

12th International Workshop

Neural Coding 2016



Cologne, Germany

Aug 29 – Sep 2, 2016

<http://neural-coding-2016.uni-koeln.de>

Foreword

Welcome to the 12th International Neural Coding Workshop held at the Biocenter of the University of Cologne.

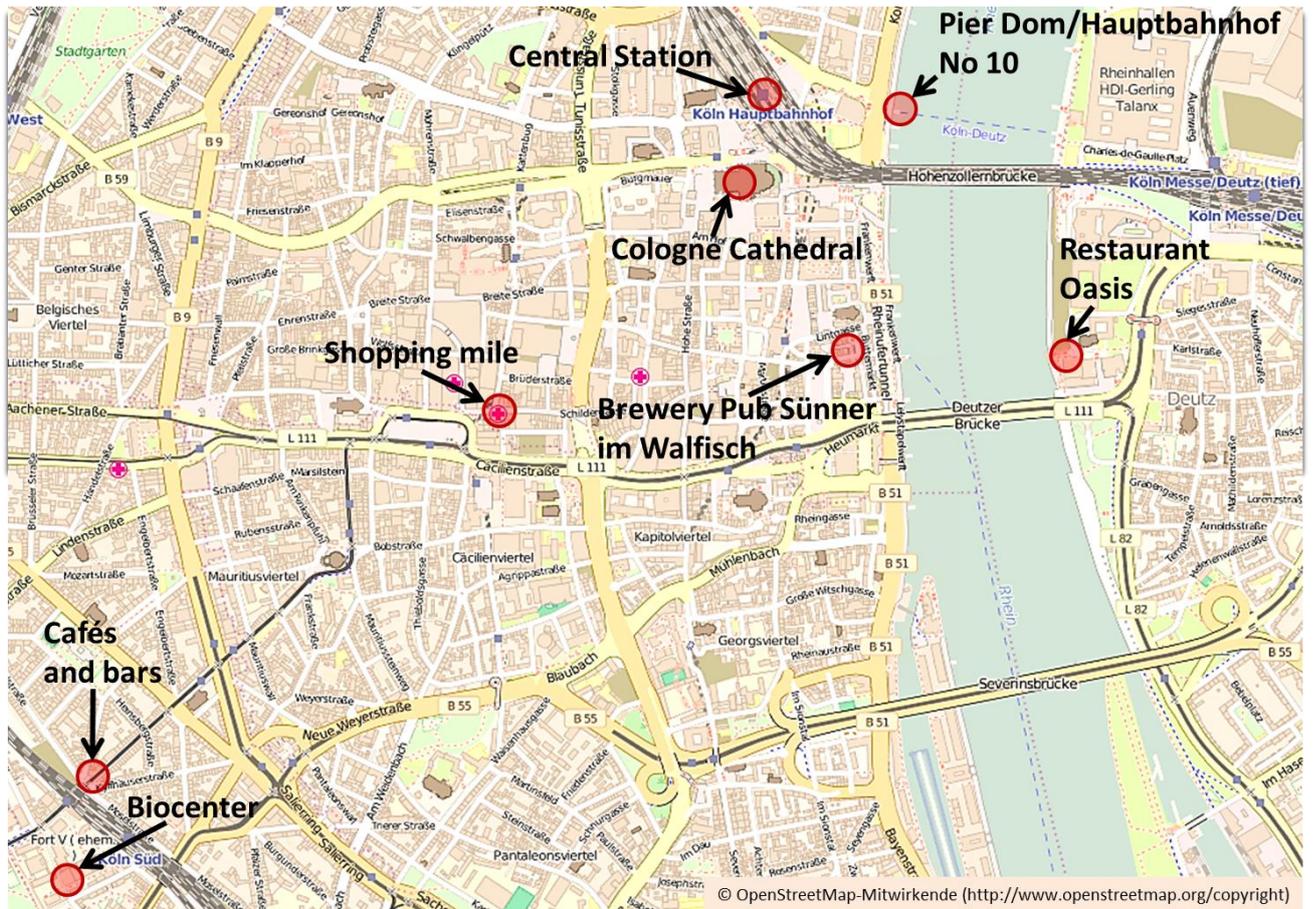
Over more than two decades the NC workshop has taken a pioneering role in bridging disciplines and introducing theoretical ideas and methods to neuroscience research. This concept of combining theoretical and experimental approaches has proven highly successful and nowadays plays a pivotal role in the modern neurosciences.

Research in neural coding covers neural representation, processing, and modulation of information at various levels of the nervous system. The program of NC 2016 reflects many aspects of neural coding and topics range from the theoretical mechanisms underlying single neuron function to sensory computation, memory formation, behavioral control, and robotic embodiment.

In keeping with its tradition, NC 2016 is a single-track meeting allowing for both, a deeper insight into individual topics and a broader look at the bigger picture. Extended poster sessions and an enjoyable social program shall provide ample opportunity for fruitful discussions and personal contacts.

We wish you all an interesting meeting and an enjoyable time in Cologne!

Martin Nawrot, Peter Kloppenburg, Moritz Deger, Ansgar Büschges
(local organizing committee)



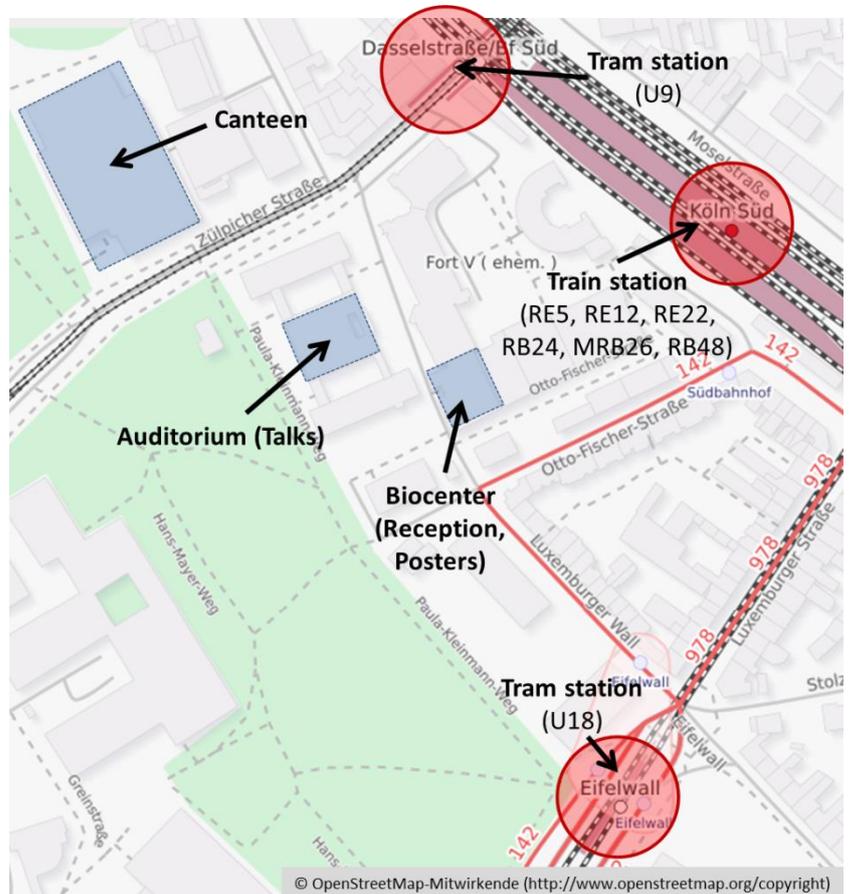
Biocenter:
Zülpicher Straße 47b

Auditorium:
Geo-/Bio-Hörsaal
Zülpicher Straße 49a

Brewery “Süner im Walfisch”:
Salzgasse 13, 50667 Köln
Tram station “Heumarkt”

Restaurant “Oasis”:
Kennedy-Ufer 1, 50679 Köln
Tram station “Köln Messe/Deutz”

Banquet Ship on the Rhine:
Konrad-Adenauer-Ufer,
Pier Dom/ Hauptbahnhof No 10
Tram station “Köln Hauptbahnhof”



Practical Information

The workshop will take place at the Biocenter of the University of Cologne situated in the city center (Zülpicher Str. 47b, 50674 Köln) close to Cologne south train station (“Köln Süd”).

Talks and coffee breaks will take place in and in front of the geology/biology auditorium („Geo-/Bio-Hörsaal“), situated in the building opposite of the Biocenter (Zülpicher Straße 49a).

At registration you will receive a conference badge, vouchers for all lunches, and a **ticket for the public transport** in the Cologne city area. With this ticket you can reach all the restaurants and get to the Cathedral for the guided tour.

