR) of the feedback channel affects the control performances of a human controller during a closed-loop compensatory tracking task.

The task for the subject was to control a zero order system (pure gain) using a joystick so that the system followed a reference trajectory in the form of a pseudorandom multi-sine (10 sinuses, 0.1-0.3 Hz). The current tracking error was delivered to the subject via ELCUS (i.e., a closed loop control with tactile feedback) [3]. Two electrodes were placed on the volar and dorsal side of the forearm to communicate positive and negative errors, respectively. Additionally, the stimulation intensity was proportional to the absolute value of the error (pulse width modulation, 10 bits). The DTR of the feedback channel was decreased progressively by sampling the tracking error and delivering the corresponding pulses at a range of decreasing frequencies (100, 50, 25, 10, 5 and 1 Hz). In the two additional tests, the DTR was "artificially" increased by delivering the same information multiple times. i.e., the tracking error was sampled at low frequency (1 and 5 Hz) while the pulses were delivered at a much faster rate of 50 Hz (i.e., 1/50 and 5/50 conditions). Three young, healthy subjects participated in the experiment. After a period of training (60 min), the subjects performed the compensatory tracking task 5 times at each of the conditions. The control performance (quality of tracking) was measured by using the cross correlation between the reference and generated trajectory (i.e., Square Pearson Correlation Coefficient (SPCC)), and Root Mean Squared Tracking Error (RMSTE) normalized to the peak to peak value of the reference signal.

The results have shown that the control performance decreased with the decrease in DTR. However, between 100 and 10 Hz, this decrease was only moderate; the mean SPCC \pm SD (mean RMSTE \pm SD) was 87.1 \pm 4 % (2.25 \pm 1.7 %) at 100 Hz and 78.3 \pm 5.7 % (2.5 \pm 0.7 %) at 10 Hz. The quality of tracking deteriorated more at 5 Hz with SPCC (RMSTE) equal to 70.4 \pm 5.3 % (3.5 \pm 1.1 %) and deteriorated significantly at 1 Hz with SPCC (RMSTE) 29.9 \pm 2.9 % (7.7 \pm 1.5 %). Finally, "artificial" increase in DTR considerably recovered the control performance to SPCC (NRMSTE) 53.4 \pm 8.5 % (6.1 \pm 1.4 %) for the 1/50 condition and SPCC (NRMSTE) 77.4 \pm 6.2 % (2.6 \pm 0.62 %) for the 5/50 condition.

Preliminary results of this study suggest that the human cognitive control of the sensory motor loop during a compensatory tracking task is relatively robust with respect to the DTR of the feedback channel for the frequencies between 100 and 10 Hz. Moreover, in the conditions in which the information is available at lower rates, the control improves markedly if the information is sent redundantly. In this case, the increase in DTR likely increases the information transfer rate through the channel. These are preliminary conclusions and further experiments with more subjects need to be conducted. The insights from this study are relevant for the closed loop control of prosthetic systems. The study characterizes the behavior of a human controller with respect to DTR, and this can facilitate the selection of optimal system parameters (stimulation frequency, sensor sampling rate).

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[F 47] On the estimation of 3D shape from image orientations

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One of the most important functions of vision is to estimate the 3D shape of objects in our environment. Many different cues (e.g. disparities, shading, texture) provide information about shape, but how the visual system estimates shape is poorly understood. Here, we present evidence that crucial information is extracted from the way local image orientation signals vary continuously across the surface of an object ('orientation fields'). We used computer renderings to create images of shaded and textured objects and measured the responses of populations of oriented filters to the images. We find some striking statistical regularities that demonstrate the orientation fields are systematically related to 3D shape. We also find that when illumination conditions and texture patterns change, it can lead to systematic changes in the orientation fields. This makes specific predictions about how the perceived shape of objects should change depending on the illumination or texture on the surface. We tested these predictions psychophysically and find that the model correctly predicts both successes and failures of human 3D shape perception. Together these findings suggests that the visual estimation of shape from shading, highlights and texture may have more in common than previously thought and that orientation fields could act as a 'common currency' for the visual estimation of shape.

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[F 48] Did I do that? Causal inference of authorship in goal-directed actions for impoverished stimuli

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The perception of own actions is affected by visual information and internal predictions [1] of consequences to those actions. The integration of these cues depends on their accuracies [2,3], including the association of visual signals with one's own action or with unrelated external changes [4]. This attribution of authorship should thus depend on both the consistency between predicted and actual visual consequences and their signal accuracy.

METHODS. We used a virtual-reality setup to manipulate the consistency between pointing movements and their visual consequences. Subjects were instructed to perform fast outand-back movements with their right hand without direct vision of their hand. Instead, we presented terminal visual feedback about their movement direction. This feedback could be experimentally manipulated with rotations randomly drawn from a given set. We investigated the influence of the consistency between true movement direction and the presented feedback direction on authorship judgement while additionally impoverishing visual feedback saliency. We asked whether a causal inference model accounts for the empirical data, assuming a latent authorship-variable: if the visual stimulus was attributed to one's own action, visual and internal information should fuse in a Bayesian optimal manner, otherwise not.

RESULTS & CONCLUSION. The model, fitted to motor responses, correctly predicts authorship-ratings, showing attribution of visual signals to self-action for small, and stronger reliance on internal information for large deviations. Presently, we test predictions of the model for variations of the visual saliency.

Acknowledgements

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[F 49] The influence of prior experience and symbolic cueing on human path integration

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Perception and action are the result of an integration of various sources of information, such as current sensory input, prior experience, or the context in which a stimulus occurs. As we have shown, human visual path integration behavior in a simple homing task can be described as the optimized result of a probabilistic combination of the current sensory input and short-term prior experience gathered over the preceding trials (Petzschner and Glasauer, J Neurosci 31, 2011). The observed trial-to-trial modifications in performance are explained by a rapidly adapting prior that does not depend on error feedback.

Here, we investigate whether additional information given by symbolic verbal cues can influence the path integration behavior and how the observed results can be explained by probabilistic modelling. Thus we extended the mentioned distance production-reproduction task to include a symbolic cue that supplied additional, but initially uncertain information about the stimulus value. The symbolic cue values were provided as a written instruction prior to each trial and indicated whether the distance to be reproduced would be 'short' or 'long'. The cue values corresponded to two ranges of distances. We investigated whether (1) subjects could use such a symbolic cue that provided reliable but imprecise information about the sample distances and (2) how this abstract information influenced their estimation process. To evaluate the behavioral results in the cue condition we used two control conditions that mimicked the extreme cases of cue usage. In the first control condition, we presented participants with exactly the same distances in the same order, but without the symbolic cue. In the second control condition the 'short' and 'long' ranges of displacements were presented in a separate order. Thus, if subjects ignored the symbolic cue, we expected that the performance in the cue condition would resemble that of the first control condition. If subjects however separated their estimates based on the symbolic cue, the behavior should be similar to the second control condition.

Our results show that subjects are able to utilize the additional symbolic information given in the 'cued' condition to modify their estimate of self-displacement. To explain these effects, we propose two models of distance estimation by iterative Bayesian inference, the categorical and the cue-combination model, which are founded on qualitatively different assumptions about the causal relationship between the sensory stimulus and the symbolic cue and consequently, about how the mapping of the symbolic cue to the stimulus dimension is learned during the experiment. Both models combine 1) the current noisy sensory input, 2) a prior expectation of the presented distance adaptively adjusted with each trials, and 3) the information provided by the discrete symbolic cue into a single estimate of displacement and perform equally well for the observed behavior.

We conclude that the probabilistic modelling approach to understanding 'cognitive' influence, such as prior experience or symbolic cues, on action production can lead to simple but powerful models, which can explain a range of previous psychophysical findings.

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[F 50] Effect of ivabradine on the activity of retinal ganglion cells

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Ivabradine is a new bradycardic agent which was approved for symptomatic management of stable angina pectoris and acts by blocking of HCN4-channels in the sinoatrial node (1). About 15 % of patients treated with ivabradine report slight and completely reversible luminous phenomena (phosphenes), which occured after 2 month of medication (2).

Ivabradine is thought to induce phosphenes by blocking hyperpolarization-activated and cyclic nucleotide-gated (HCN) channels in photoreceptors. These channels play an important role in shaping the membrane potential after activation and are therefore thought to be essential for efficient encoding of stimuli at high-frequency (3). Blocking HCN channels causes prolonged hyperpolarization of photoreceptor inner segments, and knock-out studies revealed the importance of retinal HCN-channels for mesopic cone vision (4).

Yet, experiments investigating the pharmacological induction of phosphenes by ivabradine have so far focused on histology, photoreceptor electrophysiology (5) or electroretinograms (6).

Complementary to these studies, we here focus on the effect of ivabradine on the encoding of visual signals at the output stage of the retina that is in the activity of retinal ganglion cells. In particular, we search for spike pattern in RGC activity after administration of ivabradine that could underlie the reported phosphenes.

To do so, we mounted isolated mouse retina on a 252-channel multielectrode array to record spikes from individual ganglion cells. We measured spontaneous activity as well as response to a series of light stimuli (steps in light intensity, different types of temporal and spatio-temporal flicker) before, during and after administration of 3 μ M ivabradine.

Preliminary results show altered spontaneous activity in RGCs during ivabradine administration, with ON-type RGCs primarily showing increased and OFF-type RGCs rather decreased spontaneous activation.

We hypothesize that this imbalanced spontaneous activity by ON-type and OFF-type RGCs may contribute to luminous phenomena reported by patients treated with ivabradine.

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[F 51] The encoding of object motion and motion direction in the retina

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Visual perception requires eye movements, passive or active, even while fixating an object. These eye movements prevent image fading. At the same time they cause an apparent motion of the image on the retina. This suggests that mechanisms exist for decorrelating eye movements and image information. An important step for understanding these mechanisms is to analyze different encoding strategies at the level of the retina. This could provide a better picture of motion processing in general.

It is already known that some retinal ganglion cells respond preferentially to certain directions of motion. Furthermore, a new functional property has been observed where cells respond to object motion on a moving background, but not when the whole visual field moves. These object-motion-sensitive (OMS) cells are considered to play a crucial part in the decorrelation of eye movements and object motion. Here we study the interplay between these different aspects of motion encoding.

We project visual stimuli onto isolated salamander retina and record the responses of retinal ganglion cells using a multi-electrode array. To study local motion and motion direction, we deploy jittering images following a random walk. Using reverse correlation analysis of the cell responses with the movement pattern, we obtain temporal filters, which indicate direction preferences and temporal integration. We found both direction-selective and OMS cells. Although these properties show up independently, some OMS cells also reveal direction selectivity. This suggests the existence of OMS subclasses.

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[F 52] Classifying retinal ganglion cells using responses to naturalistic stimuli

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Retinal ganglion cells (RGCs) integrate sensory information in the retina, acting as the output layer of a complex neural network, formed by amacrine, horizontal, and bipolar cells. Many different types are identified in morphological studies. Primates, for example, are known to have at least 17 distinct RGC types. A common assumption is that these morphological classes can be associated with functional properties. Research has been done on identifying RGCs based on their responses to steps in light intensity, direction selectivity, receptive field size and dynamics. Usually, the receptive field is characterized using a spatio-temporal white noise as stimulus, with pixel intensities drawn independently from a binary or Gaussian distribution. Reverse correlation (spike-triggered average, STA) is then used to reveal the temporal and spatial characteristics of the receptive field.

However, natural stimuli are both spatially and temporally correlated, with power spectra shown to follow a power law, and one may expect that responses to correlated and uncorrelated stimuli differ. Correlated stimuli have already been shown to be more efficient in driving RGCs, evoking higher firing rates.

For our experiments, we place a salamander retina with the ganglion cell layer down on a multi-electrode array of 252 electrodes. The stimulus is projected on the photoreceptor layer. Data are saved for offline spike-sorting and analysis. We use a stochastic process to generate a naturalistic stimulus correlated both in space and time, with similar statistical and power properties as natural images (pink noise). To recover the spatio-temporal receptive fields of the recorded cells, the STA is appropriately corrected for the correlations contained in the stimulus.

As expected, cells show a higher firing rate for the correlated stimulus. Surprisingly, some of the detected cells do barely respond to spatio-temporal white noise stimulation, if at all, but can be well analyzed with our pink noise stimulus. We further discuss how these findings can be used for cell identification.

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[F 53] Layer specific neuronal activities in response to visual object images in the inferior temporal cortex revealed by current source density analysis

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Neurons in the inferior temporal (IT) cortex show selective responses to specific sets of complex visual objects (Tanaka, 1996). They are structurally organized in columns, within which neurons have similar object selectivity (Tanaka, 2003). Anatomical studies revealed specific intra- and inter-laminar connectivity structures within a column (Fujita and Fujita,1996), suggesting that neurons in different layers are involved in different aspects of the visual information processing. Several studies tried to reveal spatio-temporal profiles of the information processing performed within a column and explored the layer dependent differences in the neuronal spiking responses (Shinomoto et al., 2005; Sato et al., 2009). However, no clear evidence of layer specificity has been reported so far.

To tackle this issue, we recorded from areas TE and TEO of anesthetized macaque monkeys the multi-unit activities (MUA) as well as the local field potentials (LFP) using linear electrode arrays while the animals were visually stimulated using various types of simple and complex visual object images. The electrode array spans 1.55 mm with 32 electrode contacts separated by 50 um and was inserted into the cortex perpendicularly to the surface. From the LFP recordings we reconstructed the current source density (CSD) (Pettersen et al., 2006), which reflects the local current flows induced by synaptic inputs to the local neuronal population.

We examined whether and how the responses to the visual stimuli in the CSD signal differ across layers. We identified a current sink at about 100 ms after stimulus onset at a depth of

approximately 1.2 mm from the cortical surface, likely corresponding to layer IV and thus reflecting the afferent input to these areas. In 200-300 ms after stimulus onset subsequent current sinks occurred in upper positions, supposedly corresponding to synaptic activities in layers II and III. The location and timing of the sequential activations were consistent with the feed-forward connectivity known for columns in the primary visual cortex, but on a much slower timescale compared to previous studies using electric or full-field flash stimulation (Mitzdorf, 1985, Schroeder et al., 1998). We calculated the object selectivity based on the magnitude of the CSD sinks in a time dependent manner, using the F-value of ANOVA (i.e. the ratio between across-stimulus and across-trial response variabilities) as a measure. We found that the initial sink in layer IV showed a significant but only weak object selectivity, while the subsequent sinks in upper layers showed a much stronger object selectivity. These results suggest that object selectivity in IT develops dynamically by activity propagating across cortical layers within the columnar structure.

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[F 54] Learning invariance in visual perception.

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The human visual system has the remarkable ability to largely recognize objects invariant of their position, rotation and scale. In part, this is likely achieved step by step from early to late areas of visual perception. But how could this invariance be achieved by the visual system? One key point is the stable world, which, however, is perceived through rapid variations of the image on the retina. Thus, the visual system has to learn to represent this rapid varying information as stable as the entity of the world is (cf. Berkes, 2005).

Obviously, exploiting the fact that the world is temporally coherent could be an appropriate neural learning strategy by making use of a trace in the learning rule (e.g. Földiak, 1991). We show that such a strategy could be implemented in a biologically plausible way and could be used to learn invariant representations from natural scene inputs. Furthermore, we show how one concept of neuronal learning can be applied to build a model for invariant object recognition being able to recognize and invariantly represent object properties of different complexities.

Therefore, we propose a learning rule based on the conceptual design of the previously developed learning rule for simple cells (Wiltschut and Hamker, 2009). The previous rule has been developed on the ideas of normalized Hebbian learning, covariance learning, and anti-Hebbian decorrelation. It leads to largely independent responses of V1-simple cells when trained on natural scenes. Our new rule expands these ideas by incorporating aspects of BCM learning and the calcium dependency of learning processes (Shouval et al., 2002), particularly by using the level of calcium rather than neural activity in the learning rules.

We have implemented this rule in a model learning the invariance properties of so-called V1-complex cells. It is important to generate appropriate image transformations simulating the rapidly varying retinal image. For this purpose, we use small shifts of the input simulating fixational eye movements. For the learning of invariance representations in higher visual areas it is required to simulate more complex and realistic object transformations.

The rule enables us to learn neurons sharing the invariance properties of V1-complex cells (Teichmann et al., 2012). We are able to show that the degree of temporal information used in the learning influences the development of invariant and temporally slowly fluctuating neuronal responses. Importantly, the derived learning rule is not special for this particular purposes: the same learning rule differing only in the length of the trace allows neurons to learn simple-cell like receptive fields.

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[F 55] Changes in functional connectivity support changes in visibility

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The neural basis of stimulus visibility is tightly linked to the quest for the neural correlates of conscious perception. Experimentally, stimulus visibility can be altered using stimulus manipulation techniques such as visual masking. In visual masking a target stimulus is rendered invisible by varying the timing of a mask that is followed by the target stimulus. Importantly, the physical appearance of the target stimulus is not changed during stimulus presentation. Here, we used functional magnetic resonance imaging (fMRI) to investigate to what extent the visibility of the target stimulus is reflected by functional connectivity changes in the human brain. Oriented grating

stimuli were presented under varying visibility conditions created by backward masking. Visibility was manipulated by using four different stimulus onset asynchronies (SOA), which created a continuum from invisible to highly visible target stimuli. Masking performance was tested in a separate behavioral experiment prior to the fMRI experiment. In addition, subjects were asked to report the orientation of the grating with a button press during the fMRI scan. Subjects who responded correctly to the highest visibility condition and were at chance level to the lowest visibility condition were selected for the fMRI analysis. First, we selected regions of interests from brain activations that were activated independent of different visibility conditions. This revealed intraparietal sulcus, dorsolateral prefrontal cortex, inferior frontal gyrus, early visual, and higher visual areas. We computed a parametric functional connectivity analysis using these regions of interests and showed that increased stimulus visibility is reflected in the coupling between early and higher visual areas. Specifically, higher visual areas are significantly more correlated with early visual areas when the visual stimulus presented is visible to the subject than when it is invisible. This provides evidence that dynamic changes in functional connectivity reflect conscious perception.

[F 56] Electrically Evoked Responses Of Retinal Ganglion Cells In Wild Type and Rd10 Mouse Retinas.

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Abstract Over the years, retinal implants have been developed to restore limited functional vision in patients blinded by outer retinal diseases like retinitis pigmentosa (RP) and age-related macular degeneration through electrical stimulation of the surviving neurons. The most extensively characterized animal model is the rd1 mouse. Howev-er, the recently identified rd10 mouse, which has a relatively delayed onset and slower progression of degenera-tion may be a more appropriate model for human RP. To support ongoing efforts to optimize prosthetic retinal stimulation [Zrenner 2011], optimal stimulation paradigms need to be established for this new mouse line. Here we investigate retinal ganglion cell (RGC) responses to different stimulation paradigms in adult wt and rd10 mice.

Introduction

Retinitis pigmentosa (RP) and age-related macular degeneration (AMD) are two forms of outer retinal diseases which result in a substantial loss of photoreceptors. Although, the remaining inner retina undergoes some physiological and morphological changes, the characteristic cellular layering is still preserved, offering the opportunity to restore vision by electrical stimulation of the residual neurons via retinal implants. The most extensively characterized animal model is the rd1 mouse. However, the recently identified rd10 mouse, which has a relatively delayed onset and slower progression of degeneration, may be a more appropriate model for human RP. In order to support ongoing efforts to optimize prosthetic retinal stimulation, paradigms need to be established for this new mouse line. Here, we in-vestigate retinal ganglion cell (RGC) responses to elec-trical stimulation in adult wt and rd10 mice.

Materials and Methods

RGC spiking responses were recorded in vitro from patches of wild-type and rd10 retina using a planar multi-electrode (Multichannel Systems, Reutlingen, Germany). Prior to electrical stimulation, spontaneous activity was recorded. Stimuli were applied epiretinally via one of the 60 electrodes of a multielectrode array (MEA) while the remaining electrodes recorded electrically evoked responses (MC Rack, MC-Stim Multichannel Systems; Fig. 1 & 2). Stimuli consisted of square-wave, monophasic (either cathodic or anodic) constant-voltage pulses with varying voltages and durations. Stimulus randomization was employed to compensate for recording instability-induced biases that have been previously observed. The stored data were processed and analyzed offline (Offline Sorter, Plexon Inc, TX; Neuroexplorer, Nex Technologies; and Matlab) to generate rastergrams, peristimulus histograms, and stimulus-response curves.

Results

In agreement with recent reports, spontaneous activity was higher and more oscillatory in rd10 retina than in the wild-type [Goo 2011]. For the wt retina, we found pulse voltage and duration requirements that are in agreement with previously published reports. In both wt and rd10 cells, a dependence on duration was seen only for a few transitional voltages (near threshold; Fig. 3-5). Both above and below these voltages the influence of duration was not significant. A subset of cells demonstrated an asymmetric preference for either negative or positive voltage pulses (Fig. 6 & 7). Additionally, ganglion cell responsiveness decreased with increased interelectrode distance out to around $800\mu m$ from the site of stimulation. Finally some cells in rd10 retina showed an initial suppression of spontaneous activity upon epiretinal stimulation.

Conclusion

Our preliminary findings present one of the first examinations of electrical stimulation in rd10 retina. Based on these findings, we propose tentative stimulation parameters appropriate for activation of rd10 retina. The relevance of our results to the continued devel-opment of efficient stimulation protocols for retinal prostheses is examined.

Figure Legends

Fig. 1 Standard planar MEA (30µm diameter electrodes, 200µm interelectrode distance, Multichannel systems, Reutlingen, Germany).

Fig. 2 Simultaneous epiretinal stimulation and recording from the retina [image from Eckhorn 2001].

Fig. 3-5 Sample voltage-duration response functions for an rd10 retinal ganglion cell.

Fig. 6 & 7 Asymmetric voltage responses.3D plots showing asymmetric voltage responses to cathodic and anodic pulses in rd10 retinal ganglion cells.



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[F 57] Generating a diverse repertoire of receptive fields in mouse visual cortex

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In mouse visual cortex (V1), the receptive fields and responses of neurons are highly diverse [1]. Selectivities for the orientation, direction and visual field location of visual stimuli are arranged nearly randomly across local groups of neurons. In this model study we show that to a very good approximation this organization naturally arises in a very large class of generic random recurrent networks without the need of any stimulus dependent plasticity.

We consider a recurrent random network of neurons in V1 layer 4 receiving input from the LGN. Neurons are modeled as firing rate units with a nonlinearity. Assuming the network receives weakly orientation but not direction selective afferent inputs, we show that as a function of average strength of recurrent connections, most neurons increase their orientation selectivity and become also direction selective. For sufficiently strong recurrent connections the distributions of both orientation and direction selectivity closely approaches the experimentally observed distributions in mice [2]. In this regime, neurons show diverse levels of average activity with the majority of cells firing at relatively low rates. Computing the structure of the neurons' receptive fields we find that they are often composed of several ON- and OFF regions reminiscent of cortical simple cells [1]. We discuss the effect of excitatory and inhibitory connections and the robustness of selectivities with respect to different recurrent connections and visual stimuli.

We conclude that a diverse repertoire of receptive fields arises naturally in networks with sufficiently strong recurrent connections. Our results account for the recent observations that neurons in mouse V1 are orientation and direction selective already shortly after the time of eye opening and that dark rearing appears to have little effect on these properties [2].

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[F 58] Multi-Stable Visual Motion Perception

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Perceptual multi-stability is established when the brain fails to reach a single interpretation of the input from the external world. This issue intrigued scientific minds for more than two hundred years. This phenomenon has been found in vision (Leopold & Logothetis, 1999), audition (Repp, 2007), olfaction (Zhou & Chen, 2009) and speech (Warren & Gregory, 1958). Crucial features are similar within and across modalities (Schwarts et al., 2012).

In the visual modality, a number of ambiguous visual patterns have been described such as the Necker cube, motion plaids, and binocular rivalry. Multi-stable stimuli can provide unique insights into visual processing, as changes in perception are decoupled from changes in the stimulus. Understanding of how multi-stable perception occurs might help one to understand visual perception in general.

A key question in multi-stable perception is what the brain processes are responsible in the identification and alternation of the percepts. Some investigators suggest that both top-down and bottom-up processes are involved (García Pérez, 1989) but others argue that multi-stable perception does not need high-level processing but happens automatically as low-level competition between the stimulus features (Akman et al., 2009; Wilson et al, 2000). Furthermore, it is well known that changes in stimulus features can bias perception in one or another direction, (Klink, et al., 2012).

In order to explore this question, we used multi-stable motion stimuli and specifically moving plaids consisting of three superimposed gratings moving in equidistant directions (difference of 120 deg). These stimuli induce the perception of component and pattern motion simultaneously since any two component gratings bind together and are perceived to move in the opposite direction of the third grating component. We modulated properties of the stimuli such as grating speed and size and recorded the responses of human subjects reporting the direction of the single grating using one of three buttons for each direction. Preliminary results show that perceptual dominance is greatly affected by the selection of grating speeds. Grating size did not greatly change the predominance of the different gratings. We find that gratings with speed closer to physiological values have greater probability to be perceived and that gratings with similar speeds tend to group more often than gratings with different speeds. Further manipulations of other stimulus features like contrast and spatial frequency allow parametric variations of the relative probabilities of different interpretations. Our future goal is to use this information to built models of perceptual alternations using probabilistic inference.

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[F 59] Information processing in the Drosophila Olfactory System: From Odors to Kenyon cells

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Insect navigation in natural environments, for instance to seek food or to find a mate of the same species, relies on the efficiency of the insects' olfactory system to detect, memorize, associate and retrieve olfactory information. The olfactory system of Drosophila (including Antennal Lobe and the Mushroom Body) consists only around 3000 neurons (Newquist, 2011) and is thus an ideal model to study the information processing of learning and memory (Masse et al. 2009). Although the system is very simple, experimentally assessing all parameters is still very difficult if not impossible. An important example for information processing is the threshold of coincidence detection in Mushroom Body neurons, the so called Kenyon cells. Here, coincidence detection means that a neuron can detect the occurrence of timely simultaneous but spatially separate input signals. In computational studies (Nowotny et al., 2003; Smith et al., 2008) the number of coincidentally active input neurons that suffice to trigger Kenyon cell firing (i.e. the threshold) is usually set arbitrarily and to our knowledge there exists only one study that addresses this question theoretically (Huerta and Garcia-Sanchez, 2003). As Kenyon cells are involved in associative odor learning (Galili et al., 2011), a detailed understanding of their function and parameters is advantageous for a better understanding of learning and memory in Drosophila.

The quality of information processing in a computational model of the olfactory system can give us a lead on physiological and structural parameters of this system. For this purpose we use an information theoretical measure, the mutual information, which relates to the capacity of information transmission (Paninski, 2003). The greater the mutual information between, for instance, the presented odors and the Kenyon cells, the more information about the presented odor(s) is in the Kenyon cell firing and, thus, the more efficacious is the information processing. When we model the olfactory system with experimentally verified parameters and the environment in such a way that the system has to rely on the discrimination of distinct odors, we find, for instance, a clear optimum in mutual information for coincidence threshold values between 3 and 5. Additionally, non-synaptic modulatory input (Szyszka et al., 2008) modifies the optimal threshold values and can by this compensate dynamic environments or changing motivational states. This study shows the potential of using mutual information to extract basic structural and functional properties of such neuronal systems.

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[F 60] Space-Time receptive fields in the optic tectum of the chicken (Gallus gallus)

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The optic tectum plays a key role in visual processing. While the input from the retina is spatially topographic in the superficial layers, the deeper layers project to the thalamic rotundus with a functional topography. The spatial receptive field is classically defined as the area of space within which the discharge of a neuron can be modulated. The receptive field increases in both size and complexicity along the different layers of the optic tectum. Although the spatial properties of tectal neurons are described in detail for the superficial and deeper layers, a description of the receptive field in the temporal domain is still lacking.

We stimulated the eye with white and black squares on 225 (15x15) positions on the monitor in fast progression while recording extracellularly from single neurons in the optic tectum of chicken. Space-time receptive fields were calculated by reversely correlating the occurrences of each spike with the stimulus present 0-200 ms ago.

Our results show that neurons in the deeper layers of the optic tectum tended to respond stronger to black flashing stimuli than to white flashing stimuli. For some neurons the receptive field was changing over time.

These results suggest that the receptive fields of neurons in the deeper layers of the chick optic tectum show temporal modulation. Whether or not the dynamics of the receptive field are related to the processing of the properties of the visual stimulus remain to be elucidated.

[F 61] Intraparietal sulcus represents audiovisual space

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Previous research has demonstrated that human observers locate audiovisual (AV) signals in space by averaging auditory (A) and visual (V) spatial signals according to their relative sensory reliabilities (=inverse of variance) (Ernst & Banks, 2002; Alais & Burr, 2004). This form of AV integration is optimal in that it provides the most reliable percept. Yet, the neural systems mediating integration of spatial inputs remain unclear. Multisensory integration of spatial signals has previously been related to higher order association areas such as intraparietal sulcus (IPS) as well as early sensory areas like the planum temporale (Bonath et al., 2007). In the current fMRI study, we investigated whether and how early visual (V1-V3) and higher association (IPS) areas represent A and V spatial information given their retinotopic organization. One subject was presented with synchronous audiovisual signals, at spatially congruent or discrepant locations along the azimuth and at two levels of sensory reliability. Hence, the experimental design factorially manipulated: (1) V location, (2) A location, (3) V reliability. The subject's task was to localize the A signal. Retinotopic maps in visual areas and IPS were measured with standard wedge and ring checkerboard stimuli. At the behavioral level, the perceived location of the A input was shifted towards the location of the V input depending on the relative A and V reliabilities. At the neural level, the cue locations represented in retinotopic maps were decoded by computing a population vector estimate (Pouget et al., 2000) from the voxels' BOLD responses to the AV cues given the voxels' preferred visual field coordinate. In early visual areas (V1-V3), the decoded cue locations were determined by the V spatial signal but were independent from the A spatial signal. In IPS, the decoded cue locations were determined by the V and the A spatial signals if relative V reliability was low. In conclusion, our results suggest that the brain represents AV spatial location in IPS in qualitative agreement with reliability-weighted multisensory integration.

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[F 62] Eyes are not cameras: Deriving properties of retinal ganglion cells from the natural input

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The shape of retinal ganglion cells has been related to the statistics of the natural environment under the efficient coding hypothesis. The statistical regularities present in natural images have been measured and neurons have been shown to reduce the redundancy present in these stimuli. This analysis reveals that retinal Ganglion cells' properties can be related to the second order dependencies present in natural images. While such analysis has used the convenient assumption that photographic pictures of natural environments are equivalent to the natural input to the visual system, we here consider quantitatively the influence of the imaging process of a model eye on these statistics. This analysis reveals strong dependencies of the local intensity statistics on the position across the visual field thereby explaining substantial anisotropies of retinal Ganglion cells reported in the literature.

First, we generated artificial scenes with three-dimensional edge elements and quantified the resulting distributions of orientations by applying the perspective projection onto a spherical surface. These distributions show a strong influence of the imaging process on the statistics of the input to the visual system. Secondly, image data from a naturalistic virtual environment was obtained. The second order statistics were computed as a function of eccentricity and radial distance from the center of projection. This analysis confirms strong dependencies of the second order statistics on the position across the visual field. Finally, we repeated the analysis to commonly used natural image databases including the van Hateren database and

quantified the second order dependencies as function of the position across the visual field using a new generalized parameterization of the power spectra.

We conclude by providing a detailed quantitative analysis of the second order statistical dependencies of the natural input to the visual system and making novel predictions about retinal Ganglion cells' receptive field profiles as function of their position.

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[F 63] Baseline states and odour evoked responses of mitral and tufted cells in the awake mouse

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Odour stimuli evoke activity patterns in the olfactory bulb, which are transformed in multiple steps by local microcircuits, before arriving to the cortex. Since inhibitory and excitatory synapses both exhibit short-term plasticity in this network, the baseline activities and properties of odour-evoked responses strongly determine, how much the individual neurons can influence information processing within the olfactory bulb. Therefore, gaining an unbiased picture about the states of different neurons of the network in the behaving animal is essential for understanding how inputs from different channels are transformed.

We have performed blind whole-cell patch-clamp recordings in awake head-fixed mice to gain detailed and unbiased measurements of the spontaneous activity and odour-evoked responses of olfactory bulb neurons. Mitral and tufted cells show great diversity in their baseline resting membrane potentials and spike rates. Both in awake and anesthetized animals, a large proportion (>33%) of cells have very low spontaneous firing rates (<1 Hz). In awake animals, mitral and tufted cells exhibit both inhibitory and excitatory subthreshold and suprathreshold odour-evoked responses. Strong, phasic excitatory responses can be observed in a subset of cells, and these cells have hyperpolarized membrane potentials relative to other cells. Tufted cells exhibit strong excitatory responses more frequently than mitral cells.

Granule cells are characterized by exceedingly hyperpolarized resting membrane potentials (-66.3 \pm 3.4 mV), and the virtually complete lack of spontaneous spikes. In response to specific odours they show prolonged subthreshold and only rarely suprathreshold excitatory responses.

The observed large heterogeneity in base firing rates and odour-evoked responses suggests that different subpopulations of principal neurons, defined by their internal states, have distinct roles in local processing and points to the importance of intracellular recording techniques for studying olfactory networks.

[F 64] Predicting morphological and electrophysiological cell classes in glomerular neurons of the mouse olfactory bulb

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In the olfactory glomerulus, olfactory nerve input is relayed onto mitral and tufted cells, the principal output neurons of the olfactory bulb. A network of juxtaglomerular (JG) interneurons shapes this input, thereby representing the first site of odour information processing. Three morphotypes of JG interneurons have been described: external tufted cells, superficial short axon (SSA) cells and periglomerular (PG) cells. Especially classification of PG and SSA cells has proven to be more difficult than previously thought because of the great heterogeneity of these cell types.

Prompted by this diversity, we aimed to introduce a comprehensive inventory of JG neurons based on morphological and electrophysiological criteria. We therefore performed whole cell patch clamp recordings in acute mouse brain slices in the glomerular layer of the olfactory bulb with post-hoc biocytin labeling in order to relate the electrophysiological behaviour of these neurons directly to their morphology. 15 parameters were measured from average voltage responses and neurolucida reconstructed neurons for >50 JG cells and subsequently tested for their potential discriminatory power. Cells were then subjected to cluster analysis and grouped according to these distinct functional and anatomical parameters. Furthermore, paired recordings of JG neurons were conducted to gain insight about the connectivity rates between specified cell types.

In the future, this classification of JG neurons may serve as a data base for in vivo studies where cell recovery for reconstruction is sparse, facilitating attribution of functional data to a specified cell type when morphology of the examined neuron is unknown. Vice versa, electrophysiological properties may be inferable from morphological features of cells, e.g. as obtained from electron microscopy.

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[F 65] Temporal features of pain evoked spike trains

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A large portion of peripheral nociceptors are unmyelinated C-fibers. Most C-fiber nociceptors are polymodal, responding to multiple noxious modalities such as thermal and mechanical stimuli. Nevertheless, distinct noxious modalities can be dissociated behaviorally [1], raising the question how the nervous system achieves to determine the modality of the stimulus.

To shed light on this question, we investigated the response of C-fiber nociceptors to noxious heat and mechanical stimulation at the earliest stage of sensory processing. We recorded the afferent responses of single-C-fiber receptive fields to both graded mechanical pain and heat stimulation in an in vitro mouse skin-nerve preparation. In accordance to previous reports, we could observe the cells roughly into three classes on the basis of their response characteristics: C-M, C-H and C-MH fibers [2]. C-M fibers responded to mechanical stimuli and not to heat, C-H fibers were sensitive mainly to heat but also responded with lower firing rates to mechanical stimuli. We found that each neuron class exhibited characteristic features in response to each modality. For example, the heat responses in C-H fibers were rather uniform during a heat ramp. Similarly, C-MH fibers mainly responded strongly during the onset and offset of mechanical stimulation with little response in between, while C-M fibers maintained their response during the stimulus duration, albeit with fluctuating firing rates.

These multimodal responses suggest that noxious stimuli may be encoded by a combinatorial code at the earliest stage of sensory processing, instead of having a "labeled line" for each modality. Downstream neurons might exploit the different response characteristics to determine the quality of the stimulus, or to resolve its temporal characteristics.

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[F 66] Heterogeneous short-term plasticity enables spectral separation of information in the neural spike train

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In order to understand how information is processed in the brain, it is vital to investigate how a single neuron responds to inputs that encode multiple signals. As each neuron receives input from many other neurons, such a situation is no exception but the norm. Previous studies have investigated how the transmission of one signal is influenced by others that can be considered background noise [1]. However, when looking at signal gating and processing, we also need to ask how the information content of more than one input signal is reflected in a neuron's output.