Your **badge** is the key to access the conference rooms, coffee breaks, lunches and all the social activities. Please be ready to present your badge at all times.

Each **talk** is allocated a 20-minute time slot plus discussion. Speakers are requested **not to exceed the time limit** and to present the file with their slides to the chairman at the latest during the break before the session. If you prefer to use your own laptop for the presentation please test the setup during one of the breaks before.

All **posters** should be posted on Aug 29 in the morning. The posters can stay there for the whole conference but should be removed not later than Thursday Sep 1, 16:00, after the last session.

Lunches will be served in the Canteen (“Mensa”) of the University of Cologne, which is across Zülpicher Straße (address is Zülpicher Str. 70). Participants will receive lunch vouchers when they register along with the conference badge (one voucher per day).

For each **voucher** you can **choose either** of these offers:

- Main dish, small salad (NOT the buffet one), dessert & drink, or
- One mixed plate from the buffet (salads, etc), dessert & drink.

However, do not mix buffet and main dishes because that is not covered by the voucher, and you cannot pay with cash, leading to a deadlock situation at the cashier.

Wireless internet access is available through the network Uni-Koeln-802.1X. Access credentials were distributed by Email on Aug 17. Alternatively you may use eduroam access if your home institution provides it.

Post-workshop publications

Reviewed papers will appear in special issues of two journals – *Biosystems* and *Biological Cybernetics*. The details of the submission procedure and deadlines will be given on the web page of the workshop (<http://neural-coding-2016.uni-koeln.de>) and the participants will be informed by email.

The expected deadline for submission is **December 15, 2016**. The number of slots in each journal is limited. Therefore, the prospective authors are requested to confirm their intention to submit a paper by **30 September 2016** by email to neural-coding-2016@uni-koeln.de, and to indicate, which of the two journals they prefer and if their choice is exclusive.

For the special issue in *Biological Cybernetics* we welcome combined experimental-theoretical contributions and purely theoretical contributions of high quality. We specifically encourage „prospect“-type articles that provide an outlook into future research. *Biological Cybernetics* has a high reputation in the field and stands for a long tradition in biological information processing and in particular information processing in nervous systems. This is also expressed in the journal’s subtitle - Advances in Computational Neuroscience.

In line with the tradition of Neural Coding workshops, delegates of NC2016 are also invited to consider submitting full high quality contributions for a planned special issue of *BioSystems*. Neural Coding meetings and NC2016 in particular bring together computational and experimental neuroscientists that are interested in fundamentals of neural processing and coding, in both vertebrates and invertebrate systems. Topics include sensory coding, perception, plasticity and learning, and the neural control of behavior, which all fall within the wider aims and scope of *BioSystems*. Mechanisms are explored at the single neuron and the network level. Submitted manuscripts will be rigorously peer-reviewed.

Programme overview

12th International Neural Coding Workshop – Cologne, Germany – Schedule

	Sunday 28.08.16	Monday 29.08.16	Tuesday 30.08.16	Wednesday 31.08.16	Thursday 01.09.16	Friday 02.09.16
08:00 – 09:00		08:30 – 09:15				
09:00 – 10:00		Registration	09:00 – 10:30	09:00 – 10:30	09:00 – 10:30	9:00 – 11:00 Round table (optional)
10:00 – 11:00		09:15 – 10:30 Intro & Sg N M 1	Single Neuron Math 2	Methods	Motor	
11:00 – 12:00		Coffee break	Coffee break	Coffee break	Coffee break	
12:00 – 13:00		11:00 – 12:30 Invertebrates	11:00 – 13:00 Network Structure &	11:00 – 12:30 Synchrony	11:00 – 12:30 Variability	
13:00 – 14:00		12:30 – 14:00 Lunch	Plasticity 13:00 – 14:00 Lunch	12:30 – 14:00 Lunch	12:30 – 14:00 Lunch	
14:00 – 15:00		14:00 – 16:00 Posters 1 and Coffee		14:00 – 15:00 Math Network	14:00 – 15:30 Robotics	
15:00 – 16:00				Coffee break 15:30 – 16:30		
16:00 – 17:00		16:00 – 17:30 Vision	Guided tour of Cologne Cathedral	Math Network 16:30 – 18:30		
17:00 – 18:00				Posters 2 and Refreshments		
18:00 – 19:00	18:00 – 20:00 Reception / Registration					
19:00 – 20:00		Dinner "Oasis"	Dinner Brewery "Walfisch"	Dinner at Biocenter	Banquet Ship on the Rhine	

Conference Programme

Sunday, August 28th

18:00-20:00 Registration & Reception

Monday, August 29th

8:30 Registration opens

Introduction – 9:15 – 9:30

9:15 Welcoming and practical information

Single Neuron Math 1 – 9:30 – 10:30

9:30 *Marie Levakova* - Signal-enhancing effect of spontaneous activity in latency coding p. 43

10:00 *Massimiliano Tamborrino* - Neuronal response latency estimation in presence of a background signal p. 88

Coffee break – 10:30 – 11:00

Invertebrates – 11:00 – 12:30

11:00 *Jan Clemens* - The organization of adaptation in the auditory receptor neurons of *Drosophila* p. 14

11:30 *Thomas Nowotny* - The early olfactory code in bees p. 60

12:00 *Roman Borisyuk* - A computational model for decision making and behaviour selection in *Xenopus* tadpoles p. 7

Lunch – 12:30 – 14:00

12:30- Canteen (“Mensa”), Zülpicher Straße 70. Use voucher! map

Poster Session 1 – 14:00 – 16:00

14:00 Even numbered posters are presented, all are visible.
In the lobby of the Biocenter, Zülpicher Str. 47b.
Coffee will be available during the poster session.

Vision – 16:00 – 17:30

16:00	<i>Björn Kampa</i> - Specific excitatory connectivity for feature integration in mouse primary visual cortex	p. 28
16:30	<i>Jens Kremkow</i> - Principles underlying sensory map topography in primary visual cortex	p. 37
17:00	<i>Markus Diesmann</i> - Multi-area model of macaque visual cortex at cellular and synaptic resolution	p. 16

Dinner

19:00	Restaurant Oasis, Kennedy-Ufer 1	map
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Tuesday, August 30th

Single Neuron Math 2 – 09:00 – 10:30

9:00	<i>Laura Sacerdote</i> - Integrate and fire like models with stable distribution for the interspike intervals	p. 76
9:30	<i>Luisa Testa</i> - Ito excursion theory: an application to the firing paradigm in stochastic neuronal models	p. 82
10:00	<i>Lubomir Kostal</i> - Neural coding accuracy and stimulus information in variable frames of reference	p. 33

Coffee break – 10:30 – 11:00

Network Structure & Plasticity – 11:00 – 13:00

- 11:00 *Gaia Tavosanis* - Structural correlates of olfactory conditioning in the mushroom body calyx of adult flies p. 3
- 11:30 *Wulfram Gerstner* - Synaptic plasticity controlled by surprise p. 20
- 12:00 *Nestor Parga* - The dopamine signal under sensory and temporal uncertainty p. 63
- 12:30 *Kei Ito* - Understanding neuronal circuits and their functions using expression driver systems of the fruit fly *Drosophila melanogaster* p. 26

Lunch – 13:00 – 14:30

- 13:00- Canteen (“Mensa”), Zülpicher Straße 70. Use voucher! map

Guided tour of Cologne Cathedral 16:00-17:30

- 15:50- There are two tours to choose from: (i) cathedral roof map
17:30 tour (“Domdachführung”) or (ii) archeological excavations tour (“Ausgrabungsführung”). All tours are in English, take 90 minutes, and start at 16:00 sharp, so please be there at 15:50. We meet in front of the main portal of Cologne Cathedral (“Dom”).

Dinner

- 18:30- Brewery-restaurant „Sünner im Walfisch“, map
Salzgasse 13

Wednesday, August 31st

Methods – 09:00 – 10:30

- 9:00 *Aubin Tchaptchet* - Numerical implementation of neural diversity p. 90
- 9:30 *Michael Stiber* - Bringing high performance neural simulation to the desktop with BrainGrid p. 84
- 10:00 *Taro Tezuka* - Neural Decoding by Spike Train Factor Analysis Kernel p. 92

Coffee break – 10:30 – 11:00

Synchrony – 11:00 – 12:30

- 11:00 *Benjamin Lindner* - Synchrony coding by neural populations - theory and experiment p. 45
- 11:30 *Angelo Di Garbo* - Nonlinear quantification of inter-hemispheric coupling in neocortical epilepsy in mice p. 97
- 12:00 *Farzad Farkhooi* - Phase transition to stochastic synchrony in the balanced networks p. 18

Lunch – 12:30 – 14:00

- 12:30- Canteen (“Mensa”), Zülpicher Straße 70. Use voucher! map

Math Network 1 – 14:00 – 15:00

- 14:00 *Ryota Kobayashi* - Testing statistical significance of synaptic connectivity p. 31
- 14:30 *Tilo Schwalger* - Stochastic mean-field theory for finite-size populations of spiking neurons p. 80

Coffee break – 15:00 – 15:30

Math Network 2 – 15:30 – 16:30

- 15:30 *Matthieu Gilson* - Correlation coding in noise-diffusion networks: from experimental basis toward a theory of distributed representations p. 21
- 16:00 *Alessandro Villa* - Clique topology and dynamics in neuronal network simulations p. 52

Poster Session 2 – 16:30 – 18:00

- 16:30 Odd numbered posters are presented, all are visible. In the lobby of the Biocenter, Zülpicher Str. 47b.

Dinner

- 17:00- Food and drinks will be provided during the poster session at the Biocenter.

Thursday, September 1st

Motor – 09:00 – 10:30

- 9:00 *Yifat Prut* - Excitation-inhibition interplay controls timing and coordination of motor actions p. 67
- 9:30 *Alexa Riehle* - Variability of motor cortical spiking activity is modulated by the behavioral context p. 71
- 10:00 *Sonja Grün* - Behavioral related synchronous spike patterns in macaque motor cortex during an instructed-delay reach-to-grasp task p. 22

Variability – 11:00 – 12:30

- 11:00 *Thomas Rost* - Variability dynamics in balanced networks with clustered inhibitory and excitatory connectivity p. 74
- 11:30 *Tomokatsu Onaga* - Criticality in the emergence of spontaneous fluctuations in spiking neuron networks p. 62

12:00 *Petr Lansky* - Variability in neural spike trains p. 68

Lunch – 12:30 – 14:00

12:30- Canteen (“Mensa”), Zülpicher Straße 70. Use voucher! map

Robotics – 14:00 – 15:30

14:00 *Yuichiro Yada* - Goal-directed behavior of a cultured neuron robot through reservoir computing p. 102

14:30 *Nicholas Szczecinski* - MantisBot is a robotic model of visually guided motion in the praying mantis p. 86

15:00 *Tim Landgraf* - Neural correlates of flying insect navigation: from simulation to electro-physiology on a quadcopter p. 39

15:30 Final remarks by the organizers.

Conference Banquet

18:30- The conference banquet will take place on a boat map
22:00 which will cruise on the Rhine river.

Please be at the pier before 18:30 because the ship will not wait for long before we leave.

Pier name: „Anleger Köln Hbf (10)“ (pier no. 10, close to Cologne main train station). This is at the street “Konrad-Adenauer-Ufer”, opposite of the “Musical Dome” (see map).

Friday, September 2nd

9:00 Round table (optional), in the Biocenter. map

Poster Overview

All posters will be set up on their poster board (see No.) for **both** poster sessions. However, presenters should **primarily** present their poster during the indicated presenting session, to avoid stepping on each others feet (even numbers: session 1, odd numbers: session 2). Therefore neighboring posters are assigned to poster sessions alternatingly.

All posters should be posted on Aug 29 in the morning!

Presenter	Authors	Title	No.	Pres. Sess.
Susanne Hindennach	Susanne Hindennach, Debora Fusca, Martin Nawrot, Peter Kloppenburg	Dynamical processing of olfactory input in different types of antennal lobe neurons of the american cockroach	1	2
Alexander Vidybida	Alexander Vidybida	Fast Cl-type inhibitory neuron with delayed feedback has non-Markov output statistics	2	1
Alessandra Lintas	Takeshi Abe, Yoshiyuki Asai, Alessandro E.P. Villa, Alessandra Lintas	Neural dynamics in the mouse basal ganglia-thalamocortical circuit	3	2
Kseniia Kravchuk / Alexander Vidybida	Kseniia Kravchuk	First passage time of leaky integrate-and-fire neuron driven by a jump process	4	1
Irina Sinakevitch	Irina Sinakevitch, George R Bjorklund, Jason Newbern, Brian H Smith	Comparative study of chemical neuroanatomy of the olfactory neuropil in mouse, honey bee and human	5	2
Brian Smith	Thiago Mosqueiro, Martin Strube-Bloss, Brian Smith, Ramon Huerta	Accelerated information transmission with stable sparse code in strongly divergent-convergent feedforward networks	6	1

Presenter	Authors	Title	No.	Pres. Sess.
Tzai-Wen Chiu	Tzai-Wen Chiu, I-Chieh Huang, Paul Wai-Fung Poon, John F. Brugge, Hiroyuki Oya, Richard A. Reale, Hiroto Kawasaki, Kirill Nourski, Haiming Chen, Matthew A. Howard III	Variations of single-trial sound-evoked responses over the human temporal cortex	7	2
Michael von Papen	Michael von Papen, Esther Florin, Lars Timmermann, Joachim Saur	Nonparametric Granger causality of parkinsonian tremor	8	1
Sidney Lehky	Sidney R. Lehky, Ahn Huy Phan, Andrzej Cichocki, Keiji Tanaka	Coding of Faces by Tensor Components	9	2
Vezha Boboeva	Vezha Boboeva, Alessandro Treves	Beyond random correlations to learning structured correlations among concepts of a semantic cortical network	10	1
Ondrej Pokora	Ondrej Pokora, Jan Kolacek, T. W. Chiu	Functional data analysis of the recordings of auditory evoked potentials	11	2
Silvia Daun-Gruhn	N. Rosjat, S. Popovych, L. Liu, B. Wang, T. Tóth, C. Grefkes, G. R. Fink, S. Daun-Gruhn	Differences in movement-related, inter-regional phase-locking in young and elderly healthy subjects	12	1
Fioralba Ajazi	Tatyana Turova, George M. Napolitano, Fioralba Ajazi	Random distance graphs on torus	13	2
Christina Zavou	Christina Zavou, Achilleas Koutsou, Chris Christodoulou	Correlating pre-synaptic synchrony with experimentally recorded intracellular membrane potential	14	1
Joscha Schmitz	Joscha Schmitz, Matthias Gruhn, Ansgar Büschges	Adaptive motor control: task-specificity of movement feedback processing during the generation of steps in a curve walking insect	15	2

Presenter	Authors	Title	No.	Pres. Sess.
Rosanna Migliore	Rosanna Migliore, Xavier Leinekugel, Michele Migliore	Effects of electric fields on cognitive functions	16	1
Petr Marsalek	Petr Marsalek	Quantitative description of neural computations in the auditory brainstem using the ergodic hypothesis	17	2
Hubert Löffler	Hubert Löffler	Subthreshold oscillations facilitate memory of precise temporal spike trains: A computational approach	18	1
Iulia-Alexandra Lungu	Iulia-Alexandra Lungu, Alexa Riehle, Martin Nawrot, Michael Schmuker	Predicting arm movement direction with spiking neural networks and neuromorphic hardware	19	2
Hannes Rapp	Hannes Rapp, Martin Nawrot, Moritz Deger	Modeling of EEG time-series by conditional probability neural networks	20	1
Maria Francesca Carfora	Maria Francesca Carfora, Enrica Pirozzi	A stochastic model for the firing activity of neurons in a network	21	2
Masahiro Furukawa	Masahiro Furukawa, Shigeru Shinomoto	Spectral analysis of local field potential	22	1
Christina Zavou / Chris Christodoulou	Antria Kkoushi, Achilleas Koutsou, Chris Christodoulou	Synchrony measure for a neuron driven by excitatory and inhibitory inputs	23	2
Aaradhita Upadhyay	Aaradhita Upadhyay, Svenja Schneider, Anna Kaczmarek, Laura Torres Benito, Vanessa Grysko, Min Jeong Kye, Markus Riessland, Natalia Kononenko, Brunhilde Wirth	MOD2, potential SMA modifier and much beyond?	24	1

Presenter	Authors	Title	No.	Pres. Sess.
Aubin Tchapchet	Hans A. Braun, Aubin Tchapchet	Connecting mathematical modeling with electrophysiological experiments: The virtual laboratories SimNerv and SimNeuron	25	2
Olha Shchur	Alexander Vidybida, Olha Shchur	Role of neuronal firing in reduction of dynamical states set in reverberating neuronal network	26	1
Enrica Pirozzi	Enrica Pirozzi	Towards modeling of stochastic correlated inputs and adaptation in neuronal firing	27	2
Shinsuke Koyama	Shinsuke Koyama	Approximate methods for the inference of stochastic reaction networks	28	1
Abdulraheem Nashef	Abdulraheem Nashef, Oren Cohen, Yifat Prut	Thalamocortical mechanisms controlling motor timing in behaving primates	29	2
Martin Nawrot	Rinaldo Betkiewicz, Benjamin Lindner, Martin Nawrot	Odor representations in a spiking model of the insect olfactory system are optimized by lateral inhibition and cellular adaptation	30	1

Abstract Book

talks and posters

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Neural dynamics in the mouse basal ganglia-thalamocortical circuit

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The reticular nucleus of the thalamus (RTN) is formed by a thin sheet of neurons, whose majority are GABAergic cells expressing parvalbumin (PV), located on the medial aspect of the internal capsule and partially surrounding the dorsal thalamus. The RTN is a unique gateway in filtering and sorting sensory information that passes through the thalamocortical and corticothalamic axis and its activity is strongly regulated by the basal ganglia via the dopaminergic (DA) afferences from the substantia nigra compacta and by the GABAergic inhibitory projections from the pallidum and from the substantia nigra pars reticulata.