The interaction of signals is made complex not only by the nonlinearity of neuron dynamics, but also by short-term synaptic plasticity (STP) [2], which makes the amplitude of postsynaptic response dependent on the recent pre-synaptic spiking history. Synapses can exhibit qualitatively different kinds of STP. For instance, they can be predominantly facilitating or predominantly depressing. Previous studies have investigated the consequences of STP for information processing [3] and particularly pointed out that it can only lead to spectral filtering in the presence of noise or other signals [4,5]. In this study, we consider a scenario in which a neuron receives two stimuli through populations of purely facilitating and purely depressing synapses, respectively. Although such a setting is certainly an idealization, it resembles the difference in short-term plasticity of synaptic connections that parallel fibers and climbing fibers make to a Purkinje cell. Following the rate-coding paradigm, we model the input spike trains as inhomogeneous Poisson processes and use spectral measures such as the coherence to assess information throughput.

We find that STP leads to a spectral separation of information into high and low frequency bands. This spectral separation is based on the respective other signal acting as a kind of noise in the disfavored frequency band. Further, we show that the total information transfer about one signal can still benefit from the presence of the other signal through a form of stochastic resonance.

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[F 67] Evidence for brightness constancy in the mongolian gerbil

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The mongolian gerbil (Meriones unguiculatus) retina is composed of a combination of two cone photoreceptors that are maximally sensitive at a wavelength of 360 nm and 493 nm, respectively, and one rod photoreceptor with a maximal sensitivity at 501 nm [1]. It is the only known mammal that has a rod receptor with a peak sensitivity at longer wavelength than all the cone receptors. Gerbils therefore exhibit photopic vision with a peak sensitivity at shorter wavelength than that of the scotopic mechanism [2]. Since gerbils can be trained to visual discrimination tasks, their visual capabilities can be analysed in behavioral experiments [1,2]. However, so far little is known about visual processing in these animals.

In our behavioral experiments we used a virtual reality (VR) setup with a spherical treadmill that is surrounded by a 360° toroidal screen onto which the virtual environment is projected. This design permits a fixation of the animal such that it can freely rotate around its vertical body axis. The VR setup offers a highly controlled environment for sensory testing. Visual stimuli were presented as a two-alternative choice task using a virtual y-maze in which the animal had to run to the end of the chosen arm to receive a reward. First we trained gerbils to discriminate between bright and dark walls at the ends of the maze arms. In a second set of experiments, we trained the gerbils on the brightness of a central spot relative to its local background. One group of animals had to choose the side with the relative brighter spot and the other group the side with the relative darker spot. Despite differences in the absolute luminance of the stimuli the animals chose the ones with the correct relative brightness. These results are an indication of brightness constancy in the mongolian gerbil.

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[F 68] Theory of reconstruction of stationary objects by the blind cave fish Mexican tetra using flow sensing

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The blind cave fish uses its lateral line organ to sense and navigate its surroundings. By gliding through water the blind cave fish creates a flow field which is disturbed by objects around it. Sensing this disturbances the cave fish can map its surroundings and avoid obstacles.

For the case of a fish swimming along a stationary object with an arbitrary form I present a mathematical method based on a explicit solution of the Euler equations in Fourier space for calculation of the stimulus to the lateral line organ. The method is verified by flow simulations using the boundary element method. I present calculated stimuli for various distances to show how the hydrodynamic image of the object form is dampened with increasing distance.

The functional dependence of the lateral line stimulus given the object form is invertible. Therefore an approximate reconstruction of the object form and flow field can be calculated given only the flow velocities at the lateral line. The complete flow field around the fish can be calculated online and in real time by convolution of the lateral line stimulus with an appropriate kernel. This operation can be performed by a neural net and is therefore a biologically plausible reconstruction mechanism. Plots of simulated flow field reconstructions are shown. The dependence of the reconstruction quality on the distance to the object is analyzed.

This method can also be used by underwater vehicles, e.g. the AUV Snookie from TUM, to passively sense obstacles and avoid collisions with them. An implementation effort is in progress.

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[F 69] A Vision Architecture Based on Fiber Bundles

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We offer a conceptual framework for the construction of an artificial visual system. It serves as basis for the integration of sub-modalities (texture, depth, motion, color, contours, segment markers, illumination, ...) and for autonomous learning. The architecture will decisively reduce the effort necessary to achieve better visual functionality.

Visual sub-modalities are conveniently formulated as two-dimensional sheets of neurons with local connectivity. Such sheets can be formalized as manifolds. The points of a sheet carry internal feature spaces of different dimensionality (texture, e.g., may be formalized as a space of Gabor responses, stereo depth, motion and color as 1D, 2D and 3D spaces, respectively), constituting what mathematicians call fiber bundles. Manifolds admit spatial coordinate frames. Different sets of manifolds carry retinal, object-centered or scene-centered coordinate frames.

Manifolds are connected by mappings (which in the brain are realized by massive sets of axons). These mappings connect not only coordinate points but also feature spaces. For pairs of manifolds with different coordinate frames mappings are dynamical, that is, they change to keep track of relative motion. Dynamic mappings are governed by local control spaces, which encode relative position and motion. Dynamic mappings thus are themselves fiber bundles. Mappings between fiber bundles implement constraints between their feature values. These constraints connect feature values that refer to the same point in the environment. When looking at a point on the surface of a moving body, for instance, a kinematic constraint connects values for depth and motion of the point, translational and rotatory motion of the body acting as latent parameters. The representation of local surface point motion, in turn, serves to dynamically control the mapping between manifolds with retinal and in object-centered coordinates.

Visual input leaves many variables uncertain due to imprecise, ambiguous or absent information. The sub-modality spaces reflect that in terms of more or less broad probability distributions. There is a large number of constraints between different qualities referring to the same point in an image. Many of these constraints are implemented in the mappings between fiber bundles. These mappings typically are forming loops, such that a given variable value is influenced (strengthened or weakened) by several converging mappings. Under the influence of these constraint signals, probability distributions dynamically collapse to delta functions. Thus, the system has contractor dynamics on the short-term level of image interpretation.

The system has contractor dynamics also on the long-term level of learning, converging on detailed circuits in a coarse-to-fine manner. Topological mappings between neural sheets have long been shown to be subject to attractor dynamics. Mismatches in constraint loops are repaired by adapting them to each other. Models of recurring patterns are stored by plasticity in horizontal connections.

[F 70] Nonlinear processing of natural stimuli explains multiple color categories in dichromats

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In color-normal humans, the retina possesses three different cone photoreceptor classes that are sensitive to short (S), medium (M), and long (L) wavelength regions of the visible light spectrum. In the retina of dichromats, one class of cones is absent. It is often assumed that protanopes and deuteranopes, which do not possess M and L receptor classes, respectively, lack the perceptual "red-green" axis (Brettel et al 1997; Sharpe et al 1999). Nonetheless, it has been shown that dichromats use all basic color terms ("red", "green", "blue", and "yellow") to describe their visual percepts (Boynton & Scheibner, 1967; Wachtler et al 2004), which would suggest a greater perceptual dimensionality than one would expect from the spectral dimensionality of the retinal signals. Here, we investigate the possible role of natural image statistics as a basis for color categories in dichromats. We derived human cone response estimates from hyperspectral images and simulated retinal processing of protanopes and deuteranopes by selecting signals from S and M, or S and L cones, respectively. Cone responses were filtered with a center-surround kernel and fed into on and off rectifying channels, corresponding to on and off-center retinal ganglion cells. Independent Component Analyses was performed on the resulting signals to find an efficient representation. Despite the spectrally two-dimensional inputs, the chromatic selectivities of the learned basis functions formed four distinct clusters, corresponding to distinct regions in color space. Our results confirm that the number of perceptual color categories is not restricted by the spectral dimensionality of the photoreceptor input, and indicate that the retinal bifurcation in parallel on and off channels together with the distribution of chromatic signals in natural scenes may enable dichromats to form the same number of color categories as trichromatic observers.

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[F 71] The effect of surface material on colour constancy in real world scenes

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The visual appearance of real world objects depends on their reflectance properties, illumination and geometrical factors. We asked how human colour constancy performance deals with the depth-mesostructure of surfaces, which may provide additional cues or, alternatively, worsen colour constancy. In our experiments we presented samples (circular patches, 90 mm) of different materials (paper, fur, tile, cloth, leather), each mounted on a black sample holder (front 30×15 cm, 60 deg slope) and presented in the middle of a black viewing box ($1.0 \times 1.0 \times 10^{-10}$ 0.8 m). All samples appeared nearly achromatic under daylight. The samples and the box were illuminated by a computer controlled, calibrated LCD-projector (Panasonic PT AE 1000E) which was mounted above the observers' head. The observers (2 male, 2 female) viewed the samples frontally (viewing distance 90 cm). The chromaticity of the standard illuminant was D65, the equiluminant test-illuminants were chosen from one of the cardinal axes. After viewing the samples under the standard illuminant for 15 s, the respective test-illuminant was presented for 5 s. Colour constancy was quantified by a hue-cancellation method, whereby the observer adjusts the appearance of the sample so that it appears achromatic ("gray") under the respective test illuminant. Colour constancy for the different materials was found not to differ significantly, but there was a trend for compensating illumination changes best for fur and worst for tile surfaces, across all illuminants and observers, with paper ranking in the middle. The possible role of depth-mesostructure as a cue for colour constancy is discussed.

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Motor control, movement, navigation

[F 72] Deriving motion primitives from naturalistic hand movements for neuroprosthetic control

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With its 21 degrees of freedom, the human hand is one of the most versatile tools at our disposal and the loss of function in one or both hands constitutes a severe handicap. Whilst state-of-the-art robotic hands achieve, in theory, the same degrees of freedom, achieving comparable dexterity is challenge. Moreover, in neuroprosthetics, the control information has to be decoded from brain-derived signals - a challenge yet to be met. To meet this challenge, we demonstrate how to derive primitives of hand movements so as to significantly reduce the complexity and amount of brain-data required to control natural hand movements. We collected natural hand movement statistics with a portable motion capture glove (CyberGlove Systems LLC (CA) USA) obtained from subjects during their daily-route to inform our understanding of hand motor control. The data is analysed using a novel machine learning technique in order to extract a subset of naturally occurring, elementary motion primitives. These motion primitives enable us to control the hand with significantly fewer variables then the mechanical degrees of freedom, yet enable us to span the complete space of daily encountered human hand movements.

Controlling our hands during everyday tasks requires a specific motor programme for each condition as we need to interact with objects of different shapes and weights, avoiding obstacles and minimising effort. Computing a trajectory for each joint of the hand each time we want to carry out a task would not only be computationally wasteful, but it would also completely neglect the high amount of overlap which exists across daily tasks and the high correlation between the joints of the hand [Belic & Faisal 2011]. Motor primitives on the other hand may allow for complex movements at minimal computational cost and without the need for high-frequency feedback. Extracting these motor primitives from data is, how-ever, an open challenge.

Our probabilistic, local dimensionality reduction technique segments automatically daily tasks (such as opening doors or drawers, manipulating a fork, etc.) into a small number of – occasionally overlapping – local segments characterised by the activity of certain primitives. The activation of motion primitives in sub-tasks is highly reproducible across task repetitions, yet the motion primitives are general, as they are encountered across different tasks. Furthermore, we show that the primitives derived from one subject's data generalise well to other subjects, suggesting that these motor primitives found are not unique to the subject or task, but capture generalised features of how the brain controls the hand across subjects. This enables us to design smart prosthetic hand controllers to simplify mapping user intentions to prosthetic hand actions.

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[F 73] Phase tuning properties of the Local Field Potentials during reach movements in the fronto-parietal areas PRR and PMd of rhesus monkey

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The fronto-parietal reach network in primates comprises the dorsal premotor cortex (PMd) and the parietal reach region (PRR). The spiking activity of neurons in these areas is typically highly selective for the direction of a planned reach movement. For a large-enough population of motor-tuned neurons, the preferred movement direction (PD: direction of highest firing rate) of the individual neurons cover the full range of possible directions [1]. An important consequence of this heterogenity of the tuning properties is that any reach direction can be decoded from the population response equally well. This is a useful property for the design of neuroprosthetic devices, but long-term recording of isolated single neurons is challenging. Local field potential (LFP), on the other hand, represent the activity of a wider range of tissue, and are less sensitive to small electrode displacements or glial tissue growth, making them a more stable and putatively attractive source of information for decoding systems. LFP signals in the fronto-parietal reach areas also have been shown to be spatially selective [2-5]. Yet, LFP-tuning based on signal power can show substantial similarities across channels, which reduces the information content of the population data significantly. In this study we aim to derive movement related information from LFPs, maximally independent from common information across channels, to alleviate this problem.

Two rhesus monkeys were trained to perform a memory-guided center-out reach task to four peripheral, visually instructed target positions while keeping central ocular fixation. LFP power and LFP phase between channels were computed for each time and frequency and analyzed in the movement planning phase following visual instruction. Our preliminary results indicate that not only LFP power, but also LFP relative phase exhibits directional tuning during movement planning. While tuning based on LFP amplitude shows highly similar PD values across channels, the relative LFP phase seems to provide more distinct PD values. This makes LFP phase a potentially highly interesting candidate to be included in decoding system for the design of neuroprosthetic devices.

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[F 74] On the feed-forward control of eye-head coordination

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Large human gaze shifts consist of two parts: one where eye and head move together towards the target and one where gaze has reached the target and is stabilized while the head continues to move. During this stabilization phase, the eyes counter-rotate to account for the ongoing head movement. This counter-rotation could be actively performed as a part of a pre-programmed plan or mediated via a sensory, e.g., vestibular, feedback-loop. Recently, we proposed an optimal control model based on a physiologically consistent criterion, which ensures that the impact of two types of noise, namely signal-dependent and constant (signalindependent) noise, on the variability of the final gaze position is minimized (Sağlam et al., 2011). Our model, which accounts for the main features of eye and head kinematics, shows that the compensatory counter-rotation of the eyes is cost efficient in terms of end-point variability. This suggests that a feed-forward strategy to drive the counter-rotation would be beneficial. To examine whether humans use such a strategy to stabilize gaze, we investigated healthy subjects and labyrinthine-defective patients while they performed large horizontal gaze shifts to a flashed target in darkness. After a block of natural gaze shifts, their head moment inertia was increased by means of a helmet with eccentrically attached masses. Under natural conditions, similar to normal subjects, labyrinthine-defective patients stabilized gaze by eye counter-rotation. In both groups, increasing the head moment of inertia led to head oscillations that originated from the mismatch between the altered head and the control command, which was appropriate for the natural head. The eye movements of healthy subjects compensated for these oscillations. Labyrinthine-defective patients however could not compensate for the head oscillations and thus showed gaze oscillations. This suggests that humans make use of feed-forward control to perform accurate gaze shifts with a counterrotation strategy and, in addition, are able to counteract undesired head movements with vestibular feedback. Although the head oscillations are compensated for by the vestibular feedback, healthy subjects minimize head oscillations within the first 10 trials by updating their motor command. This suggests that the feed-forward plan is pre-programmed without taking the vestibular feedback mechanism into account, probably because the vestibular system cannot perfectly eliminate the impact of head oscillations.

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[F 75] Eye Velocity Gain Fields in the Medial Superior Temporal Cortex

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Lesion studies have shown the involvement of the Medial Superior Temporal cortex (MST) in the generation of optokinetic eye movements (Dürsteler and Wurtz, 1988). Most of the neurons in this cortical area show activity when presented with a moving large-field visual stimulus. This visual response is modulated by eye movements (Bradley et al., 1996). However, the exact interaction between the retinal image velocity and the eye velocity signals is not yet fully understood. Using a novel information-theoretic approach for determining neuronal tuning functions (Brostek et al., 2011), we show that the majority of MSTd neurons exhibits Gain Field-like tuning functions The degree of modulation of the visual response by eye velocity differed across the population. These physiological findings were reflected by emergent properties of intermediate layer units of a neural network model trained to perform coordinate transformation. MSTd Gain Fields may thus constitute an intermediate step for transforming retinal image velocity to a head- or space-centered stimulus velocity signal.

Acknowledgements

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[F 76] Neural Representation of Space: Relation between one- and two-dimensional Environments.

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In the medial entorhinal cortex of rats, a special type of neurons, called grid cells, can be found. The activity of these cells correlates with the animal's position in space, such that it is high when the rat is in certain regions, called firing fields, and low when it is elsewhere. In two-dimensional environments, the firing fields are arranged similar to the lattice points of a hexagonal Bravais lattice. In environments where the rat's movements are restricted to one dimension, the layout of the fields is less periodic and depends on the direction the rat is running in. It is an open question whether the structures of firing fields in one dimension are cuts through two-dimensional hexagonal lattices or if the neural representation of space changes fundamentally for one-dimensional environments.

To solve this question, we compare the firing patterns for both directions on linear tracks and show that their similarity does not depend on the spatial distance between the paths. This suggests that the firing pattern on the linear track is not a simple cut through a two-dimensional hexagonal map.

[F 77] Grid cells discharge with less variability than place cells

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The brain's representation of external space is reflected in spatially modulated firing of hippocampal place cells and grid cells in the entorhinal cortex (EC). Experiments in hippocampus suggest that varying levels of attention underlie the high variability of place cells [Fenton et al. 2010]. Whether the same is true for grid cells, is an open and intriguing question. To tackle this question, we study the variability of grid-cell spiking for runs through firing fields, both on linear tracks and in the open field, using recordings that were made available by E. Moser (Trondheim). By analyzing the factors leading to variability, we find that most of the variability on the linear track can be attributed to trial-to-trial variability of the rat's path, while the spatial firing map remains stable. This result is in stark contrast to the much higher variability of place cells [Fenton et al. 2010; Fenton and Muller 1998; Jackson and Redish 2006]. Fenton and colleagues report that the variability in hippocampus depends on the context, with the lowest variability occurring during tasks in which the animals had to navigate precisely [Fenton et al. 2010]. The variability we find for grid cells is lower than this minimum. This lends additional support to the hypothesis that the variability in the hippocampus comes from other sources, such as the lateral EC [Rennó-Costa et al. 2010], and not from the grid cells in the medial EC.