The DA-mediated effect on the GABAergic inhibitory neurons expressing PV affect the balance between Excitation and Inhibition at the level of the basal ganglia-thalamocortical system. We recorded simultaneously several spike trains recorded at different levels of the mouse basal ganglia thalamocortical circuit of wild-type and PV deficient mice [1]. We used time-domain, frequency-domain and Granger causality analysis [2] to study the fine dynamic relationships within different elements of that neural circuit (see Figure 1).

Prefrontal areas sending projections to RTN are involved in the control of attention and RTN is involved in rapidly moving the center of attention between external input, based on a decision made by the frontal cortex. Relevant psychiatric disorders such as ADHD and schizophrenia have been associated with a dysfunction of the RTN. It is therefore likely that a perturbation of the E/I balance within the basal ganglia-thalamocortical circuit is associated with abnormal activity patterns in RTN.

Keywords: basal ganglia, thalamocortical circuit, spike train analysis, Granger causality, crosscorrelogram, coherence analysis

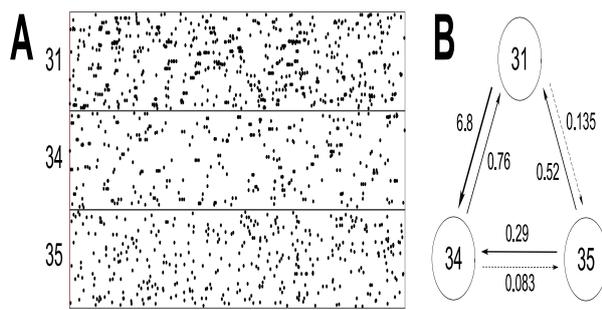
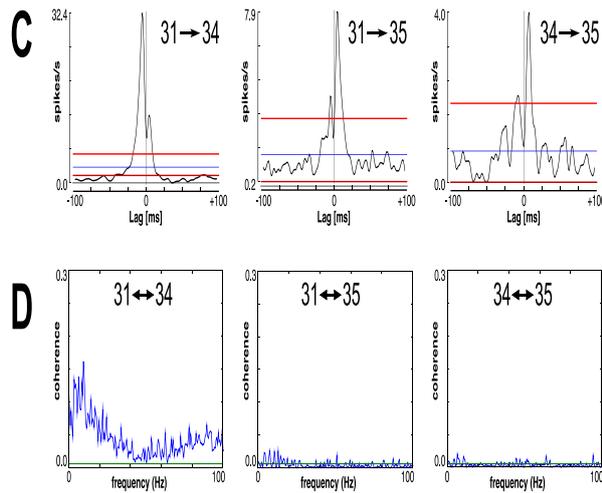


Figure 1: A. Raster display of three cells (#31, #34 and #35) recorded in the mouse reticular nucleus of the thalamus. The horizontal time scale corresponds to 1000 ms. B. Connectivity diagram as determined following the Granger causality analysis using autoregressive model of order 20. C. Crossrenewal density histograms in the range 0-100 ms using a Gaussian bin smoothing of 5 ms. Negative values refer to the opposite trigger-follower curve. D. Coherence analysis in the range 0-100 Hz.



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Structural correlates of olfactory conditioning in the mushroom body calyx of adult flies

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The fly mushroom body (MB) is essential for olfactory associative memory formation and retrieval. In the MB calyx the Kenyon cells (KCs) receive presynaptic input from second-order cholinergic projection neurons (PNs) delivering olfactory information. Together, they form distinct synaptic complexes called calycal microglomeruli (MGs). Those consist of a single presynaptic PN bouton, enclosed by claw-like postsynaptic sites of several KCs. We asked whether appetitive associative olfactory learning is accompanied by changes of synaptic connectivity between PNs and KCs in the mushroom body calyx. We trained adult flies in the classic two-odor appetitive-conditioning paradigm using the pheromone 11-cis-vaccenyl acetate (cVA) and geranyl-acetate (GA). Although flies exhibit preference for cVA after starvation, we found that females and males display clear long-term memory of the appetitive conditioning at 24 hours after training. To observe potential structural changes correlated with long-term associative memory formation, we labeled only those PNs responsive to cVA with a specific driver line expressing the fluorescently-tagged presynaptic active zone marker Brp-short-cherry. We additionally visualized the postsynaptic compartment of MGs using a GFP-tagged subunit of the acetylcholine receptor expressed in most KCs. A high throughput, automated 3D reconstruction method allowed analyzing morphological changes in the calycal MGs. We specifically addressed whether the MGs connected to the DA1 antennal lobe glomerulus responding to cVA displayed changes in flies conditioned to cVA after long-term memory formation. This analysis revealed that MGs responsive to cVA decreased in size in trained flies compared to the unpaired control. Furthermore, the number of the MGs responsive to cVA increased. Neither of these changes was detectable in flies that expressed short-term appetitive memory or in flies in which long-term memory formation was impaired by blocking protein synthesis after the training. These data reveal that long-term appetitive memory formation correlates with changes in size and number of the responsive calycal MGs. These changes suggest extensive rewiring during consolidation. We propose that the modulation of MG size and number might lead to a facilitated response to the conditioned odor.

Keywords: *Drosophila*, mushroom body, long-term memory

Odor representations in a spiking model of the insect olfactory system are optimized by lateral inhibition and cellular adaptation

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To understand the underlying mechanisms behind sensory processing we investigate odor representations in two principal stages of the insect olfactory system. In the antennal lobe (AL) odor representations are dense and dynamic. In the Mushroom Body (MB) representations are sparse. The neural odor code in these animals emerges within 50ms after stimulus onset and neural representation changes dynamically during and after an odorant is present [1, 2]. We present a comprehensive spiking neural network model of the olfactory pathway that reproduces the spatial and temporal patterns of the odor code in the AL and the MB observed in neurophysiological experiments [1, 3].

We find that odor responses at the AL and the MB are shaped by two mechanisms: (1) uniform lateral inhibition within the AL, and (2) cell intrinsic spike-frequency adaptation. Together, both mechanisms underlie dynamic odor representation in the AL and robustly regulate the spatial and temporal sparseness in the KC population. In addition, time decoding classification of odor representations reveals that representations are optimized for decoding odor identity during stimulus on- and offset. Interestingly, at the AL level odor identity can be decoded well beyond stimulus offset, whereas at the MB level a prolonged stimulus trace is only found in intrinsic adaptation currents but not the spiking response.

Keywords: olfaction, sensory processing, spiking networks

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Beyond random correlations to learning structured correlations among concepts of a semantic cortical network

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Hierarchical tree-based models have long been the classic way of thinking about how semantic information is organized in the brain. However, such approaches have been proved to be insufficient and even inconsistent with a variety of observations [1], leading to the hypothesis that seemingly "category specific" deficits arise as an emergent property of a semantic system organized in a non-categorical manner. The introduction of distributed representations of concepts, each being an ensemble of features, is able to explain and predict many deficits without assuming a categorical organization of this knowledge in a tree [2].

There have been data-driven attempts to derive feature norms for words and encode them in a network [3], but such attempts have been limited in their scope because the data they can use is limited. The multi-parent algorithm with which we generate activity patterns in the Potts network, which serve as model word representations, is a simple concrete way to go beyond hierarchical trees toward models which envisage multiple influences [4]. Our approach offers the advantage of allowing the generation of representations of arbitrary scope and correlation, which in turn allows for a systematic quantitative study of the behaviour of the network

One natural question arising in the study of a such a network is that of the storage capacity. To address this question, we have developed a signal-to-noise analysis that we have so far applied to random correlations. Currently, there is still a slight mismatch in our results between the theoretical curve obtained analytically and that derived from computer simulations, that derives from the fact that stable states do not coincide with the exact memory patterns stored in the network. In fact, when gradually increasing the memory load initially, at low loads, one does not observe too many variants of each prototypical memory item: all simulations tend to end up in one of very few distinct states, with energy levels that are very close to one another. As the loading increases, however, stable states begin to proliferate in the vicinity of the prototype. Close to and beyond the storage capacity, there is almost a continuum in the multiplicity of stable states, with variable degrees of mixing with other memory items.

This combinatorial increase in the number of accessible states, referred to as the Potts glass phase, may be related to an interesting phenomenon, that of a unfounded distinction between for example, exact recall and confabulation [5]. Notably, the Potts glass phase has been largely neglected in associative networks, where the focus has been on the retrieval phase, mainly because we tend to think that a memory system should work by storing exact copies of items and then retrieving the stored copy, as in a computer database. We can understand the relevance of the Potts Glass phase if we go beyond this psychological construct and view

memory as a dynamic, reconstructive process, in which each particular recall can be described as the trajectory of the network from an initial cue point to a local minimum in the rugged energy landscape of the very high dimensional phase space of activity.

The follow-up of this reasoning leads to a count of the number of these stable states. For the Hopfield model, Treves and Amit [6] have shown that there is an exponentially high number of stable states. The application of a similar computation for our model is currently on hold for mathematical reasons, but the results from our simulations point to similar results. Finally, a new information theoretic perspective [7] may re-open the way to concluding our estimation of these stable states.

Keywords: semantic memory, Potts network, storage capacity

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A computational model for decision making and behaviour selection in *Xenopus* tadpoles

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A general approach to decision making postulates that signals from different sensory modalities are integrated to select from amongst multiple options. This integration process is important due to the noisy nature of sensory signals. A computational model describing dynamics of behaviour responses to the input signals from an environment is presented. We implement the integration of noisy sensory signals in a computational model that can describe the behavioural switching observed in hatching *Xenopus* tadpole [1]. This animal is a good place to study decision making process because its repertoire of behaviours and sensory signals is rather small and many biological details are known from experimental studies. At the same time the computational model can clarify the key universal neurobiological mechanisms and formulate the theoretical principles for understanding the decision making process as well as to provide new ideas and hypotheses for experimental testing. The model includes 26 ordinary differential equations describing the average activities of various neuronal populations at the head and on the left and right sides of the spinal cord.

The model has two parts. The first part of the model relates to the central pattern generator (CPG) neurons that generate locomotor behaviour. The repertoire of possible locomotor actions includes: (a) starting swimming; (b) stopping swimming; (c) accelerating swimming; (d) starting struggling; (e) stopping struggling. To model these actions we consider neural populations of excitatory and inhibitory neurons on both sides. Each population is represented by the Wilson-Cowan model [2, 3], which describes the dynamics of the average neuronal activity in the population. Bifurcation analysis of excitatory and inhibitory population activities can determine the region in the parameter space where oscillations exist [2]. Thus, a pair of interactive populations forms a neural oscillator. In paper [3] we have studied two coupled neural oscillators and found a broad range of possible dynamical regimes: steady-state activity, in-phase and anti-phase oscillations, quasiperiodic (modulated) activity, and chaotic dynamics. These studies give us a possibility to select parameter values to mimic swimming activity (anti-phase oscillations on two sides of the spinal cord) in a range of appropriate frequencies (including acceleration and slowing of the swimming). A regime of struggling behaviour is modelled by bursting activity. Fast in-phase oscillations on opposite sides of the spinal cord are modulated in an envelope by slow anti-phase oscillations. Also, bifurcation analysis highlights how parameters can be changed to control dynamics and switch from one mode to another.

The second part of the model describes sensory pathways and signal integration. This modelling is based on recent neurobiological findings on neuronal coordination of the initiation of locomotion [4]. The model includes four sensory signals: (1) touch trunk skin; (2) touch head; (3) dim light and (4) press the head or cement gland (inhibitory signal). These signals arrive at an integrating population where decision making and action selection from the CPG repertoire occurs.

We demonstrate how an arbitrary sequence of external environmental inputs (represented as noisy sensory signals) are processed by sensory pathways and passed to the integrating population, which selects an appropriate sequence of actions and generates the tadpole's behaviour. For example, following simulated touch of the tadpole's skin, the animal starts swimming (locomotor action (a)). If the light is subsequently dimmed the swimming frequency temporarily increases (locomotor action (c), accelerated swimming). If during swimming a long enough skin touch has been applied to both sides of the body (e.g. a dragonfly catches the tadpole) then the model makes the decision to select locomotor action (d) - start of struggling and continues this action until the skin touch input from both sides disappear. At that time locomotor action (e), stop struggling, is selected and the model returns to action (a), start of swimming. Thus, any prescribed temporal sequence of external signals results in a corresponding sequence of selected actions.

Keywords: population model, sensory modalities, integration of signals

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Connecting mathematical modeling with electrophysiological experiments: The virtual laboratories SimNerv and SimNeuron.

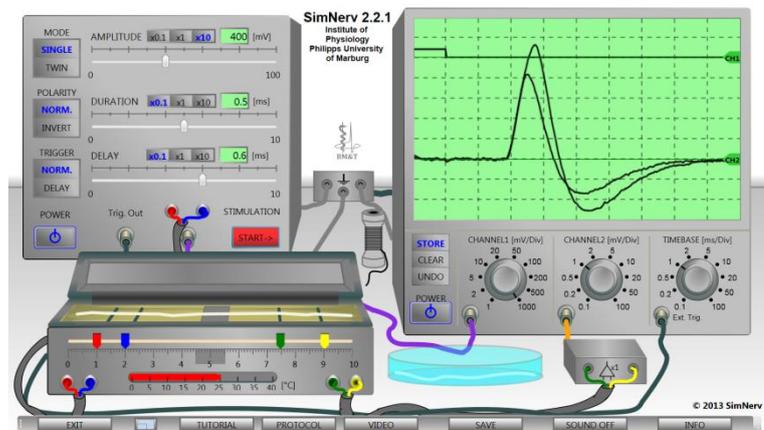
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Experts in mathematical modeling often do not have many insights into the problems of experimental neurophysiologists while many electrophysiologists do not know how to make use of their data for mathematical modeling. Many attempts have already been made, also by our group, to overcome such obstacles to broader use of physiologically adequate mathematical simulations in direct relation to experimental data [1-3]. Among others we have designed virtual laboratories like SimNerv and SimNeuron for experimentation in simplified but realistically appearing lab environments on the computer screen (see figures). All stimulation and recording devices are freely adjustable and mathematical algorithms guarantee for the physiologically adequate reactions of the virtual neurons and nerves, also considering their physiological diversity [4].

Figure 1: The virtual SimNerv laboratory for extracellular recordings of compound action potentials from peripheral nerves. One of the nerves is placed in recording chamber. The electrodes on the left are connected to a stimulator for the application of current pulses. The recording electrodes (right) are connected to an oscilloscope via a differential amplifier. The two recordings on the oscilloscope screen have been obtained with exactly identical current pulse. Can you imagine what has been changed to make the one potential bigger than the other one?



These virtual laboratories have originally been designed for students' experimentation in practical courses without the use of animal tissue. However, it turned out that the laboratories can also provide new insights for experienced neuroscientists. This especially holds true for SimNeuron which includes a "Neuron Editor" (Fig. 2) showing the complete set of the mathematical equations with all numerical parameter values that the user themselves can change.

For experimentalists it is important that the Hodgkin-Huxley type equations are given in a modified form which allows direct overtaking of the experimentally determined key values. Moreover, the algorithms also consider experimentally often modified parameter like ion concentrations. The mathematicians can make their own voltage and current recordings to see how basic current- and voltage-clamp data from conventional experiments are reflected in the model parameters. In contrast to real experiments, also the time course of ion conductances and current can be plotted in addition to voltage traces.