[F 78] A Physiologically Inspired Model for Global Remapping in the Hippocampus

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Population activity patterns (place maps) in the hippocampus change dramatically if the animal is exposed to the same maze in different lab environments (global remapping) [Leutgeb et al. 2007, Science]. Such decorrelated patterns are essential for many models of associative memory: they sustain flexibility and allow many patterns to be stored. This remapping could have its root in an observed shift of grid cell firing patterns: During hippocampal remapping the spatial activity pattern of grid cells undergoes locally coherent rotations and translations [Fyhn et al. 2007, Nature], but it is not known whether this coherence extends over different spatial modules, which are anatomically separated within entorhinal cortex [Witter, Moser 2006, Trends in Neurosciences]. Also, the environment's size and shape are of importance for the remapping. We studied the influence of these realignments of grid cells on the formation of place cell firing patterns in the hippocampus and find that global remapping can indeed be caused by realigning a realistic number of grid cell modules. Also the size of the environment (relative to the grid field's period length) has influence on the remapping. To support these hypothesis, we employed a model with physiologically plausible connections in which grid cells give rise to place cells for a single environment [de Almeida et al. 2010, Hippocampus]. We investigate the behavior of the place cell output layer in response to incoherent rotations and translations of the spatial patterns in the grid cell modules in different sized environments, while leaving the synaptic weights from the grid to place layer unaltered. Simulations of the full model with noise create rate remapping for small shifts, leaving strong spatial correlations, while larger shifts produce strong rate fluctuations as well as spatial decorrelation of place fields. This recreates the findings in experiments by Fyhn et al. [Fyhn et al. 2007, Nature]. Furthermore the population vector decorrelation depends on the size of the environment, such that smaller shifts suffice to achieve the same decorrelation in larger environments.

[F 79] Mechanisms of human place recognition

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Human place recognition can be based on visual 'snapshots' alone, i.e. on raw images lacking object information (Gillner et al., 2008). The basic underlying mechanism consists in matching of the current input image with a stored snapshot obtained at an earlier visit of the goal location. Recognition will occur when the matching error decreases below some threshold, i.e. at the intersection of the approach trajectory with the 'confusion area' of the place (Franz et al. 1998a). This mechanism predicts recognition points which are systematically offset towards the approach direction. If the stored snapshot is updated at each visit (as might be useful in dynamic environments), we expect increasing offsets for repeated approaches from a fixed direction. Here we analyse the confusion area of humans performing a simple place recognition task in virtual reality and present a quantitative model of the results.

The experiment is realised in desk top virtual reality using a 30° Monitor. Subjects started in front of a pond and had to move to a goal on the other side using a plus-shaped boardwalk. At the crossing, turns to the left or right were required to perform the task. In the experimental phase, i.e. after training, the boardwalk was covered by ground fog. With the boardwalk invisible, the only way to find the turning point was to navigate according to four distinguishable landmarks, i.e. rocks or patches of reed appearing within the pond. All four approach directions were used in the trial sequence. Starting points were repeated up to two times to test for increasing recognition offsets.

Our results show a significant offset of recognition points towards the approach direction, but no significant change of recognition point offset with prior approach direction. In addition, we found a significant systematic error based on landmark configuration, displacing the recognition point in the direction of the landmark centre of gravity.

Effects of landmark configuration are not expected in plain snapshot navigation, but quantitative models are needed draw strong conclusions. We developed a scalable place recognition model which is based on the snapshot approach but at the same time is able to incorporate object-based cues such as landmark configuration. Model features include: (i) The current snapshot entering the matching procedure depends on the instantaneous view but also information from previous views and spatial updating. This is accounted for by a working memory stage containing a panoramic snapshot with varying resolution ("visual array"). (ii) The reference snapshot is assumed to be a panoramic view at constant resolution. (iii) The matching stage is based on the "morphing" algorithm (Franz et al., 1998b). (iv) Different types of place codes (raw snapshot, landmark center of gravity, etc) are generated by applying different amounts of visual pre-processing to produce the memorized snapshot. With this model, we will be able to identify the place-codes underlying the subject's performance.

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[F 80] A Virtual Musculoskeletal Model for Variable Compliance and Joint Stabilization of a Walking Hexapod

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It has long been acknowledged that muscles work as motors. In fact, they can also perform as dampers, springs, and struts. While under tension or during motion, they may lengthen, shorten, or remain the same. Due to their elastic property, they can generate compliant motions and achieve joint stabilization. These two characters facilitate interactions between robots and the environment. For example, compliant joint motions can prevent robots and human from damages owing to the 'soft' property.

Many traditional methods imitate muscle functionalities to produce compliant joint motions and achieve joint stabilization. Series Elastic Actuators (SEAs) enable robots to lower impact force and achieve joint stabilization by physical spring and damper mechanisms. But tunable SEAs are usually bulky, heavy and mechanically complex. This is unsuitable for small walking robots. A software control method is an alternative for joint compliance and stabilization. Active compliance uses force control (also known as impedance control) to change stiffness of actuators for compliance and stabilization of the robots. Active compliance, however, relies on position and torque feedback. This property slows down joint reactions to external loads. In addition to active compliance, VMC (Virtual Model Control) is another simple force control approach. It applies simulations of virtual mechanical mechanisms to yield real actuator torques. The torques produces compliant behaviors as if physical mechanisms are connected to the real robot. However, its major disadvantage is that many parameters need to be tuned by hand, which mainly limit structures of robots and over-depend experiences of developers.

In this study we propose a virtual musculoskeletal model for a biologically inspired six-legged walking machine, i.e. AMOS (Advanced MObility Sensor driven-walking device). This virtual musculoskeletal model enables AMOS to easily adjust joint stiffness and reduce leg contact force when confronted with external disturbances. Each AMOS joint can be virtually driven by a pair of antagonistic mechanisms. 'Virtual' here means joint can mimic antagonist muscle behaviors without physical spring and damper components. With external excitation, these virtual mechanisms drive joints as if the joint is driven by agonist and antagonist muscles. The agonist and antagonist muscles are mathematically modeled by a spring-damper mechanism.

The AMOS joint stiffness can be variably tuned by a stiffness coefficient when being excited by a sensory feedback, e.g. a contact force feedback. This simple stiffness regulation differs from mechanically complex SEAs and sophisticated VMC (Virtual Model Control) controllers. Moreover, only a contact force feedback can excite joint movement, which distinguishes from active compliance overdepending on position and torque feedback. The virtual musculoskele-tal model has been tested on AMOS leading to variable compliance with simple tuning, joint stabilization to external perturbations (e.g. hand pushing and releasing AMOS body, object dropping on AMOS body), as well as a reduction of contact force during AMOS walking.

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[F 81] Object or grip type representation? A comparative population study of macaque hand grasping areas M1, F5, and AIP

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Primate grasping movements are complex behaviors that rely largely on cortical control. In particular, the hand area of primary motor cortex (M1), the ventral premotor cortex (area F5), and the anterior intraparietal area (AIP) are crucial for the planning and execution of hand and finger movements(Rizzolatti and Luppino, 2001).

To investigate the visual and motor representation in these areas, we trained a macaque to grasp 44 different objects in a delayed grasping task (Fig.1). The monkey first placed its hand at rest and fixated a red LED before a randomly selected object was presented for grasping (cue epoch). The animal then had to withhold movement execution until, after a short delay (planning epoch), the fixation LED dimmed. Spiking activity was recorded on 192 channels using six chronically implanted micro-electrode arrays (Microprobe Inc.)(Townsend et al., 2011); arm and finger kinematics (27 degrees of freedom) were recorded with a novel instrumented glove based on electromagnetic sensors (Schaffelhofer and Scherberger, 2012).

To correlate hand kinematics with activity of the neuronal population, we extracted the mean firing rates of all recorded cells and determined the principal components of the neuronal population activity in specific task epochs. To describe the difference of the neuronal population in the 44 grasp conditions, we performed a cluster analysis and calculated the Mahalanobis distance (MD) between individual pairs of grasp conditions. Similarly, the same analysis was applied to the population of joint angles (27 dimensions) of the hand kinematics. Expressing all MDs in a distance matrix then allowed correlating the neuronal population activity in AIP, F5, and M1 with each other as well as with the hand kinematics (Fig. 2).

Computing the Pearson Correlation coefficient (r) revealed that M1 reflects hand kinematics best during motor execution (r=0.64) whereas F5 showed the highest correlation in the planning epoch (r=0.5). In comparison, hierarchical clustering revealed a predominant tuning of AIP to visual object features. Furthermore, between-area correlations are consistent with a strong collaboration of AIP and F5 for visuomotor transformation and of F5 and M1 during motor execution. These results demonstrate for the first time clearly distinct roles of AIP and F5 at the population level.

Figure 1: Monkey grasping for a wide range of different objects presented on a turntable within a delayed grasping task.

Figure 2: Correlation diagrams



Figure 1

Figure 2

Acknowledgements

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[F 82] Motor equivalence as a method to reveal movement invariants/primitives

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How do humans avoid obstacles while making arm movements? Are such complex movements generated by scaling and combining movement primitives? And how may we detect such invariants/primitives of movement?

To approach these questions we investigate naturalistic 3D human arm movements in tasks that involve moving an object toward a target while avoiding obstacles. We vary the position of the obstacle (near vs. far obstacle condition) along the path to the target and obstacle height. In previous work, we examined the end-effector spatial path finding evidence for two movement primitives: the transport primitive (movement from start to target position) and the lift/descend primitive (movement perpendicular to transport within the movement plane) (Grimme et al, 2011).The lift component was invariant in near vs. far obstacle conditions, while the transport component adapted to obstacle-induced perturbations.

Here, we extend this research by an analysis at the level of the joint angles. Motor equivalence can be defined as reorganization of movement components following a perturbation that preserve important performance variables such as the end-effector path in reaching. We apply an analysis of motor equivalence that is based on the concept of an Uncontrolled Manifold (Scholz & Schöner 1999) to investigate how the joint configuration changes in the two movement primitives when obstacles are either near or far from the start position.

We find motor equivalence in the lift component while changes in joint configurations due to different obstacle distances strongly affect the transport component. This non-motor equivalence in the transport primitive was scaled with growing obstacle height.

The motor equivalence in the lift component results from an invariant lift component in endeffector space accompanied by variable joint configurations that are due to the perturbed transport component. Our investigations show that the motor equivalence analysis is useful to characterize movement invariants/primitives.

Overall, the results of the motor equivalence analysis support our previous results at the end-effector level that naturalistic 3D obstacle avoidance movements are surprisingly regular. Their kinematic structure can be understood in terms of independent and invariant movement primitives: lift/descent and transport.

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[F 83] Adaptive matched filter for egomotion estimation

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The so-called tangential cells in the lobula plate of the fly are sensitive to motion stimuli. The local sensitivities and preferred motion directions of these cells can be represented as vector fields that resemble flow fields generated by egomotion. This finding has led to the hypothesis that the tangential cells function as matched filters for egomotion estimation. However, flow fields generated by translation depend also on the depth structure of a scene. In previous matched filter approaches to egomotion estimation, the statistics of the environmental distances had to be known a priori to set the parameters of the estimator. Here we propose an adaptive matched filter model that can react to changing global characteristics of the environmental distances, which are described through spherical harmonic functions. We show that if the field of view covers the whole sphere, only the dipole and the quadrupole moments contribute to the solution of egomotion estimation. For the field of view of flies that does not completely cover the viewing sphere these moments are by far the dominanting elements. This finding is reflected in our model, which solves the egomotion problem in varying environments while representing the depth structure by just nine parameters. We present results from a simulations with artificial flow fields and compare the proposed model with a previously described matched filter approach and a technical solution.

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[F 84] Internal forward models with efference copies for state estimations in adaptive hexapod locomotion

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Animal locomotion mechanisms seem to largely rely not only on central pattern generators (CPGs) and sensory feedback but also on internal forward models [1]. These components are used in different degree in different animals. In general, CPGs generate basic rhythmic patterns which can be considered as motor commands. They are usually shaped by sensory feedback (like, proprioceptive signals) to achieve appropriate coordinated movements during walking. Besides, the internal models transform motor commands copied (efference copies) within the central nerve system (CNS) into expected sensory inputs (or sensory prediction). This allows to compare the expected ones to the actual incoming sensory signals for state estimations. As a consequence, the internal models with efference copies together with local leg control [2] allow animals to adapt their locomotion to deal with environmental changes or during traversing over difficult terrain.

Based on these biological findings, we extend our existing neural CPG-based locomotion control of the hexapod robot AMOS [3] by introducing six internal forward models here. Each of them serves to transform a motor signal generated by a CPG (efference copy) into an expected sensory signal (i.e., foot contact signal) of each leg. Utilizing the discrete-time dynamical properties of a recurrent neuron (e.g., hysteresis effect) for signal transformation, each forward model is configured as a single recurrent neuron [4] with synaptic plasticity. Gradient descent learning is applied to adapt its presynaptic and recurrent weights. This way it can learn online to correctly transform the motor signal into the expected foot contact signal of each leg during normal walking (e.g., walking on flat surface). After learning the outputs of the learned models (i.e., expected foot contact signals) are used to compare with the actual incoming foot contact signals for the estimation of its walking state. The differences between the expected and actual sensor values are used to adapt leg motion (e.g., extension or elevation) through local leg control mechanisms. As a result, this neural closed-loop controller with the neural forward models enables the robot to perform a variety of locomotion behavior including insect-like walking and climbing. In addition, it allows the robot at the same time to adapt its locomotion to deal with terrain changes, losing of ground contact during a stance phase, or hitting obstacles during a swing phase (see supplementary video at http://www.manoonpong.com/BCCN2012/InternalForwardModels.wmv). We believe that all these biologically inspired components (i.e., CPG, internal forward models, and local leg control mechanisms) are at least important parts for developing robust and adaptable walking robots.

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Learning, plasticity, memory

[F 85] **Remapping-like changes in place field activity through dopaminergic action**

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The phenomenon of hippocampal remapping has received sustained attention ever since its discovery. Remapping is striking because usually, most place cells in the rodent hippocampus show stable response properties over weeks and more. However, strong changes in the environment lead to global remapping, whereby most place cells change their firing fields drastically or shut down altogether, while new, previously silent cells become active. While the kind of environmental cues that elicit remapping have been studied in detail, it is still unclear what kind of internal signal prompts the otherwise so stable place representations to change all at once. Dopamine is often discussed as a potential novelty signal and here we investigated the effects of dopamine agonists on place cell activity. To this end, we recorded the spatial response properties of pyramidal cells in the dorsal hippocampus of rats while they freely explored an environment. Systemic injection of the nonspecific dopamine agonist apomorphine, but not of saline, led to changes in place field locations of many cells, similar to changes observed in global remapping. In further experiments, the dose-dependence, role of the specific receptor subtypes, and the effect of dopamine antagonists were examined. The finding that dopaminergic action induces remapping-like place field changes shows that global remapping can occur in the absence of environmental changes. Pharmacological manipulation opens up new avenues to analyze the mechanisms underlying global remapping.

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[F 86] The distribution of synaptic strengths and possible mechanism for synaptic plasticity arise in the model of inter-spine molecular transport of PSD-95 molecules.

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The scaffolding protein PSD-95 is the most abundant molecule in the post-synaptic density (PSD) located in the spine, where it forms a cluster to which the membrane synaptic receptors are bound. The amount of PSD-95 molecules inside an individual spine determines the size of the PSD cluster and is strongly correlated with the synaptic strength. It is observed that these molecules have high turnover rates and that neighboring spines are constantly exchanging individual molecules.

Here we present a model of non-equilibrium molecular transport between spines in neuronal dendrites describing the dynamics of PSD-95 molecules. When the molecules interact with each other inside the spines of a dendrite due to binding to PSD cluster, the corresponding trapping times inside the spines depend on the size of the PSD cluster and become much

longer than the diffusion times in the dendritic shaft. This allows us to obtain the stationary distributions of PSD cluster sizes that emerge from such inter-spine molecular dynamics. Our results suggest that spines are competing for a shared pool of PSD-95 molecules in a weak "winner-take-all" regime that is restrained by the finite lifetimes of the PSD-95 molecules.

Furthermore, we propose that in the model non-equilibrium inter-spine dynamics of PSD-95 molecules can provide the basis for locally controlled synaptic plasticity through activity-dependent ubiquitination of PSD-95. Thus local rapid destruction of a fraction of the PSD-95 cluster can lead to its growth due to self-organization phenomena, providing the molecular mechanism for maintenance of late long-term potentiation (LTP) required for synaptic plasticity. In this scenario, the geometrical filling fraction of the PSD cluster is suggested to be an important characteristic of the synapse that carries the information of the previous LTP events.

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[F 87] Effective and functional connectivity patterns during contextual fear conditioning

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In contextual fear conditioning, an initially neutral context-stimulus (CS) is paired with an aversive unconditioned stimulus (US) which evokes fear or anxiety responses. Repeated pairings of the CS with the US result in an association of both stimuli that causes the occurrence of the CS alone to elicit an emotional response. It has been suggested that neocortical regions are able to represent the single features of the context, whereas the implementation of features into a unitary conjunctive representation necessitates the binding capacity of the hippocampus. We carried out a pilot study with young healthy subjects to test a novel paradigm, which utilizes two cue-array contexts with identical physical properties, only differing in the arrangement of context components to force subjects to uncontaminated contextual processing. T-contrasts revealed sustained BOLD activity of the electrical-shock-associated context, relative to the non-shocked context (CS+unpaired > CS-), in right rostrolateral prefrontal cortex and bilateral insula. Transient activity for the same contrast was found in regions of the right hippocampus and the right amygdala. An analysis of functional connectivity showed that the posterior hippocampus was significantly stronger connected to the right superior orbital gyrus during unpaired CS+ contexts relative to CS- contexts. An additional analysis of effective connectivity revealed that activity of the right anterior hippocampus influences activity in the amygdala and the primary somatosensory cortex (Brodmann areas 3a and 3b) as a result of its interaction with the electrical-shock-associated context. A functional decoupling between hippocampus and prefrontal cortex has been suggested as one of the major dynamical signatures of depression and age-related cognitive decline. Therefore we started to investigate healthy elderly subjects and depressive patients using the same paradigm. It is expected that, compared to young individuals, elderly subjects will be hampered in their ability to differentiate the visually similar contexts, resulting in a diminished contingency awareness and weaker connection of hippocampus to amygdala and prefrontal cortex. Furthermore, depressive subjects are expected to show a stronger tendency to overgeneralize the aversive electrical stimulus (CS+) to both context-images relative to healthy controls. We expect depressed patients to show hyperactive amygdalae which are weakly connected to hippocampus, anterior cingulated cortex and prefrontal areas with a similar impairment of identifying the correct US-CS+ association. The data will serve at constructing and validating biophysically and anatomically detailed models of the prefrontal cortex and hippocampus that will serve to investigate these relationships. In a further step, dynamical and behavioural predictors will be derived from highly realistic model simulations for additional imaging experiments in humans.