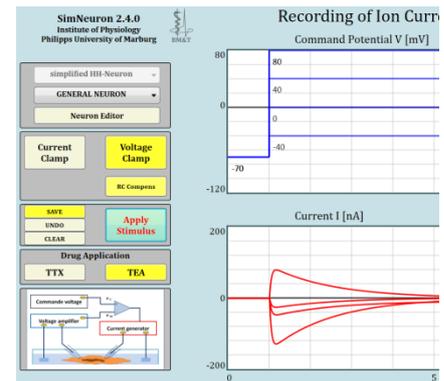
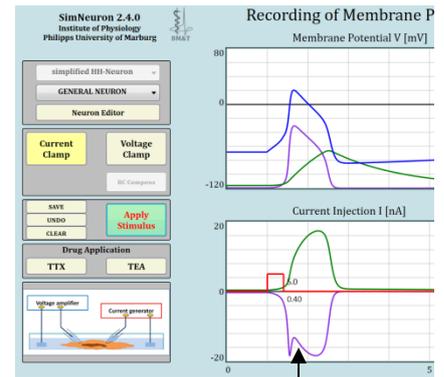
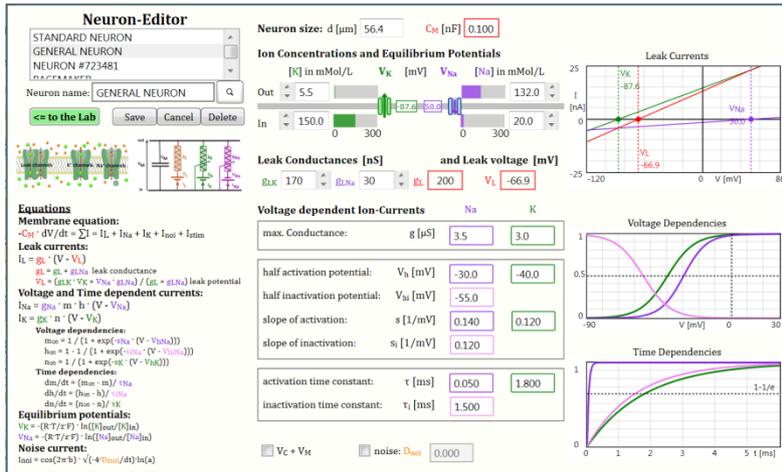


Figure 2: The Neuron Editor and parts of the current- and voltage-clamp labs of SimNeuron including recording examples. In the upper right current-clamp lab, in addition to the stimulus induced action potential, also the Na^+ - and K^+ -conductances and currents are shown. Do you understand the curves and can you explain the transient reduction of the Na^+ current (arrow)? The recordings of selective Na^+ currents in the voltage clamp lab in response to different command potentials may give a hint. Do you understand why the Na -current changes its direction? Would you know how to determine the reversal potentials, also of the K -current?

Everybody may check whether he/she immediately understands the example recordings in the figures and can answer the questions. These and more phenomena are described in detailed tutorials and protocol forms with which the programs are coming along. Fully functioning demo versions can be downloaded from www.virtual-physiology.com. More information and demonstrations will be given at the poster.

Keywords: Hodgkin-Huxley type neuron, voltage clamp, ion conductances

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A stochastic model for the firing activity of neurons in a network

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In the last decade an increasing attention has been paid to the representation of the dynamics of interacting neurons in little and large networks [6, 7, 8, 9] through different stochastic models. We recently proposed [1, 2, 4] a model suitable to describe the interactions between two neurons, where we also included a time-dependent synaptic current conveying external stimuli. Here we extend such previous model to a finite-sized network of linked neurons. As a first step, we consider three linked stochastic LIF-type equations, each one describing the evolution of the membrane voltage of a neuron in this little network (see Fig.1 – left). The interaction linkages are realized by including a function H for the synaptic current that jumps when one or both the other neurons fire. So in the small network depicted in Figure, the stochastic differential equation (SDE) for the membrane potential V_{22} of neuron N_{22} is

$$dV_{22}(t) = \left[-\frac{1}{\theta}V_{22}(t) + \frac{\rho + \mu\theta}{\theta} + i_0e^{-t/\alpha} + k_{22}(1 - e^{-t/\alpha})H_{22}(t) \right] dt + \sigma dW(t)$$

where the linking function H_{22} is a linear combination of the indicator functions of the spikes of the two other neurons and weights are chosen based on symmetries and distances in the network; k_{22} modulates intensity and sign of this random input. In this theoretical setting, we are able to determine three Gauss-Diffusion (GD) processes suitable to describe the above dynamics by obtaining their mean and covariance functions. The mean of such processes involves the distribution of the firing of the other neurons. Then we determine an approximation of the first-passage-time distributions (FPT Df) of each process, by solving a system of non-singular second-type Volterra integral equations via a numerical procedure. In this interactive scheme, under suitable hypotheses, the possibility to investigate on the Interspike Intervals (ISIs) by using the FPT density of each neuron will be considered. Moreover, under the hypothesis that the membrane potentials of one or two neurons (say, that of the neurons N_{11} and N_{12}) stay in a particular asymptotic regime we exploit closed-form expressions for their FPT to obtain approximations of the firing density of neuron N_{22} . We also compare both these numerical approximations of the FPT pdf with histograms of simulated FPTs, obtaining a satisfactory agreement between our numerical predictions and simulated results for each neuron in the interconnected network.

As a second step, we model a network of four interconnected neurons, graphically represented as a square matrix of dimension two with several connecting edges along which information is transmitted. In this case, our stochastic model comprises four SDEs linked by indicator functions of the firing activity of the other neurons. Suitable GD processes are used also in this case to provide evaluations of FPT pdf for the estimation of firing densities; an asymptotic analysis is also done. Finally, along these lines, a general model for a network of

$N \times N$ neurons is proposed (as an example, see Fig.1 – right). We deal with some additional investigations, such as the study of joint distributions of the dynamics of involved neurons, the correlation of the firing of the neurons, the study of the effect of successive spikes [5] of one or more neurons on the dynamics of the other neurons in the network, the effect on the whole network of a superimposed current on one neuron, the phenomenon of spike-frequency adaptation [3]. Suitable simulation algorithms have been realized for such networks: their results can be useful for a large range of investigations and comparisons.

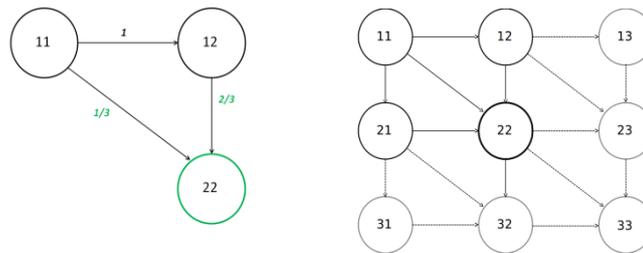


Figure 1. Schematic representation of a 3 neurons network (left) and of a 9 neurons network (right).

Keywords: time inhomogeneous LIF model; interaction linkage; simulation.

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Variations of single-trial sound-evoked responses over the human temporal cortex

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Knowledge on the neural coding of complex sounds in the human auditory cortex is important for understanding speech processing. To this end, we studied the variations of single-trial sound-evoked responses (electrocorticogram, ECoG) from 10 consented patients with intracranial multiple-electrodes as part of the treatment plans for epilepsy (protocols approved by the University of Iowa Institutional Review Board). ECoGs were recorded with two sets of electrodes over the temporal lobe on one side: (a) a subdural electrode grid (8x12 contacts) placed over the association area (superior temporal gyrus, STG), and (b) a 4-contacts depth electrode placed in the primary area (Heschl's gyrus, HG). Three types of sounds were presented repetitively under passive listening: (a) dynamic AM tone bursts (a 2 kHz tone modulated from 40 to 150 Hz with linear rising/falling phases); (b) FM tones that emerged from a 'random FM' tone (250 to 750 Hz) with two different modulating profiles (sweeping from 500 Hz to 2 kHz, with linear rising/falling phases); and (c) a click train (5 clicks, 10 msec intervals). Each listening session lasted for 5-min during which each type of sounds was presented for 100 episodes at jittered intervals (1.5 -4.5 sec). Single-trial ECoG responses were first extracted from the background EEG with an adaptive filter. The strength of each evoked response was represented by the root-mean-square (RMS) value, and the variation of the strengths within a session was represented by the standard deviation (SD). In silence, RMS and SD levels showed a linear relationship reflecting an underlying Poisson process. Upon episodic sound stimulation, this linear relationship deviated from Poisson, suggesting a change in neural dynamics by sound. Furthermore, the spatial patterns of RMS and SD over the temporal lobe varied depending on the stimulus sound type. Typically, a larger area over STG showed a characteristic drop in SD closed to (but not overlapping with) a more restricted area showing strong RMS response. The reduced SD in the background EEG activity could be explained by suppression (if not synchronization) of the underlying neural elements induced by sound. At the HG, RMS values were large at the medial part (auditory core), whereas SD values were large at the lateral part (auditory belt). On the STG, areas with large SD values were consistently found distal to the area of large RMS values. The distal locations of large SD values over STG were consistent with their role as association processing areas (auditory parabelt). Results were consistent with the roles of different parts of the temporal cortex in processing different sound features. This study also showed for the first time that the variation of single-trial response to sound could be a novel response metric for characterizing functional localization of the auditory cortex.