[F 88] Separating spiking input correlation structures: an inhibitory STDP approach

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Correlations of activities in networks of neurons are believed to take part in representations of sensory or cognitive processes [1]. Detecting correlation patterns in the input is therefore of functional importance in neural computations. Synaptic plasticity enables neurons to "learn" structure in input signals and/or to become selective to specific input pathways. In neural network models, Spike-Timing Dependent Plasticity (STDP) can capture correlations at a short temporal scale [2].

Though this issue has been addressed in networks of excitatory neurons, it is not well known whether STDP can support detection of correlation that is shared between excitatory and inhibitory inputs. Recent investigations have just begun to address the issue [3-4].

In particular, a recent investigation indicated that combined excitatory and inhibitory (Hebbian) STDP can lead to globally balanced inputs, while correlation structure in excitatory inputs remains detectable [4]. Moreover, the study revealed that the presence of inhibition increases competition between subgroups of correlated excitatory inputs.

With numerical and analytical methods, we extend on their findings by addressing the interplay between the postsynaptic response to correlated input structure and different STDP learning curves for inhibitory synapses. Using a single neuron model (Fig. 1), we examine conditions with differently correlated subgroups under which nontrivial structure in excitatory and inhibitory synapses is developed. For instance, cases where subgroups in excitatory and inhibitory inputs share correlation (Fig. 1 A) or are independently correlated (Fig. 1 B) are addressed.

A preliminary result is shown (Fig. 2). We can quantify the structure development in the synaptic weights by the ratio between correlated and uncorrelated weights. If the ratio is >1, structure in synaptic weights is developed. The top left figure shows that for shared correlation between excitatory and inhibitory inputs, structure is developed for both excitatory and inhibitory synapses, if correlation is weak (c = 0.1). However, if correlation is increased, or if correlation is independent between excitatory and inhibitory inputs, no structure is developed for inhibitory synapses. We ask how excitatory and inhibitory STDP can cooperatively isolate multiple correlation sources to elucidate the importance of inhibitory plasticity in detecting correlation patterns in neural activities.



Figure 1

Figure 2

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[F 89] From reinforcement learning to automaticity: How basal ganglia pathways are superseded by cortico-thalamic fibers

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Basal ganglia (BG) contain distinct pathways that differentially process cortical signals and relay their outputs to thalamus. Synaptic learning within these pathways is differentially modulated by dopamine, a neurotransmitter that encodes reinforcement signals [1]. As reinforcement learning converges and gives rise to automatic performance of a task, BG activity becomes less specific [2], while 'shorter' fibers are assumed to bypass BG circuitry to ensure fast responding [3].

In a computational framework, we show how the pathways' differences in dopaminergic modulation of synaptic plasticity explain why they develop distinct functions. Novelly, we do not pre-specify connectivity in BG pathways but let the model self-organize. We apply our framework to a stimulus-response task that requires learning, automatic performance and relearning of stimulus-response associations. Thereupon, we observe the 'direct' BG pathway to learn facilitation of appropriate responses, the 'hyperdirect' pathway to learn inhibition of inappropriate responses, and the 'indirect' pathway to learn inhibition of previously correct responses during re-learning of stimulus-response associations. Cortico-thalamic fibers develop when BG pathways have converged on a solution; they ensure fast automatic responding and thereby supersede BG activity.

Our computational framework accounts for recent empirical findings on how brain processing changes from reinforcement learning to automatic responding (e.g. [2,4]). It furthermore explains re-learning of automatic stimulus-response associations and thereby expands previous theoretical accounts of automaticity [3].

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[F 90] Neuromodulation in spiking networks through short-term changes in synaptic transmission

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We present our model for modulated synaptic transmission, in which the gain of each synapse is directly influenced by a global concentration of some neuromodulatory signal (e.g. Dopamine). By changing the synapse-local properties of information transmission, we achieve a network-level learning effect that favours the learning of polychronous input patterns at high levels of the neuromodulator, and penalises or even resets learnt patterns at low neuromodulator levels. At medium (baseline, tonic) levels of neuromodulation, network learning smoothly switches from reinforced to unsupervised learning, that is only dependent on the innate time structure of the incoming patterns.

Neurons in the network are able to re-tune from their unsupervisedly learnt pattern preference to another input pattern that repeatedly correlates with high global levels of the neuromodulator.

As the modulatory factor needs to be present during the arrival of inputs, we do not approach the distal reward problem through our model, but assume for the case of delayed reward an involvement of hippocampus and cortical working memory instead of direct application of reward into an STDP rule.

The presented effect does not rely on any direct modulation of synaptic modification (threefactor STDP), so standard (asymmetric) STDP rules can be used. However, our rule for modulated synaptic transmission can be combined with existing rules for modulated synaptic modification if wanted.

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[F 91] Consolidation of synaptic patterns from proximal into distal dendrites of a hippocampal CA1 pyramidal neuron

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The initial formation of declarative memories depends on hippocampal circuits. On a timescale of weeks or longer, the newly formed memories gradually become independent of the hippocampus and more reliant on neocortical networks. Little is known about how this process of memory consolidation takes place.

We study the process of memory consolidation at the level of a single neuron, specifically focusing on pyramidal neurons in the hippocampal CA1 area. These cells receive Schaffer collateral (SC) input from the CA3 area at the proximal dendrites, and perforant path (PP) input from entorhinal cortex at the distal dendrites. Both pathways carry sensory information that has been processed by cortical networks and that enters the hippocampus through the entorhinal cortex. We hypothesize that memory patterns are initially stored in the recurrent CA3 network and proximal dendritic SC synapses during an exploration/online-learning phase; during a subsequent consolidation phase, these CA3/SC synaptic patterns are then partly copied to the PP synapses in the distal dendritic tuft.

Using numerical simulations and mathematical analysis of the input processing by CA1 pyramidal neurons, we show that this consolidation process occurs as a natural result from the combination of (1) spike timing-dependent plasticity at SC and PP synapses, (2) the integration of SC and PP inputs in electrotonically segregated compartments of the CA1 pyramidal neuron, and (3) the temporal correlations between SC and PP synapses: the SC input is delayed compared to the PP input (5-15 ms), because the indirect SC pathway has to pass through dentate gyrus and CA3 before reaching CA1.

We demonstrate that during the ongoing cycles of learning and consolidation phases, the memory patterns stored in the PP path constitute a low-pass filtered version of the memory patterns stored in the SC path: information that has been stored most recently in the SC path is represented most strongly. The information stored in PP synapses is gradually replaced due to the consolidation of new memories. The memory pattern in the PP path decays with a time constant that is determined by the degree to which the SC path memory is copied during a single consolidation phase. In turn, this fraction is primarily set by the learning rate of the PP synapses, together with the duration of the consolidation phases and the pre- and postsynaptic firing rates.

Our work proposes a novel, single-neuron mechanism that implements one step in the process of memory consolidation. We suggest that a cascade of such steps underlies the gradual consolidation of memories from hippocampus to neocortex.

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[F 92] The N400 component of the ERP as semantic network error: Insights from feature-based connectionist attractor models of word meaning

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The N400 component of the event-related brain potential (ERP) is widely used in research on language and semantic memory. Although the component's relation to semantic processing is well-established, the specific computational mechanisms underlying N400 generation are currently not clear. We explored the mechanisms underlying the N400 by examining which parameters in a connectionist model of word meaning most closely covary with N400 amplitudes. The model has 30 input units representing word form that map onto 2526 directly interconnected semantic feature units representing word meaning, according to semantic feature production norms. We simulated a number of N400 effects obtained in human empirical research: influences of semantic priming, lexical frequency, number of features (NOF; also possibly a proxy for concreteness), and repetition, as well as influences of frequency and NOF on repetition effects. Cross-entropy error values were consistently in the same direction as N400 amplitudes. Like N400 amplitudes, error values were larger for low frequency words, larger for words with many features, and decreased for semantically related target words as well as repeated words. Furthermore, the repetition-induced decrease was stronger for low frequency words, and for words with many semantic features. In contrast, there was less of a correspondence between total semantic activation and the N400. Like N400 amplitudes, activation was larger for words with many semantic features. However, activation also tended to increase with frequency, repetition and semantic priming which is opposite to well-established N400 results, and may be more in line with increased activation facilitating decision latencies in lexical and semantic tasks. Our results suggest an interesting relation between N400 amplitudes and error values in connectionist models of meaning. In psychological terms, error values in connectionist models have been conceptualized as implicit prediction error, and we discuss the possibility that N400 amplitudes may reflect this implicit prediction error in semantic memory.

[F 93] Single-trial coupling of EEG and fMRI during recognition reveals the generators of ERP old/new effects

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Recognition means the ability to decide if information was encountered previously. This can be featured with additional details from the encoding episode or not. Various behavioural, electrophysiological and imaging studies have pinpointed that two differential processes are involved in recognition memory, namely recollection and familiarity. Recollection describes the conscious retrieval of contextual information about a specific episode, while familiarity means only a feeling of knowing without additional contextual details. These processes may be differentiated electrophysiologically by means of event-related potentials (ERPs). In contrast to correctly rejected new items, items correctly classified as old yield a more positive ERP deflection which is termed old/new effect. One earlier frontally localized old/new effect emerging from about 300 ms after stimulus onset relates to familiarity processing whereas a functionally distinct later parietal effect is associated with recollection. Functional magnetic resonance imaging (fMRI) has revealed that within the medial temporal lobe, extrahippocampal cortical areas and the hippocampus proper support independently recognition based on familiarity or recollection, respectively. In order to examine the relation between hemodynamic changes and the modulation of ERP old/new effects during memory retrieval, we conducted a simultaneous EEG-fMRI study in 16 young healthy volunteers. Standard ERP analvses revealed an early mid-frontal and a later parietal old/new effect, presumably associated to the differential use of familiarity and recollection during recognition. FMRI old/new contrasts showed activity modulation in the hippocampus as well as in the precuneus, the retrosplenial cortex and the medial frontal gyrus. An EEG-informed fMRI analysis was performed to relate single-trial ERP amplitudes to hemodynamic signal changes, thus accounting for trial-to-trial fluctuations. By orthogonalisation to the standard stimulus-coding predictors the variance explained by the trial-to-trial modulation of the old/new effects was isolated. The results complement rare data from intracranial ERP recordings and patient studies. The results from this multimodal fusion analysis will be embedded into biophysically and anatomically detailed models of hippocampal-prefrontal interaction which will in turn generate predictors for the outcome of future imaging studies.

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[F 94] Continuous variable models of voltage-based STDP

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Voltage-based spike-timing dependent plasticity (STDP) [2] can explain the results of many plasticity experiments that were previously not adequately accounted for by spike-pair based STDP models such as frequency dependence [6] and triplets dependence [3]. Recently, we have shown that anti-hebbian plasticity at distal dendrites of layer 5 pyramidal neurons [4] can be accounted for using a generalized form of the original voltage dependent plasticity model [1], where the pre-synaptic spike train in the long term depotentiation (LTD) component is replaced by its low pass filter. However, these models use a mixture of discrete (pre and post-synaptic spike trains) and continuous variables (low pass filter of membrane potential) to ensure spike-timing specificity. Here, we investigate whether models based purely on continuous variables can have the same explanatory power as the previously developed discrete-continuous models.

We test their ability to account for the sign and amplitude of synaptic plasticity in frequency, triplets and anti-hebbian protocols. A model inspired by Shouval's calcium concentration model provides a good account of all three experiments and is less complex than the original formulation [2] of voltage-based STDP.

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[F 95] A spiking neuronal network model of fast associative learning in the honeybee

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Numerous experimental studies on classical conditioning in the honeybee (Apis mellifera) have provided insights into the physiological processes of olfactory learning and memory formation. On the basis of these findings, several theoretical studies have proposed different model hypotheses for sensory processing and learning in the insect brain. However, the actual dynamics of associative learning as evident from behavior in individual animals is typically neglected. For the honeybee, recent analyses suggest that individual animals learn to associate between odor and sugar reward within a single trial (Pamir et al. 2011).

Here we present a spiking neuronal network model which processes sensory stimuli defined by classical conditioning protocols of the proboscis extension response in the honeybee. We compare and implement different hypotheses on physiological mechanisms that support fast associative learning in their ability to reproduce both behavioral and physiological constraints as observed in experiments. The behavioral constraints of our model are defined by the learning performance of individual animals during absolute, differential, backward and trace conditioning. Physiological constraints comprise several recordings of neuronal activity from different processing stages along the sensory-to-motor pathway.

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[F 96] A biologically realistic approach for learning inverse motor-sensor models.

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Song birds learn to reproduce a memorized tutor song from sensory experience. This implies that they learn to create precise patterns of muscle activations which reproduce that same sensory impression. This phenomenon is mostly studied within the framework of reinforcement learning. Recently a different framework for bird song learning was proposed by Ganguli and Hahnloser (Cosyne 2011). They propose that birds learn by establishing an inverse model that maps the sensory representation of the song to the corresponding motor patterns. By this inverse mapping, the bird can then produce the tutor song without further training by feeding the previously formed sensory representation of the tutor song into the inverse model. In contrast to reinforcement learning this mechanism can explain one-shot-learning of sounds as observed in humans or parrots. Furthermore, the training of an inverse model is consistent with the experimentally observed babbling behavior in young song birds.

Ganguli and Hahnloser showed that in case of a linear forward mapping from the motor representation to the sensory representation, the inverse model can be learned by a generalized Hebbian learning rule. However, it is not clear, how realistic Hebbian learning can account for the learning of an inverse model, in particular when the forward mapping is non-linear. The main difficulty is that activations of neurons, which occur at different points in time, locally have to be compared in magnitude in order to close the motor-sensory loop and thus learn the corresponding inverse mapping. Here we propose a different local learning rule by which non-linear motor-sensory mappings can be inverted. Considering a dynamical system in which the activation in each neuron leaves a trace over time inducing after-hyperpolarization in each neuron, we employ the echo of the original signal through the motor-sensory loop at the level of each individual neuron to solve the difficulty mentioned above. Given this type of dynamics, we find that an anti-Hebbian learning rule is required to learn the inverse mapping. We extend our model to include spiking neurons and investigate it for a range of nonlinear transformations. Furthermore, we discuss its relation to other approaches to bird song learning.

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[F 97] Predicting of retinal ganglion cell responses with spiking neural networks and stochastic dynamic synapses

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We apply biologically inspired spiking neural networks with dynamic synapses to predict precise time of retinal ganglion cell (RGC) spike trains while achieving the concept of synchrony (the temporal correlations) between the signals of grouped neurons. We present a learning rule to develop a training algorithm for a multi layer network of Integrate and fire neurons. Two groups of parameters are evolved based on history of pre- or postsynaptic activities. First, a subset of internal hidden variables that govern synaptic efficacy changes based on presynaptic activities, and second those parameters are selective to change the amplitude of the postsynaptic response. We show that this model can exhibit acceptable level of synchrony by including the feedback parameter of cross correlation coefficients of the responses of all the neurons. We compare our model with previous works in order to demonstrate its capability of spike time prediction, by considering the number of neurons use in the network, the predefined pair of spike times which are taken into consideration to perform an update, generation of synchrony state between neural responses, and the evolution model of synaptic efficacy.

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$[F \ 98] \ \ \text{Modelling the role of } \beta CaMKII \ in \ regulating \ bidirectional \\ plasticity \ at \ parallel \ fibre-Purkinje \ cell \ synapses$

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Synaptic plasticity, the strengthening and weakening of connections between neurons, is crucial for learning and memory in neuronal circuits. However, a better comprehension of the mechanisms of many forms of synaptic plasticity is limited by the complexity of the underlying intracellular signalling pathways.

Cerebellar long-term depression (LTD) and potentiation (LTP) are calcium-dependent forms of synaptic plasticity that weaken and strengthen synapses between parallel fibres (PF) and Purkinje cells (PCs). While LTD is induced by large increases in intracellular calcium concentrations in response to paired PF and climbing fibre (CF) input, smaller calcium concentration increases that result from PF input alone lead to LTP. The induction of LTD and LTP is mediated by enzymes such as calcium/calmodulin-dependent kinase type II (CaMKII) and protein phosphatase 2B (PP2B) that regulate the phosphorylation and dephosphorylation of postsynaptic AMPA receptors.

The CaMKII holoenzyme is composed of α CaMKII and β CaMKII isoforms. Recent experiments with Camk2b knockout mice have revealed that β CaMKII, which is the predominant CaMKII isoform in the cerebellum, controls the direction of plasticity at the PF–PC synapse (van Woerden et al., 2009). More specifically, protocols that induce LTD in wild-type mice result in LTP in knockout mice that lack β CaMKII, and vice versa.

Here, we use a simple model of the phosphorylation and dephosphorylation of AMPA receptors by CaMKII and PP2B to investigate the mechanisms that underlie the regulation of bidirectional plasticity at the PF–PC synapse. The model is based on our recent model of CaMKII activation (Pinto et al., 2012). In the model, the binding of calcium to calmodulin (CaM), the activation of CaMKII and PP2B by calcium/calmodulin (Ca4–CaM), and the AMPA receptor phosphorylation and dephosphorylation are represented by coupled ordinary differential equations.

Van Woerden et al. (2009) suggested that the sign reversal of synaptic plasticity in the Camk2b knockout mice is due to a biochemical difference between the α and β CaMKII isoforms. The β CaMKII, but not α CaMKII, subunits can bind to filamentous actin (F-actin), which could result in clustering of the CaMKII holoenzyme to F-actin, making it unavailable for AMPA receptor phosphorylation. We included the binding of CaMKII to F-actin in our simulations of synaptic plasticity induction in wild-type mice, whilst omitting it when modelling plasticity induction in Camk2b knockout mice. Moreover, Purkinje cells contain about four times as much β CaMKII as α CaMKII, and the loss of β CaMKII did not result in up-regulation of α CaMKII in the knockout mice. Thus, we also included the corresponding reduction in CaMKII concentration in our simulations of knockout mice.

We simulate the induction of synaptic plasticity in response to PF stimulation with and without paired CF stimulation in our model by applying calcium pulses with concentrations that reflect experimental data, and we record the resulting phosphorylation and dephosphorylation of AMPA receptors. Our simulations replicate the experimental findings by van Woerden et al. (2009), suggesting that the binding of β CaMKII to F-actin can indeed contribute to the control of bidirectional plasticity at PF–PC synapses. Our model predicts that the sign reversal of synaptic plasticity is based on a combination of three mechanisms operating at different calcium concentrations. At the low calcium concentrations that result from PF input alone, the loss of F-actin binding in the knockout mice leads to increased availability of active CaMKII compared to the wild-type mice, and to induction of LTD rather than LTP. At the high calcium concentrations that are triggered by paired PF and CF input, the reduced CaMKII concentration in the knockout mice favours the dephosphorylation of AMPA receptors by PP2B, and the induction of LTP instead of LTD. This effect is exacerbated by the increased availability of Ca4–CaM that results from the decreased CaMKII levels, which further increases the activation of PP2B.

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[F 99] Prolonged odor information in the antennal lobe of Drosophila melanogaster

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Trace conditioning, an associative learning task in which the behaviorally neutral stimulus and the meaningful stimulus (reward or punishment) that elicits the response do not overlap in time, requires some sort of sensory memory which keeps information about the neutral stimulus after its termination, e.g. a stimulus trace. In this study, we investigated whether and how olfactory information is maintained and changed on a short temporal scale in the first olfactory brain area, the antennal lobe, of Drosophila. Using in vivo calcium imaging and the GAL4/UAS system, we selectively measured responses from two types of the olfactory network neurons: the receptor neurons itself, and the projection neurons that pass the information to higher brain areas. We analyzed the spatio-temporal response patterns that are elicited during the stimulation, as well as the subsequent patterns after stimulus offset. Odors evoked stimulus specific response patterns of activated and inhibited functional subunits of the antennal lobe, the glomeruli, which convey information in a combinatorial manner (see http://neuro.uni-konstanz.de/DoOR). With the stimulus offset, the odor response pattern changed to a new and dissimilar post-odor pattern. Although odor specific, these post-odor activity patterns differed from the initial response pattern, and were invariant to changes of the preceding stimulus length. Taken together, these results show that odors elicit a specific trace in the antennal lobe network activity of Drosophila. Whether this activity trace is used as a substrate for the trace found in behavioral responses remains to be determined.

[F 100] Representations in a recurrent network model of motor sequence learning reveal unified view of procedural memory consolidation and structure learning

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Humans can improve their performance in procedural movement tasks through practice, but such motor learning has shown puzzling and seemingly contradictory results. On the one hand, a wide variety of proactive and retroactive interference effects have been observed when multiple tasks have to be learned. On the other hand, some studies have reported facilitation and transfer of learning between different tasks, sometimes based on abstract structure similarities. Here we show how these different phenomena can all be understood based on generic learning principles in a recurrent neural network model. Specifically, we consider a self-organizing recurrent neural network model whose activity and connectivity is shaped by three plasticity mechanisms: spike timing-dependent plasticity (STDP), intrinsic plasticity, and synaptic scaling [1]. The network receives stimulus-specific input and is connected to a layer of motor neurons mediating the movement sequences through a winner-take-all mechanism. We use this network to model a series of experiments on movement sequence learning using a single set of parameters in all simulations. The network learns to carry out the correct movement sequences over trials and reproduces differences in behavior between training schedules such as blocked vs. random training. The network also shows striking similarity to human performance in tasks with similar training sequences but different training times. Previously we have shown the agreement between the output of the network and psychophysical performance across several tasks and training schedules with a single set of parameters for the recurrent network. The current work presents a detailed analysis of the underlying changes in the neuronal representations of the motor sequences across learning. Mutual information, PCA analysis of network activity, and measures of neuronal selectivity for parts of the motor sequences reveal how input representations and the trajectories of neural activity change with training. Finally, we provide testable experimental predictions. Thus, we show how training schedule and task similarity interact to produce a rich set of interference and facilitation effects thereby unifying procedural memory consolidation and structure learning in a recurrent network model with multiple plasticity mechanisms.

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[F 101] Self-Organization of Control Circuits for Fiber Projections Invariant to Position, Size and Orientation

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Dynamic mappings support the projection of the two-dimensional field of local feature descriptors within the focus of attention in primary visual cortex to an invariant space, presumably in infero-temporal cortex. These mappings must be re-established after each shift of attention or eye movement, that is, within fractions of a second. We proceed on the assumption that this rapid switching is achieved with the help of so-called control units. These are specialized neurons each of which contacts with its processes a number of projection fibers (possibly by placing its synapses in close apposition at a dendritic patch) and which perform two functions. On the one hand they test for agreement between the pre-synaptic and the post-synaptic signals at the projection fibers they contact, thus comparing the activity pattern on the whole set of incoming fibers to the activity pattern on the target neurons. If that pattern similarity is better than that of competing control units, they stay active, otherwise they switch off. On the other hand, control units gate the transmission of projection fibers (pre-activating the dendritic patch, mentioned above, when active). Control units have first been proposed by [Anderson 1987]. In previous work we have simulated a full-blown face recognition system on this basis [Wolfrum 2008].

This scheme requires highly specific connectivity patterns of control units. We are addressing here the ontogenesis and learning of these connectivity patterns. The common underlying principle of our simulations is similar to what is known about the ontogenesis of retinotopic mappings, e.g., of the fiber projections from retina to the optic tectum. There, chemical or electrical signals are induced from the retina to the tectum. Short-range signal correlations in the retina serve to code retinal geometry and allow fibers coming from neighboring positions in the retina to connect to neighboring positions in the tectum, as described in [Häussler 1983] by a set of differential equations ("Häussler equations"). To accommodate that system to the application at hand by introducing control units by a third set of indices, in addition to the "retinal" and "tectal" indices, and by letting synaptic plasticity affect not projection synapses (which essentially have to realize all-to-all connections between the source area and the target area) but the connections of the control units. In previous work we have presented simulations that addressed the generation of control circuits for a few point-to-point projection patterns that differ in relative position and size [Bergmann 2011]. We here extend this work in two directions, a continuous range of projection parameters (relative position, size and orientation) and the organization of dynamic control not only of point-to-point connections but also of feature-to-feature connections. The latter is necessary because when rotating or scaling the retinal image of an object, feature relations have to change as well.

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[F 102] 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. liquidstate 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 a cortex-like structure can 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 relearning, and 3) forgetting, which depends on the state (well- or sporadically-learned) the cluster is in.

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Neurotechnology and brain-machine interface

[F 103] Using ultra-low cost 3D gaze tracking as an intuitive, non-invasive, high information throughput alternative to BMIs.

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Eye movements provide rich information highly correlated with user intention and are often retained by patients with serious motor deficiencies (1). Despite this, eye tracking is not widely used as a brain machine interface (BMI). This is possibly because existing commercial systems of sufficient accuracy are prohibitively expensive, bulky, and their application is restricted to 2D computer interaction. Also, current gaze based interfaces use either blinks or gaze dwell to select a target which requires extended selection intervals to avoid confusion with natural blinks or fixations - often referred to as the Midas touch problem(2). Using mass produced video game hardware, we have developed an ultra-low cost binocular eyetracker with a comparable performance to commercial systems 500 times as expensive. We use our eve-tracker for both 2D and 3D gaze estimation. In a 2D gaze control experiment we demonstrate that users can successfully play the game 'pong', a game requiring real-time continuous control, without any training. The high-speed accuracy of the eye tracker coupled with the developed gaze estimation algorithms, can drive a virtual volumetric cursor in the user environment with a bit rate of 17 bits/second. This bit rate is more than ten times that of invasive and semi-invasive brain read-out interfaces that are vastly more expensive (3). The head-mounted GT3D system has a 40 USD material cost and operates at a 120 Hz sampling rate with a 0.5-1 degree of visual angle resolution. Calibration in contemporary 3D gaze tracking methods requires additional expensive equipment (e.g. a volumetric display), infeasible for our low-cost system. Instead, we use a simple calibration approach with a standard 2D visual display unit (VDU), achieving a 3D gaze performance competitive with current research systems (5cm mean Euclidean error in workspace of 1m depth) (4-6). With binocular eye-tracking, we speed up BMI target selection time by a factor of 5.6 using nonbehavioural winks rather than behavioural blinks to communicate a selection. The presented non-invasive and ultra-low cost GT3D system yields high-data rate and low latency 3D gaze information highly correlated with motor intentions, making it suitable and complementary to typical BMI approaches as well as being economically accessible for large patient groups and the elderly.

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[F 104] Adaptive multi-electrode positioning (AMEP) system for chronic extracellular recording in awake behaving primates

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Intra-cortical brain machine interfaces usually use implantable electrode arrays with fixedgeometry. The drawback of these devices is that electrode position cannot be adjusted for signal optimization in chronic preparations. Other implantable and adjustable electrode systems allow to only push the electrodes in one direction, or can not dealt with multiple electrodes. Here we present an adaptive multi-electrode positioning (AMEP) system for chronic implantation and motorized bi-directional electrode adjustments.

The AMEP fits into a standard implantable recording cham¬ber for rhesus monkeys. The system consists of a stainless-steel chamber insert that is introduced into the implanted chamber above the intact dura. It can currently hold 16 individual glass-insulated single-core microelectrodes. Electrodes can be preloaded before insertion of the system into the chamber, but can also be individually replaced on demand, without removing the insert from the chamber. Each of the 16 microelectrodes can be moved independently in its own stainless steel guide tube with 10 mm total travel distance. The rear end of the microelectrode is mechanically interfaced to a micro gripper, which couples to the microelectrode via software control. The gripper is positioned by a motorized and computer-controlled xyz-micromanipulator, which allows it to actuate each of the 16 electrode individually and to movement electrodes in both directions of the z-axis. The bottom of the chamber insert is sealed with a silicone sheet that prevents fluids from entering the electrode guide tubes and improves the mechanical stability of the electrode recording position. The metal-shielded insert houses a 16-channel low-noise preamplifier which makes the system robust against EM-noise.

In summary, the AMEP system is designed to fulfill the following specifications: 1) use of quartz glass insulated platinum tungsten microelectrodes, which are well suited for chronic recording applications, 2) use of a secure electromechanical connection between microelectrodes and preamplifier input to guarantee a low noise signal transmission, 3) good biomechanical compatibility of the microelectrodes, which reduces the risk of gliosis around the electrode tip, 4) small electrode spacing for high spatial resolution, 5) electrical shield around the recording electrodes to avoid electrical noise pick-up from the laboratory environment, 6) possibility to reposition the microelectrodes individually with an axial μ m-resolution in both directions by using a microprocessor controlled xyz-micromanipulator system with an electrode gripper. In conclusion, the newly developed AMEP will allow precise microelectrode repositioning in chronic preparations with a travel distance suitable for recordings even from non-surface areas in the cerebral cortex of monkeys. The bi-directionality of movement opens the potential to fully automatize the electrode positioning with signal-driven control algorithms.

Conflict of Interest

Thomas Recording is a private industry company who plans to commercialize the device which will be developed in this public funded R&D project and which is presented in this abstract.

[F 105] Growth-function of electrically evoked brainstem responses in cochlear implant patients

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This investigation develops a system for the objective measurement of auditory brain stem responses in awake cochlear implant patients. Electrical stimuli were delivered with MED-EL implants under computer control (via the RIB II interface) and responses were amplified with a biosignal amplifier (g.tec) and sampled synchronously with an A/D data acquisition board using custom software. Data analysis was conducted both on-line (to follow the measurement progress) and off-line to implement more complex stimulation- and muscle artifact rejection algorithms. In addition to the eBERA measurements, our patients also evaluated the perceived loudness of the pulse-trains used in these measurements.

Electrical stimulation artifacts were two orders of magnitude larger than wave V of the evoked potentials. They were removed using stimulation pulses with alternating polarity, discarding the initial part of the response (0.5 ms) and by fitting and subtracting the remaining artifact with an exponentially decaying function. We then could analyze the responses easier, identify wave V at high stimulation levels and track it by eye down to low levels. An objective threshold criterion was established based on the binomial average. For low to medium stimulation amplitudes the amplitude of wave V amplitude grew linearly with the perceived loudness, individual correlation coefficients were between 0.81 and 1. Notably, our measurements were very sensitive, the objective detection threshold was between the loudness categories "soft" and "very soft" (Würzburger Hörfeld).

In summary our results indicate that carefully measured and analyzed eBERA data provides interesting insights into loudness growth in CIs. If a systematic relation between single-pulse thresholds and burst stimulation can be established, it can be even used for objective threshold estimations.

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Conflict of Interest

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[F 106] A wireless and fully implantable recording system for ECoG signals

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Massively parallel, chronic measurements of neuronal activity over long periods of time are important for fundamental research as well as medical applications. Major requirements for such an electrophysiological recording system are medical safety and a large number of electrodes allowing recordings with high spatial and temporal resolution.

In order to address these requirements, we are developing a fully implantable, wireless recording system for electrocorticography (ECoG). Without any wired connection passing through the skull, we avoid any points of entry for infections and remove the risk of inflicting harm by pulling the cables. Our system approach is defined as follows: A thin foil carries the necessary electronics and a set of embedded electrodes interfacing the surface of the brain. These electrodes are electrically connected to an array of amplifiers and 16-bit analog-digital-converters (ADCs). The acquired data is processed by an application-specific integrated circuit (ASIC). It prepares the data for efficient wireless data transmission using a RF-transceiver and custom antennas. A base station outside the body receives the data and delivers it via Ethernet to a software application. In addition, the system is wirelessly powered via an inductive link.

To implement this concept, a $10\mu m$ thick polyimide foil, providing an active area of $135mm^2$ with 128 embedded gold electrodes, was fabricated in our clean room. The ASIC was designed in house for a 150nm standard CMOS process. It allows selecting relevant channels for recording, downsampling, reducing resolution, and power management for the analog frontend. We also designed and assembled the antennas for data transmission and coils for energy transmission through well conducting tissue. In addition, the base station including software and an extracranial prototype comprising the electronics were developed and build.

With measurements from macaque's visual area V1 using a chronically implanted foil with 128 electrodes, we successfully acquired ECoG data. Mapping the recording site's visual receptive fields revealed a high spatial and temporal resolution of the electrodes. Connecting the implanted array with the extracranial prototype, we demonstrated successful acquisition, processing, and transmission of data. Furthermore, we successfully tested the inductive energy link.

The remaining challenges in this project are to assemble all electronic components on a foldable flexible foil carrying the electrodes and to improve the system's lifetime by enhancing its protection against the environment inside the skull.

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Conflict of Interest

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[F 107] Sparsely optimized multi-electrode transcranial direct current stimulation

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Transcranial direct current stimulation (tDCS) has become a widely used technique for noninvasive brain stimulation in the last decade since its successful application to the human cortex [1]. It has shown notable potential for the treatment of neurological and psychiatric disorders, as well as for studying the basics of cognitive and behavioral neuroscience [2]. Currently, tDCS is applied using two rectangular pads placed on the scalp. However, it is well known that the induced electric field in the brain resulting from this configuration is nonfocal [3]. Focality in stimulation translates into a better understanding of the elicited effects [4] and it may reduce potential side-effects.

Researchers have recently proposed a multi-electrode stimulation paradigm, where using the superposition of sources, an optimization algorithm calculates the appropriate electrode currents in order to achieve a given intensity and orientation of the induced electric field at a target. The authors show how focality can be improved over the conventional montage [5]. However, to translate this new paradigm into practice one must take into account that there is a limited number of active electrodes which can be used. This poses a hardware constraint which should be included in the optimization techniques.

This work presents a method for realizing optimized multi-electrode tDCS which allows to specify the number of active electrodes while optimizing intensity and orientation of the induced electric field at a given target. For solving the sparsity problem, i.e. to select a subset from the available electrode set, we tested two approaches: (1) a stepwise optimal selection (SOS) algorithm, including electrodes which yield the minimal residual and thus provide the best fit to the predefined electric field and (2) an orthogonal matching pursuit (OMP) [6], a greedy algorithm which finds the most relevant projections of the residual onto the electrodes' contribution. In both approaches we employ a constrained least-squares optimization approach, taking patient safety into account. Using an anatomically realistic MRI-based finite element model, we calculate the induced electric field in the brain for the different electrode montages by solving the Laplace equation.

We show substantial focality improvement against the conventional setup, namely, 67%, 76% and 78% for four, six and eight active electrodes respectively using SOS (OMP yields a slightly worse performance). Calculating the residual sum of squares and the Bayesian information criterion (BIC), we analyze the trade-off between the number active electrodes and how well the solution matches the predefined electric field. The BIC yields the minimal number of electrodes for an optimal trade-off. We compare our method to optimization approaches with unconstrained number of active electrodes. Most importantly, our method makes optimized multi-electrode tDCS compatible with any stimulator system.



Figure 1

Figure 2

Figure 3

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[F 108] A Curious Robot Vision System

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The ability of biological organisms to learn autonomously is a challenge for future robots assisting humans in their homes, work places, or other changing environments [1-3]. Autonomous learning implies that the system can choose what activities it should engage in and hence what it can learn about. Here we introduce an autonomously learning robot vision system implemented on the iCub robot that explores a scene and learns visual object representations without any human assistance. The system integrates a number of visual competences including attention, stereoscopic vision, segmentation, tracking, model learning, and recognition.

Our system is driven by an attention mechanism that endows it with a simple form of curiosity: the system will preferentially attend to objects, for which it estimates that it can still learn something new. The basic mode of operation of the system is as follows. An attention mechanism combines bottom-up (saliency based) attention with top-down information about object familiarity and previously visited locations. It drives the system to look at interesting points in the scene. At each location, an object candidate is segmented from the background using stereo information and actively tracked if it is moving. A new object model, containing information about the spatial arrangement of local image features, is created if the object is novel. Otherwise the existing model for the object is updated. The system continues to look at and learn about an object as long as the object model can still be improved by acquiring additional features from the object. When the learning progress for the current object drops below a threshold, attention is diverted to a new location, where the process repeats. Our experiments comparing our "curious" attention system to several alternatives show greater learning speed and higher recognition accuracy when learning is focused on objects and locations where the learning progress is expected to be high.