The organization of adaptation in the auditory receptor neurons of *Drosophila*

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Adaptation is a ubiquitous property of sensory neurons and improves the quality and efficiency of stimulus representations. Adaptation to various properties of the stimulus distribution - like the mean or variance - coexist within the same sensory pathway, yet the interaction between different types of adaptation is rarely examined.

Here, we address this issue in the context of courtship song recognition in the fruit fly. During courtship, the male produces a song, the features of which inform the female's mating decision. Song is perceived using the arista, a feathery extension on the fly's antenna and idiosyncrasies of this sound receiver pose unique challenges for encoding the song pattern. First, due to the high directionality of the sound receiver, the rapid changes in distance and angle between male and female during the courtship induce strong fluctuations in sound intensity. Second, in addition to the fast, sound-induced antennal vibrations, gravity or wind also move the antenna and add a slowly varying offset to the antennal vibrations.

Both overall sound intensity as well as the antennal offset potentially interfere with an efficient representation of the song's pattern and the auditory system should hence correct for both intensity and offset through adaptation. Sound intensity corresponds to the magnitude or **variance** of antennal movement and antennal offset to the **mean** – the auditory system should thus perform mean and variance adaptation.

By combining electrophysiology and modelling, we examine adaptation in the fly's auditory receptor neurons – the so-called Johnston's organ neurons (JON). Previous studies have demonstrated mean adaptation in JON [1, 2]. This mean adaptation is subtractive and arises before spike generation, in the subthreshold currents of JON. We here show for the first time that JON also adapt to sound intensity. This form of adaptation is divisive and produces near intensity-invariant sound responses. Using information theory, we demonstrate that it maximizes sensitivity to deviations of intensity from a background.

Intracellular recordings reveal that variance adaptation arises in the subthreshold responses of JON just like the mean adaptation. That two distinct forms of adaptation are implemented in the same cellular compartment raises the issue of how both forms of adaptation interact. Ideally, the antennal offset – and hence mean adaptation – should not affect sound sensitivity.

Using a cross-adaptation paradigm in which we independently control the mean and variance of antennal position while recording from JON, we find a unidirectional interaction: mean adaptation does not affect sound sensitivity (as desired). However, intensity adaptation does reduce responses to antennal offset.

We next used modelling to gain insight into the implementation of adaptation in JON. Testing all possible serial and parallel arrangements, we find that only a serial arrangement in which mean adaptation precedes variance adaptation is able to reproduce all of our data. Moreover, we find that rectification is essential for variance adaptation. This parallels recent findings in the retina, where variance adaptation (i.e. contrast adaptation) also requires rectification [3].

Our study demonstrates for the first time that auditory receptor neurons of *Drosophila* produce intensity invariant sound representations. In addition, we show how multiple forms of adaptation are organized to support efficient sensory representations.

Keywords: adaptation, information, sensory coding

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Multi-area model of macaque visual cortex at cellular and synaptic resolution

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The cortical microcircuit, the network comprising a square millimeter of brain tissue, has been the subject of intense experimental and theoretical research. A full-scale model of the microcircuit at cellular and synaptic resolution [1] containing about 100,000 neurons and one billion local synapses exhibits fundamental properties of in vivo activity. Despite this success, the explanatory power of local models is limited as half of the synapses of each excitatory nerve cell have non-local origins. We therefore set out to construct a multi-scale spiking network model of all vision-related areas of macaque cortex that represents each area by a full-scale microcircuit with area-specific architecture. The layer- and population-resolved network connectivity integrates axonal tracing data from the CoCoMac database with recent quantitative tracing data, and is refined using dynamical constraints. This research program raises methodological as well as technological questions: Are simulations at this scale feasible with available computer hardware [2]? Are full-scale simulations necessary, or can models of appropriately downscaled density be studied instead [3]? And finally: How can dynamical constraints be built into a high-dimensional spiking network model [4]? In this talk we systematically address these questions and introduce the required technology before outlining the data integration process [5]. The simulation technology has been developed on the K computer in Kobe and JUQUEEN in Juelich and is incorporated in the current release of the NEST software. Preliminary simulation results reveal a stable asynchronous irregular ground state with heterogeneous activity across areas, layers, and populations. Intrinsic time scales of spiking activity are increased in hierarchically higher areas, and functional connectivity shows a strong correspondence with that measured using fMRI. The model bridges the gap between local and large-scale accounts of cortex, and clarifies how the detailed connectivity of cortex shapes its dynamics on multiple scales.

Keywords: simulation, supercomputing, integrate-and-fire

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Phase transition to stochastic synchrony in the balanced networks

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Networks of spiking neurons in the balanced state provide a remarkable understanding of the emergence of the temporal irregular activity in cortex [1]. In the balanced state with random coupling, the temporal variability in the firing of a neuron arises naturally from an approximate balance between its excitatory and inhibitory input. The asymptotic analysis of the balanced state requires randomness of neural connectivity. However, nonrandom features of synaptic connectivity are highly presented in local cortical circuits [2]. Here, we derive the mean-field limit and statistics of input fluctuations in a recurrent network of binary units in the balanced state in *an arbitrary connectivity architecture*. We show the dependence of average population firing rate on the system size and an average number of connections per neuron, using martingale structures in Markovian dynamics of binary neurons. This expansion enables us to represent the mean-field equation for *a finite size network* in a form of stochastic ordinary differential equation. We show that under the condition that network connectivity law is homogeneous, the diffusion term in the mean-field equation will vanish in the thermodynamical limits. This novel approach reveals a novel state that in a network with *inhomogeneous coupling micro-structures* the fluctuations in the average population firing rate survive irrespective of the network size. In these networks, the asynchronous spiking of a small subset of neurons may lead to *stochastic synchronization* in the network. Our results indicate that a synfire chain [3, 4] can be effortlessly implemented in the general theory of recurrent networks in the balanced state.

Keywords: balanced network, population dynamics, synfire chain and mean-field theory

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Spectral analysis of local field potential

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Oscillations often provide us with information of the origin. For instance, electrical oscillations measured by electroencephalograms and electrocardiograms afford clues to cognitive disorders and cardiac dysfunction, respectively.

Here we devise a Bayesian algorithm that may be applicable to the problems of inferring the origin from oscillating signals. To understand the working of the algorithm, we first consider inferring coins from the sound spectra of their collision. By devising a Bayesian learning algorithm, we reveal that optimizing the inference naturally leads the machine to select frequencies at which individual coins exhibit specific peaks in their sound spectra, indicating that inferences can be efficiently made by detecting the resonance sounds inherent in different coins. The machine has achieved a high performance of greater than 90% in correctly inferring single coins.

In the present contribution, we report the result obtained by applying the Bayesian learning algorithm to the inference of the layer location of the local field potential (LFP). The machine has also achieved a high performance and we shall discuss the problem specific to the LFP and the possibility of biological application of this spectral analysis.

Keywords: inverse problem, spectral analysis, local field potential

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Synaptic plasticity controlled by surprise

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During Hebbian plasticity, pre- and postsynaptic activity work together to cause a change of the weights. However, neuromodulators signaling reward, novelty, or surprise influence synaptic plasticity as well. We therefore have to consider in models of synaptic plasticity a total of three factors (pre, post, modulator) that control learning [1]. Such three-factor rules have also been called neo-Hebbian [2]. While the role of neuromodulators related to reward is well studied in theories of reinforcement learning, a theory of surprise-driven learning is missing. Here we discuss theories of surprise that can serve as starting point for a framework of surprise-based learning.

Two components are needed in a framework of surprise-based learning [3]: (i) a confidence-adjusted surprise measure to capture environmental statistics as well as subjective beliefs, (ii) a surprise-minimization learning rule, or SMiLe-rule, which dynamically adjusts the balance between new and old information without making prior assumptions about the temporal statistics in the environment. We apply our framework to a dynamic decision making task and a maze exploration task to demonstrate that it is suitable for learning in complex environments, even if the environment undergoes gradual or sudden changes. A synaptic implementation of learning in a network of spiking neurons with hidden neurons provides additional insights [4].

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Correlation coding in noise-diffusion networks: from experimental basis toward a theory of distributed representations

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The present study follows from the development of dynamical models of the whole cortex activity to reproduce fMRI data [1]. Typically, they rely on anatomical information obtained using diffusion-tensor imaging (DTI) to determine the skeleton of cortical interactions. The cortical dynamics are thus the product of local dynamic parameters (e.g., inputs, excitability) and the network connectivity. Building on our recent framework that estimates those parameters for resting-state fMRI data [2], we have extended the study to several datasets involving task-evoked activity. What we found is that the second-order statistics of estimated inputs in sensory areas convey information about the task; those covariances are then shaped by the recurrent connectivity to generate patterns of correlated activity over the whole network. In the context of fMRI, this allows for the characterization subnetworks that exchange and integrate relevant information to perform a given task, such as visual and auditory sensory inputs when watching a movie.