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[F 109] Modeling the neurophysiology of TMS-induced I-waves

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Transcranial magnetic stimulation (TMS) allows to non-invasively manipulate neural activity via strong magnetic fields and is currently tested for its clinical use for treating depression, stroke, schizophrenia and several other neurological disorders. However, the details of how TMS induces patterns of neural activity in cortical circuits remain poorly understood, which hampers targeted clinical application [1]. Assessing the nature of such patterns or establishing the biophysical basis underlying magnetic stimulation in purely experimental settings remains difficult given the scarce recording opportunities and high variability of results across healthy subjects. Models incorporating anatomically detailed neurons could overcome these limitations and provide valuable insight into the effects of TMS at the cellular and systems level.

We have recently presented a first computational model of how TMS stimulates cortical circuits and produces I-waves, fast rhythmic responses in descending motor pathwavs [2]. The model consists of a detailed layer 5 (L5) pyramidal cell in primary motor cortex and a population of layer 2 and 3 (L2/3) neurons projecting to it. It parsimoniously explains the mechanisms underlying I-wave generation together with some of their basic properties such as frequency, timing, and size. Here we show how the size of the L5 dendritic trees influences the amplitude of the simulated epidural responses. By removing distal dendritic branches of the L5 cell we show how later I-waves are abolished. This suggests that the complex anatomical structure of L5 neurons plays an important role in the generation of I-waves. We argue that I-waves are a product of synchronized volleys of EPSPs and IPSPs impinging onto L5 cell dendritic trees and the intrinsic membrane properties of L5 cells. This generation mechanism does not require multiple activations of chains of presynaptic elements or complex resonating circuits [1]. Our model additionally reproduces findings from paired-pulse stimulation protocols, pharmacological interventions and behavior modulation of I-waves. In conclusion, our model explains findings from a wide range of experiments and is an important first step towards designing optimized TMS protocols for specific clinical purposes.

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Data analysis, machine learning, neuroinformatics

[F 110] Spectral Analysis of Local Field Potentials from Rat Primary Visual Cortex (V1)

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In primary visual cortex (V1) of rats, orientation selective neurons do not show topographic organization on a larger scale (Ohki et al., 2005), in contrast to the columnar organization of orientation selective cells in V1 of cat and monkey. Accordingly, while orientation tuning in mass signals like the local field potential (LFP) has been described in recordings from cat V1, it can be assumed to be weak or absent in rodent V1. However, in monkey motor cortex, which also shows no clear columnar organization, information about the direction of the monkey's hand movement could be extracted from LFP power spectra with high predictive power (Rickert et al., 2005).

To reveal in how far global network tuning properties could be extracted from mass signals of primary sensory areas which do not show clear topographic organization, we performed in vivo multi-electrode recordings in V1 of anesthetized rats while presenting visual stimuli with clear direction information (moving edges and gratings). Spectral analysis of LFP signals from multiple channels was performed using adaptive multivariate auto-regression (AMVAR; Ding et al., 2000) after removing the first two statistical moments (mean and standard deviation across trials) from the signal. This method allows high spectral estimation accuracy with high temporal resolution superior to other methods of time-dependent spectral analysis like multi-tapering (Nalatore & Rangarajan, 2009). Direction tuning was assessed using circular statistical measures.

For moving edges, significant directional tuning in the LFP power spectrum can be found during the onset transient up to 500 ms after stimulus onset. Tuning strength was not distributed evenly across the whole observed spectrum (<200 Hz), however, but limited to mainly two distinct frequency bands centered around ~30 Hz and ~70 Hz. Preliminary analysis of moving grating stimuli did not reveal significant tuning either in the onset transient or the steady state during stimulus presentation. These results suggest that, even in the absence of coarse scale organization of cortical networks with respect to tuning properties, information about the stimulus properties can be inferred with appropriate methods.

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[F 111] Bayesian models for the emergence of visually moving objects

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The analysis of unconstrained, realistic, everyday dynamic visual stimuli and the interpretation of what we see as a temporally changing arrangement of objects in our environment is one of the central challenges in computational vision science.

We report on recent insights obtained in investigations that aim at this ambitious (far) goal, experimenting with motion analysis and segmentation of video streams. In the present work, we emphasize a particular interpretation of the general Bayesian approach. The term 'Bayesian', in this context, means that prior knowledge (experience, learned statistics) is actively used in the process of determining what that state of the 'world outside' is, given the current (visual) observations, and all interpretations accumulated from the past.

The required models in which a formulation of observation and estimated state of the outside world is performed can have different degrees of agreement with what is known from a physically realistic description of the process:

A simplified, though still very useful model formulates the interpretation of visual input in terms of 'regions' which a) move according to naive physical laws, b) have a shape that usually only changes slowly, and c) show a surface 'texture' that is also roughly constant over time.

On the basis of such a model, time-recursive estimation procedures can be developed which, on one hand, provide a 'dynamic segmentation' of a moving visual scene into regions (=the projections of 3D objects), and also allows to make predictions on the future visual observations.

The actual implementation of such a procedure is impeded by the mathematical structure of the underlying optimization problem: it has extremely many variates, and due to the nonlinear structure of the problem, it has local minima 'almost everywhere'. We propose decision-directed approaches for solving this very fundamental kind of problems, deliberately sacrificing guaranteed optimality against feasibility, where the term 'feasible' is meant both in a technical sense (implementable and showing reasonable run-time) as well as in a biological sense (= implementations on a neural substrate appear plausible).

We show results of fundamental investigations with a hierarchical, dynamical segmentation scheme, as well as first experiments with a Bayesian decision-directed scheme.

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[F 112] Discerning cognitive stages in a working memory and decision making task from human fMRI data using multivariate time series analysis

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The radial arm maze (RAM) task has been intensely studied in rodents to elucidate neural correlates of spatial memory, decision making and reward processes (Floresco et al., 1997; Lapish et al., 2008). Here we employ a diverse set of multivariate statistical/machine learning methods on fMRI data recorded from a group of healthy adults whilst performing a virtual reality version of the RAM task, where participants moved through a virtual park surrounded by various landmarks to find gold coins hidden at the end of 12 alleys.

Various multivariate test statistics (such as Wilk's lambda and generalized Hotelling's T-squared) were first computed separately for several regions of interest (ROIs) as a measure of the overall discriminability of different task stages (namely encoding, decision, reward expectation, reward consumption, and delay) within the blood oxygenation level dependent (BOLD) signal pattern. Mahalanobis distances were also calculated to identify pairwise differences between cognitively defined task epochs. Significance levels were determined nonparametrically through time series (block-permutation and time-shifting) bootstraps. Results demonstrate that those anatomical regions postulated to be involved in task execution, such as the dorsolateral prefrontal (DLPFC) and anterior cingulate (ACC) cortices, and the visual areas (V1) contain significant information on the task stages which distinguishes them from non-task related (control) areas, such as the Heschl gyrus and insula.

Furthermore, we found that the decoding capability of some ROIs varies with different classification schemes; e.g. the DLPFC yields the highest discrimination between low/high memory load decisions, whilst the ACC yields the highest discrimination between low/high spatial complexity decisions (defined with respect to the arms' spatial relationship to simple and salient landmarks). We also investigated the possibility of reconstructing neural system dynamics from the RAM BOLD signal. A penalized version of Fisher's linear discriminant analysis was applied to delay coordinate maps constructed for each ROI, to obtain a reduced 3-dimensional representation of the state-space and to reconstruct the neural trajectories. We found that within ROIs associated with cognitive load (DLPFC) or sensory (precuneus) processing, different task epochs occupied disparate regions of the state space. For patient (schizophrenia and depression) data, we will test whether this organization breaks down on trials with numerous behavioral errors.

Acknowledgements

This work was funded through a grant from the German Ministry of Education and Research (BMBF, 01GQ1003B). The task software was developed in close collaboration with the Experimental Radiation Oncology group (Prof. Hesser, Mannheim), and with Kai Ueltzhoeffer (Department of Psychology, Goethe University, Frankfurt am Main), using the open source 3D graphics (OGRE) virtual reality environment.

[F 113] Neuro-control with online adaptation for a Knee-Ankle-Foot-Orthosis

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A Knee-Ankle-Foot-Orthosis (KAFO) is a modular lower-extremity orthosis prescribed to people with gait disability which might be, e.g., caused by diseases or injury to brain or spinalcord. The KAFO should support, correct and assist the movement of the corresponding affected joints. Traditional KAFOs are restricted by a gait depending switch of the joints based on (electro-) mechanic non-adaptive switches. So common disturbances (floor unevenness, obstacles, ramps) cannot be mastered in a satisfactory way. Novel approaches include active elements into the orthosis, which do not directly act on the movement. Instead they adjust the compliance leading to new challenges for the controller of such actuators, which are difficult to handle with traditional approaches.

Thus new technologies have to be developed to improve control and to overcome the shortcomings of traditional non-adaptive approaches, thus solving the problem of efficient actuator control. Development of advanced orthotic devices is held back by the vast number of possible indications as well as by the wide range of neuromuscular variability within a specific patient group (Yakimovich et al., 2009). The development of advanced devices is therefore imposing the need for individual (online) adaptation of gait parameters to allow adaptation (1) to changing environments like slopes, stairs etc. as well as to gait parameters like stride length/frequency and (2) to the individual patients with respect to physiological conditions. To do so, we have employed a reflexive neuro-controller as inspired by RunBot (Manoonpong et al., 2007), embedded to a KAFO based on a controllable hydraulic damper, derived from OttoBock's C-Leg©.

Where traditional control approaches are designed with a fixed behaviour set, which is fit on the patient using an equally fixed set of parameters, the design of a neural controller allows extensive behaviour adaptation at run time, i.e. time continuous output signal modulation and modification, and smooth transitions between different time periodic output patterns. This improves the flexibility and thus the range of applications for the device. At the same time, the controller is implemented with fewer assumptions on the patient's conditions in mind and thus allows more patients to take advantage of it.

While these developments are advantageous, the patients desire for predictable and secure operation of the device are of utmost importance. In this study approaches to tackle these problems on the design level of the neural controller are presented, e.g., to achieve secure behaviour by reflexive fail safe mechanisms and predictability by restricting the possible degrees of freedom for behaviour adaptation. Thus allowing the application of unsupervised adaptation for medical devices.

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[F 114] Correspondence Priors for Binocular Image Data via Canonical Correlation Analysis

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In this work, we study unsupervised learning of correspondences relations in binocular video streams. This is useful for low level vision tasks in stereo vision or motion estimation but also for analysis of fMRI data. Still an open question is, how correspondence relations evolve and are represented in the human brain.

Correspondence estimation is often based on the principle of identifying corresponding pixels or patches and appears in many forms: in stereo vision pixel correspondences among a pair of images taken at the same point in time serve to determine a depth map [LucasKanade1981]. In motion estimation, pixel correspondences among consecutive images are sought [Horn-Schunk1981]. Most spatial feature approaches to correspondence estimation are based on the prototypical detection and matching framework. Here, correspondences are typically not determined using the raw pixel representation but rather rich feature descriptors. In the past, feature detectors have often been designed based on statistical (and biological) principles [Schmid2000,Mikolajczyk2004]. Today, there is an increased interest in unsupervised learning of such features directly from data based on energy-models and probabilistic generative models [OlshausenField1997,Hyvaerinen2009]. Furthermore, unsupervised feature learning is not restricted to model the actual image content but can also be used to learn the relationship between pairs of images , where images may be related via a spatial transformation, depth map, or the optical flow [Susskind2011,Memisevic2012].

In contrast to probabilistic methods for unsupervised feature learning, often involving rather sophisticated machinery and optimization schemes, we present a sampling-free algorithm based on Canonical Correlation Analysis (CCA, [Hotelling1936]), and show how 'correspondence priors' can be determined in closed form. Specifically, given video streams of two views, our algorithm first determines pixel correspondences on a coarse scale via learning the inter-image transformation employing CCA. Subsequently it projects those correspondences to the original resolution. After learning, for each point in video channel A, regions of high probability containing the true correspondence are determined, thus forming correspondence priors. While CCA only allows us to learn the inter-image transformation implicitly, we show how to apply a learnt transformation to previously unseen data in a principled way. Correspondence priors are efficiently encoded using second order statistics and may then be plugged into probabilistic and energy based formulations of specific vision applications. In contrast popular probabilistic models, our algorithm can be applied in closed form, only involving QR decomposition or the SVD, thus making it especially suitable within real world applications.

We experimentally verify the applicability of the approach in several real world scenarios where the binocular views may be subject to substantial spatial transformations.

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[F 115] A spiking classifier for nonlinear problems implemented on a neuromorphic hardware system

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The question how neuronal systems process sensory information is as crucial for neuroscience as it is for bio-inspired technical applications. Classification of multidimensional data is a common problem in signal and data analysis. The architecture of the olfactory system maps particularly well onto this problem [1]. Here, we present an olfaction-inspired spiking classifier network that achieves the performance of a Naive Bayes classifier on a benchmark data set, and demonstrate its ability to solve nonlinear classification problems. Moreover, we show an implementation of this network on a neuromorphic hardware system comprising 192 spiking analog hardware neurons embedded in digital control circuitry. Neuronal computations in this system operate at a speedup factor of 10^4 compared to biological real time, enabling high-thoughput neurocomputing. The neuromorphic implementation is subject to inherent device mismatch affecting analog components, e.g. neuron parameters, which leads to a decrease of classification performance. As a solution we present an algorithm for self-calibration that takes into account the specific architecture of our network in order to maximally exploit the capabilities of the hardware system. With this algorithm we were able to increase classifier performance on the hardware to a level comparable with a Naive Bayes classifier. As neuronal variation is not only a feature of neuromorphic hardware but also a hallmark of neurons in biological systems, our results provide insight into the biological relevance of neural coding hypotheses thought to operate on a neuronal substrate with heterogeneous sensitivity.

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[F 116] A simulation framework for acute extracellular recordings

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Extracellular recordings are a key tool to study the activity of neurons in vivo. Especially in the case of experiments with behaving animals, however, the procedure of electrode placement can take a considerable amount of expensive and restricted experimental time. Furthermore, due to tissue drifts and other sources of variability in the recording setup, the position of electrodes with respect to the neurons under study can change, causing degraded recording quality (non-stationarities).

Here we devloped a simulation framework for acute extracellular recordings. Neurons and electrodes are modelled as objects in a spatio-temporal state space. A generative data model allows to construct putative voltage traces at electrode positions, as the superposition of time-and-distant-dependant characteristic waveforms of the simulated single neurons. All objects

may be positioned arbitrarily during the simulation. This kind of framework allows to simulate acute experimental conditions and provides grounds to evaluate feedback-dependant algorithms (positioning systems, online/adaptive spikesorting). The simulated data was found to resemble data acquired from acute extracellular recordings from PFC of awake behaving maquace.

Acknowledgements

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[F 117] Characterizing Responses of Translation-Invariant Neurons to Natural Stimuli: Maximally Informative Invariant Dimensions

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The human visual system is capable of recognizing complex objects under possibly drastically different viewing conditions. Especially in the higher cortical areas, the sensory neurons reflect this functional capacity in their selectivity for visual features and their invariance to certain object transformations. The calculations necessary to achieve these properties are highly non-linear in retinotopic space and characterizing the response patterns of these neurons is a formidable computational challenge, such that standard generalized linear models will most often fail. This problem goes hand in hand with the fact that the neurons in question do not respond well to stimuli that are easy to treat statistically, e.g. noise. Parametrized complex shapes evoke better responses but cannot capture the full richness of natural scenes.

We present a spike-triggered method based on information theory which can characterize both the shape selectivity and the range and coarseness of position invariance from neural responses to natural stimuli. It significantly outperforms position-specific models with several relevant features on model translation invariant cells and the majority of V1 complex cells we tested.

[F 118] Combining sensitivity analysis with dimensional stacking to identify and visualize functional dependencies in conductance-based neuron model data

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Biophysically plausible neuron models are often characterized by a large number of parameters. Hence, visualization of observables derived from the simulation data, as a function of all underlying parameters is often difficult. However, visualization approaches exist, such as dimensional stacking (LeBlanc, 1990, Taylor et al., 2006), which maps a given discretely sampled (high-dimensional) parameter space onto a two-dimensional grid, that is amenable to visualization. This method does not omit information, as would, for example, a projection onto the first two principal components.

The usefulness of dimensional stacking for the identification of functional relationships depends on the choice of the so-called stack order. Only if the parameters with strongest influence on the observable are identified and ranked accordingly, the stacking method is suitable to extract information about the underlying system. Previous approaches (see, for example, Taylor et al., 2006) have solved this problem by sweeping through all possible stack orders and defining the optimal stack order as the one leading to lowest visual clutter in the resulting dimensional stack image. Here, we propose an efficient ranking procedure for the parameters by computing the impact of each parameter on the given observable. This allows a definition of the optimal stack order as the ranked impact scores, without the need of creating all possible dimensional stack images.

We demonstrate the usability of the proposed combination of sensitivity analysis and dimensional stacking, using the following example: we implemented a conductance-based singleneuron model with nine parameters that controlled the temperature dependence of the model's ion channel kinetics. Each parameter could take four values. We simulated the model at different temperatures and then computed the temperature dependence of, first, the stimulusresponse curve and, second, of the energy consumption per action potential, for each possible parameter combination. Using sensitivity analysis, we show that the mechanisms underlying these two temperature dependencies rely on largely different sets of conductance parameters. This implies that both temperature-invariance and energy efficiency can be achieved in a single neuron without compromising each other. Dimensional stacking provides a direct visual estimate of the parameter impacts and also of the presence of higher-order effects.

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[F 119] Encoding and Recall of Natural Image Sequences with Conditionally Restricted Boltzmann Machines

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The link between the ensemble of natural stimuli an organism is exposed to and the shape of the tuning functions in their sensory systems has been a subject of great interest in computational neuroscience [Karklin and Simoncelli, 2011, Lewicki, 2002, Sprekeler and Wiskott, 2011]. More specifically in the field of vision neuroscience, a number of principles have been proposed to explain the shape of tuning functions in primary visual cortex, for example redundancy minimization [Atick, 1992] and predictive coding [Rao and Ballard, 1999]. More recently, there have been suggestions that a simple hierarchical learning algorithm could learn the structure of data independently of labels and supervision through the use of deep learning approaches such as Stacked Autoencoders [Vincent et al., 2010] and Deep Belief Networks [Hinton and Osindero, 2006].

To date, much of the research in vision neuroscience has been focused on natural images as opposed to natural image sequences, due at least partly to the lack of controlled datasets of natural movies. In the current work we use the BBC Nature video collection [BBC,] as a dataset, as these provide long scenes with no zooming, therefore keeping image statistics mostly stable within scenes.

Using the framework of Deep Belief Networks to learn and reconstruct (or recall) sequences of natural images, we focus specifically on the use of the conditional Restricted Boltzmann Machine algorithm with sparse weights as proposed by [Taylor et al., 2006]. Through this method, the task of learning the networks for a set of natural image sequences becomes tractable. We present an analysis of the resulting network structure, comparing it to the tuning functions found in previous theoretical studies and in experimental studies. Furthermore we present a qualitative analysis of the performance of the network in sequence recall applied to image sequences from the dataset.

We believe this provides a solid approach to the problem of encoding of natural image sequences. This approach is very promising and deep learning studies have been proven to be very useful in the context of predicting the cortical organization of sensory areas [Lee et al., 2008]

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[F 120] Cloud Services and a Data API for Electrophysiology

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Recent progress in neuroscience has lead to rapid proliferation of data. The problem of efficiently organizing and annotating this information while allowing effortless access from different platforms becomes crucial if scientists are to fully exploit recorded experimental data.

The G-Node services provide data management in the cloud, including tools for organization, annotation, search, and backup. These services are accessed through a common application interface (API), which supports a common data model for electrophysiology and flexible data annotation[1]. Native client libraries in commonly used programming languages (including Python and Matlab^[2]) enable researchers to perform computations in familiar analysis environments while retaining the advantages that cloud storage entails. Thus, scientists may select whatever technology is most suitable for their current research with their data being available at all times and from all locations. The platform also features powerful search and query capabilities from simple full-text search to specialized query and filter mechanisms such as data slicing or fine-grained recording channel selection.

The services aim at providing an interface useful not only to produce but also to reproduce certain scientific analysis. All the changes made to any object in the system are being tracked. Scientists can go back in time to any revision, which makes the reproduction of individual analysis steps effortless and transparent.

These services are complemented by common tools for data access like neuroshare[3], NEO I/O[4], or odML[5], and provide convenient data conversion. Compatible files are automatically converted to native objects which may, in turn, be exported as needed. The platform encourages collaboration between both individual scientists and labs. Data sets, metadata, and files can be shared based on various criteria; simultaneous work on such data sets is supported.

Our platform equips every electrophysiologist with the tools necessary for integrating sophisticated data management into day to day experimental workflow, thus fostering scientific progress through neuroinformatics.

Acknowledgements

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[F 121] Predictable Feature Analysis

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Slow feature analysis (SFA) is an algorithm that has proven valuable in several fields and problems concerning signal- and data analysis. The idea is that a drastic, yet reasonable dimensionality reduction can be obtained by focusing on slowly varying sub-signals, the so-called "slow features". Typical data-analysis and recognition tasks, such as regression and classification, become much more feasible on the reduced signal and can be applied afterwards.

Our current research is focused on a way to handle interactive scenarios, which involve notions of control, planning and decision-making. In order to perform any kind of planning or intelligent control it is crucial to have a model that is capable of estimating the consequences of possible actions. In control theory, such models are usually formulated as a set of (partial) differential equations in a problem specific manner. In contrast to that, we follow an SFA-inspired approach that preserves the main advantages of SFA - namely its unsupervised nature and the ability to build a model in a self-organizing fashion. We aim to achieve this by replacing the objective of slowness by an objective of predictability, because predictability is a desired property of the needed consequence-estimating model by definition. We call this approach "Predictable Feature Analysis" (PFA).

This work deals with the involved problem of recognizing and extracting predictable features from an input signal. To this end we first have to specify the meaning of "predictable". While there exist model independent notions from information theory (cf. information bottleneck approach), we consider predictability with respect to a certain prediction model. In the current setup, we consider aspects as predictable if they can be predicted by a linear autoregressive model after an optional, non-linear preprocessing. This results in a nested optimization problem, which is quite involved. The features extracted must be optimized for predictability, but judging their predictability is an optimization problem by itself.

We present a tractable algorithm with relaxed constraints and some preliminary results on artificial data sets.

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[F 122] Separability of Adjacent Neurons Recorded with a CMOS-Multi-Transistor-Array

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Background/Aims: In order to understand the functionality of neural networks, reliable parallel spike trains must be recorded from neuronal ensembles [1, 2]. Silicon-based multi-transistor arrays ('Neurochips') are large enough to map the activity of hundreds to thousands of neurons within an area of $1 mm^2$.

In order to retrieve reliable parallel spike trains, action potentials (APs) have to be properly assigned to their corresponding units. The signal separation of adjacent neurons in neural tissue or cell culture represents a serious challenge, as their electrical coupling areas on the sensor array overlap. In this work we aim to determine whether this problem can be solved based on extracellular action potential waveforms together with their positional information.

Methods: A potential algorithm for assigning APs to corresponding units was presented in [3]. Here, we test its capabilities by using synthetic data with known positions, signal shapes and amplitudes of the extracellular signal. The synthetic data were generated from recordings of four retinal ganglion cells (RGCs). Measurements were done with a CMOS-multitransistor array (size $1 mm^2$, pitch 7.4 µm, sampling rate 78 kHz). For each RGC several hundred threshold crossings were averaged and down sampled to either 11.5 or 23 kHz respectively. Gaussian noise was added with appropriate amplitude to obtain a signal-to-noise ratio of 11 [4]. Thus a template was obtained for each RGC. Finally, synthetic data sets were generated by combining template pairs at different distances from each other (0, 7.4, 14.8 or 22.2 µm) and fed to the algorithm described in [3]. The quality of spike sorting was quantified by an error rate defined as the sum of false positive and false negative assignments with respect to the known ground truth. This procedure was carried out for two sampling rates (11.5 and 23 kHz).

Results: We compared spikes from pairs of different neuronal templates with centres of electrical coupling areas either aligned on each other or separated by multiples of 7.4 μ m. For both temporal sampling rates, spikes could be reliably separated down to the smallest separation distance (0 μ m).

Conclusion/Summary: For given conditions (signal-to-noise ratio, noise distribution and templates) our results provide parameter settings for which spiking activity can be reliably assigned to the corresponding source.

Acknowledgements

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Other

[F 123] Mixtures of conditional Gaussian scale mixtures: the best model for natural images

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Modeling the statistics of natural images is a common problem in computer vision and computational neuroscience. In computational neuroscience, natural image models are used as a means to understand the input to the visual system as well as the visual system's internal representations of the visual input.

Here we present a new probabilistic model for images of arbitrary size. Our model is a directed graphical model based on mixtures of Gaussian scale mixtures. Gaussian scale mixtures have been repeatedly shown to be suitable building blocks for capturing the statistics of natural images, but have not been applied in a directed modeling context. Perhaps surprisingly—given the much larger popularity of the undirected Markov random field approach—our directed model yields unprecedented performance when applied to natural images while also being easier to train, sample and evaluate.

Samples from the model look much more natural than samples of other models and capture many long-range higher-order correlations. When trained on dead leave images or textures, the model is able to reproduce many properties of these as well—showing the flexibility of our model. By extending the model to multiscale representations, it is able to reproduce even longer-range correlations.

An important measure to quantify the amount of correlations captured by a model is the average log-likelihood. We evaluate our model as well as several other patch-based and wholeimage models and show that it yields the best performance reported to date when measured in bits per pixel. A problem closely related to image modeling is image compression. We show that our model can compete even with some of the best image compression algorithms.

[F 124] Stochastic simulations reveal how clustering sodium ion channels in thin axons more than doubles the metabolic efficiency of action potentials

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The action potential, the fundamental signal of the nervous system, is carried by two types of axons: myelinated and unmyelinated fibres. The former type of axon is generally known to allow faster, more reliable and, as we recently showed [1], considerably more energy efficient propagation of signals than unmyelinated axons. In contrast, only the latter can reach the physical limits to axon diameter at 0.1 μ m, thus making the high connection densities of mammalian cortex possible [2].

Myelinated axons feature highly structured distributions of voltage-gated ion channels with characteristic clustering of Na channels at the Nodes of Ranvier, while unmyelinated axons are generally thought to have uniformly distributed ion channels. We recently discovered that in C-fibres, which are the 0.1 μ m diameter unmyelinated axons of the peripheral nervous system, Nav1.8 channels [3] are clustered together on lipid rafts. This localised concentration of Na channels resembles ion channel organisation at the Nodes of Ranvier. This prompted us to investigate if this structural similarity translates into functional similarity, making thin unmyelinated axons with lipid raft clustering of ion channels more efficient in terms of velocity, reliability and metabolic cost of action potentials than unmyelinated axons without lipid rafts.

We simulated both uniformly distributed and clustered channels (0.2 μ m diameter clusters of channels every 3 μ m of axon) along the unmyelinated fibre (0.1 μ m diameter), with an average channel density of 125 per m^2 in both cases. Metabolic cost was defined by the amount of ATP molecules necessary to reverse the Na current by Na-K-ATPase [4].

Biophysically realistic stochastic simulations carried on the Modigliani stochastic simulation framework [5] show that clustering Na channels on lipid raft reduced metabolic cost by over 260% (2.86×10^{-6} pmol ATP/mm vs. 1.03×10^{-5} pmol ATP/mm), while affecting propagation velocity far less (Velocity reduced by 20% with clustered channels). Crucially, deterministic simulations did not show a significant difference between the two types of axons (Velocity unchanged, metabolic cost 2.29×10^{-6} pmol ATP/mm with uniformly distributed NaV1.8 vs. 2.21×10^{-6} pmol ATP/mm). This is because channel noise and the discrete nature of ion channel currents can not be accounted for using deterministic models when the number of interacting stochastic elements is small and their effects are non-linearly boosted. Our results show the crucial impact of ion channel stochasticity and clustering on thin axons, and suggest an evolutionary advantageous specialisation in the brain: clustering of Nav1.8 on lipid rafts even in absence of myelination enables thin unmyelinated axons, in analogy to myelinated axon, to support a form of micro-saltatory [5] action potential conduction that makes them more energy efficient than unmyelinated axons with homogeneous distributions of ion channels.

Acknowledgements

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[F 125] Microstructure of Intrinisic Connections in the Inferior Colliculus of Mongolian Gerbils

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The inferior colliculus (IC) is an important information processing center in the auditory system. It acts as a hub in both the ascending and the descending auditory pathway. Previous studies suggested that the IC has anatomical fibrodendritic laminae and is tonotopically organized. The intrinsic connectivity of the IC, which is crucial to auditory processing as well, is, however, only little investigated.

We study the intrinsic connectivity of the IC with photo-stimulation using caged MNI-glutamate in vitro in Mongolian gerbils. With our stimulus protocol action potentials can be evoked within in a 100 μ m radius around the soma independent of cell type. Our data shows that IC cells receive both inhibitory and excitatory inputs from within the IC. The excitatory inputs from the region of interest show specific correlations with the cell capacitance and the cell conductance, while the inhibitory inputs only correlate with the cell conductance. By dividing the region of interest into center and periphery, we observed that the cells with many excitatory inputs are mostly located in the periphery, whereas the inhibitory inputs do not show this pattern.

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A novel control software that improves the experimental workflow of scanning photostimulation experiments Bendels et. al. Journal of Neuroscience Methods Volume 175, Issue 1, 30 October 2008, Pages 44–57

[F 126] Sequence Generation for Grasping Tasks by Means of Dynamical Systems

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Design principles for the autonomous generation of behavior in robotic systems are strongly coupled to the understanding of how cognition is emergent and linked to sensory and motor surfaces of biological systems. The concept of embodied cognition that stresses the importance of a system's physical structure for intelligent behav- ior is being embraced by an increasing number of roboticists and interdisciplinary researchers. A tight link between perception and action is crucial for autonomous robots situated in unstructured, natural environments. Learning and adapting senso- rimotor mappings from experience provides the capability to deal with increasingly complex and demanding tasks [1, 2]. On the other hand anthropomorphic robots serve as experimental platforms for the evaluation, validation and development of new models for cognition in humans and biological agents in general.

Sequences are defined by a serial order of target states of the system which can be reached by the selection of appropriate actions with respect to the current state of the sensory motor surface and the prediction of possible future state [7]. Crucial for reaching the desired target state is the time of execution which implies a coordinated process started from the intention to act, to the coupled order of single actions. The concept of timing is invariant against the kind of actions (i.e. language, reaching behavior, rhythmic movement etc.) and essential for any kind of sequences [11]. Grasping behavior involves goal directed movement of the hand, the decision about the kind of grip and the coordination between arm movement, the grasp aperture and the coordinated movement of finger joints with respect to the goal configuration of the hand [6] (a survey about the incorporated cognitive and neurological function can be found in [3]).

In the attractor dynamics approach[12], movement is generated by choosing low-dimensional, behaviorally relevant state variables and representing behavioral goals as attractors of dynamical systems over such behavioral variables. When the robot follows the dynamics of these systems, the behavioral variables will be stabilized at their attractors. Constraints can be included in a similar manner as repellers. We have recently applied this approach to generate reaching movements for manipulators under obstacle avoidance and orientation constraints [8, 9]. The suitability of the approach to deal with different constraints that are activated simultaneously in varying order has been demonstrated in [10].

The generation of coordinated sequences [13] as well as the generation of goal directed reaching movement [4] is formulated consistently by means of attractor dynamics. Some of these behaviors consist of a sequence of actions that must be acted out in a logical order one after the other. At any given moment a subset of all possible elementary behaviors is active while the rest remains inactive. Each of these activity patterns is followed by the next one in the sequence. The switching from one activity pattern to the next is triggered by an external event perceived by means of the robot's sensors. An important point for the activity pattern and the switching is that only a sparse set of all possible combinations of active and passive elementary behaviors should be allowed. The rules that specify which combinations are allowed and which are forbidden are given by the logics of the sequence itself.

In the current contribution we apply the dynamical approach to behavioral organization (elaborately discussed in [5]) to generate sequences aiming to perform grasping for an an-

thropomorphic robot. Each behavior is represented by a neuron which is initiating an action (i.e. move agent) when active or represent a state of the system (i.e. collision detection). The prediction of future states and constraints violations is provided by an internal forward simulation of the evolving solutions of the dynamical systems based on the current sensorial situation. The implementation on the anthropomorphic robot Cora show the impressive capacity of the attractor dynamics approach to integrate many constraints in a multi- degree of freedom arm-hand-system and to generate flexible and stable goal directed sequences (see Figure 1).



Figure 1

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[F 127] A Space Time Energetics Model for Intracellular Organelles of a Single Neuron - to Link Morphology with the Functions of a Brain Specific Region

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The onset of great advances in computational capability, coupled with the moral dilemma often faced with traditional brain research has prompted a non-invasive approach towards understanding the brain. Significant effort at WARFT has been routed towards capturing the spike activity of the neuron as a function of its intracellular parameters (Venkateswaran, et al). Our voltage spike - energetics model assumes a lumped nature of the mitochondria and other intracellular organelles, and doesn't consider the individual contributions of the mitochondrial cloud inside the soma and the spatial communication across the intracellular organelles. It localizes the energy budget of the neuron to a single global mitochondrion and does not consider mechanisms such as ATP communication and transportation across the organelles such as nucleus, ER, peroxisomes ,and the golgi apparatus with a commensurate level of biological accuracy. In this poster, we propose a novel distributed model of intracellular organelles, which analyzes the energetics in a three-dimensional environment, with emphasis laid on the spatial distribution of various organelles and the associated inter-dependencies across them.

The Three-Dimensional framework for the voltage-spike energetics model is set up by dividing the total mitochondria (and hence the energy budget) in a neuron among the various energy consuming entities (organelles). The plane containing these organelles is divided into infinitesimally small segments on which the mitochondria are localised. Stochastic equations are developed to model the transition of mitochondria across various "states" which represent its physical coordinates along the segment. The solution of this system of equations gives the probability distribution of mitochondria which is used to model mechanisms such as ATP consumption, restoration of ionic gradient and neurotransmitter packing. The developed energetics model for the organelles is distributed as hyper-nodes in a graph with the inter-dependencies optimised to simulate a distributed neuron. This has prompted the development of a generic framework which can analyse the commonalities present in biochemical signalling mechanisms such as the phosphorylation-dephosphrylation switch, diffusion and docking of vesicles in a simulation environment. Parallel research at WARFT is aimed at establishing a relationship across functions defined by the various regions of the visual cortex and morphological properties of the neurons in a specific layer. The morphological model provides the crucial link between functionality and energetics in the central nervous system and this highly integrated morphology-functionality-enrgetics model will lead to a more comprehensive understanding of the visual cortex .

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[F 128] A Robotic Platform for Spiking Neural Control Architectures

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Spiking neural networks (SNNs) have proven to be excellent control systems in biological organisms. Hence, they should have the potential of providing good control systems for autonomous robots. However, so far only few technical attempts to control artificial agents with SNNs have been made [2].

Here we present a robotic platform for testing biologically inspired SNNs as control architectures. The platform integrates real-time processing of sensory input and motor commands. The sensory data is fed into iqr [1], a software for the real-time simulation of SNNs. We extended its existing models of neurons and synapses to support adaptation and conditional plasticity. All communication between the robot and iqr is done via WiFi. As our platform we use a Rover based on the Arduino micro-controller [DFRobotShop Rover, RobotShop Distribution Inc.,Quebec, Canada]. A vision processing module [HaViMo2.0, fiveam robotics, Berlin] is mounted on the robot. The preprocessed image stream is transformed into spike trains which are fed into a SNN. The network processes this sensory input and generates output that is translated into motor commands. We test the robot on simple associative learning tasks, where we apply a conditional plasticity rule.

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[F 129] The location of the soma in higher invertebrates - bug or feature?

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The morphology of neurons in the central nervous system of higher invertebrates considerably differs from that of a typical mammalian neuron. Whereas in mammals dendrites and axon arise directly from the soma - often placing the soma into a central position of the space covered by the neuron - in insects the soma is "externalized": The soma connects to the axon and dendrites only via a thin process of several tens or hundreds of micrometers (the primary neurite) and is hence in a relatively peripheral position. Neurons with this morphological shape are unipolar. Their typical arrangement in ganglia allows the processes to meet in the center; somata are placed close to the surface of the ganglion. Whether the particular position of the soma - central or peripheral with respect to dendrites and axon - fulfills a functional role and provides mammals or invertebrates (or both) with specific advantages is unknown.

Here, we explore several hypotheses how evolutionary constraints may have shaped neuronal morphology in insects and mammals. To this end, we use simple multicompartmental models which locate the soma either between axon and dendrites or at the end of a primary neurite, and analyze fundamental aspects of neuronal signaling, including the efficiency of orthodromic and antidromic action-potential propagation and metabolic cost.

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