In the present study, we develop a framework where covariances are “processed” in a recurrent noise-diffusion network (i.e., multivariate Ornstein-Uhlenbeck process). More precisely, the study of the network mapping of covariances allows for a decoding of input covariances from the output covariances, and detection of corresponding changes in those. Equations for supervised learning can be derived in order to tune the recurrent connectivity and select a desired input-output mapping. Nonlinearities in the local dynamics also play a role in regulating the correlated activity between connected nodes, which may affect the whole network. This opens a new perspective for distributed coding schemes in recurrent architectures.

Keywords: noise-diffusion recurrent network, correlation coding

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Behavioral related synchronous spike patterns in macaque motor cortex during an instructed-delay reach-to-grasp task

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The computational role of spike time synchronization at millisecond precision among cortical neurons is hotly debated. Studies performed on data of limited size provided experimental evidence that low-order correlations occur in relation to behavior. Technological advances in electrophysiology that enable to record from hundreds of neurons simultaneously provide the opportunity to observe the coordinated spiking activity of larger populations of cells [1]. We recently published a method that combines data mining and statistical evaluation to search for significant patterns of synchronous spikes in massively parallel spike trains [2]. The method solves the computational and multiple testing problems raised by the high dimensionality of the data.

In the current study (also under review in [3]) we employed our method on massively parallel recordings (96 electrodes, Utah array) from two macaque monkeys, engaged in an instructed-delay reach-to-grasp task [1], to determine the emergence of spike synchronization in relation to behavior. We found a multitude of synchronous spike patterns, aligned in both monkeys along a preferential medio-lateral orientation in brain space. Consistently across two monkeys and multiple recording sessions, we found that the occurrence of the patterns is highly specific to behavior, indicating that different behaviors are associated to the synchronization of different groups of neurons (“cell assemblies”). However, pooled patterns that overlap in neuronal composition exhibit no specificity, suggesting that exclusive cell assemblies become active during different behaviors, but can recruit partly identical neurons.

Keywords: temporal coordination, cell assembly, massively parallel spike trains

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Dynamical processing of olfactory input in different types of antennal lobe neurons of the american cockroach

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The olfactory system of the American cockroach (*Periplaneta Americana*) offers a great possibility to study principles of information processing. The first station in the olfactory pathway is the antennal lobe (AL) network. Here, the olfactory input from about 200.000 olfactory sensory neurons (OSN) is processed to establish a dense odor code in about 250 projection neurons (PN) that project to higher order brain areas [1]. Efficient encoding of the olfactory information in the small number of PN channels requires dense spatiotemporal activity patterns. This odor code is structured by two different types of spiking and non-spiking local interneurons (LN, for a characterization, see [2]) that synapse with OSNs and PNs in the AL glomeruli.

We studied odor representation in LNs and PNs using whole-cell patch clamp recordings during olfactory stimulation of the antennae. The application of a broad odor spectrum enables the characterization of tuning profiles for each AL neuron type. In addition individual recordings are aggregated in pseudo-populations, such that the dense odor code generated by populations of neurons can be investigated. The spatiotemporal activity patterns allow quantifying olfactory information that can be compared across the different types of neurons. The method is particularly suitable to study the temporal evolution of the code [3]. The odor representations in the AL quickly stabilize, which is of behavioral relevance for the animal. Differences in the temporal dynamics of type-specific sub-populations provide information about their specialized roles in sensory processing.

The accessibility and high quality of intracellular whole-cell patch clamp recordings from the AL network in the American cockroach support a detailed understanding of the emergence of dense information codes. Especially interneurons and their specific contribution to shaping the spatiotemporal activity patterns complement the understanding of sensory processing networks.

Keywords: Olfactory Processing, Dense Code, Insects

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Understanding neuronal circuits and their functions using expression driver systems of the fruit fly *Drosophila melanogaster*

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To understand how information is coded in the actual brain it is a prerequisite to obtain detailed knowledge about its neuronal network architecture. Expression driver system is a powerful tool for this purpose: We first induce expression of an ectopic transcription activator (such as yeast-derived Gal4 or *E. coli*-derived LexA proteins) in a specific cell type, and then introduce a second DNA construct with the target sequence of the expression driver followed by any genes that we want to express. By inducing expression of molecules such as GFP or RFP we can visualize the structure of specific neurons, and by expressing those molecules that are fused with the proteins that are associated with the transmitter receptors or synaptic vesicles, we can identify specific localization of input and output synaptic sites.

Because of the complex and still largely unknown mechanisms that specify gene expression patterns, we cannot predict the types of cells labelled by each expression driver. Thus, we have to generate a very large collection of expression driver strains with diverse expression patterns and screen for the lines that label certain cells in the region of the brain we want to analyse. Such approach is best possible with the model organisms that are easy to maintain and generate transgenic lines. We therefore chose the fruit fly *Drosophila melanogaster* and generated several thousands of driver strains. Together with the strains that are generated recently by other groups, there are in total well more than ten thousand strains available, which should cover most if not all of the possible expression patterns in the brain.

Using the system we have conducted systematic identification of the neurons in the olfactory, gustatory, visual, and auditory sensory centres of the fly brain. Having analysed four of the five major sensory systems we now focus on the final frontier – the somatosensory system. Whereas the other four sensory stimuli are each detected by an array of essentially similar cells that are localized in a particular organ around the head (such as photoreceptors in the eyes), various kinds of mechanical stimuli, such as touch, stretch, vibration, joint movement as well as pain are detected by different types of somatosensory neurons that are distributed around the entire body surface. Thus, there should be integration of information not only between somatosensory and other sensory modalities but also within different sub-modalities of somatosensation.

Screening the expression driver lines we identified an array of strains that each label specific subtype of somatosensory cells, namely the external sensory neurons, campaniform sensilliae neurons, chordotonal organ neurons, stretch receptor neurons, and non-ciliated multidendritic neurons as well as leg- and wing-specific gustatory sensory neurons. Although their distribution in the body surface has been well known, and axonal projections of some of those cells in the central nervous system have been investigated, systematic overview of the insect somatosensory system still remained largely unknown.

By visualizing their axons and terminal synaptic sites, we found that most of those neurons

terminate in the ventral nerve cord (VNC) – an insect equivalent of the mammalian spinal cord – forming a modality-specific layered organization that is surprisingly similar to the mammalian one. A few types of sensory neurons in the legs, wings and halteres (rear wings) project directly to the brain. Each of them terminates in specific brain regions, and axons from different legs or wings terminate at different locations, forming modality-specific somatotopic sensory maps in the brain. We then screened for the secondary interneurons that send information from the VNC to the brain. Layered organization of the sensory terminals enabled us to identify interneurons whose dendrites overlap with the terminals of specific types of somatosensory cells. Those interneurons terminate in the brain regions that are close to the terminals of the directly-innervating sensory cells of the same modality, again confirming the existence of several modality-specific somatosensory centres in the brain.

An advantage of using the expression driver system for neuron mapping is that we can use the identified driver strains to express various other genes specifically in the identified neurons. We established a live Ca imaging system with a two-photon microscope to measure activity of neurons that express Ca-dependent variant of GFP called GCaMP, while the fly is held in a natural posture so that it can move legs and wings freely. Different types of directly-innervating sensory neurons and secondary interneurons showed different activity patterns while the fly stops, walks, grooms, or move their legs in the air, suggesting that each neuron type codes different types of sensory information.

We then induced expression of a K-channel protein to block electric potential change of specific neurons and observed the flies' walking behaviour. Wind flow towards the fly antennae makes flies to stop moving to crouch when they are on the ground, but does not when they are in the air. This means that certain cells should convey information to the fly brain to tell whether the animal is on the ground or in the air. Blocking of several specific types of sensory neurons or interneurons affected this arrested waking behaviour against wind, which enabled us to pinpoint the neuron types that are involved in this sensory information coding.

Combination of anatomical neuron mapping and functional analysis with specific gene expression is thus a powerful tool to understand how information is coded in the neuronal circuits. We will further continue this approach to reveal the neuronal architecture of the remaining brain regions that have not been analysed in great detail, which we call the *terra incognita*.

Keywords: somatosensory system, neuronal circuit, *Drosophila*

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Specific excitatory connectivity for feature integration in mouse primary visual cortex

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In mouse primary visual cortex (V1), local excitatory connections are more prevalent, stronger and larger between neurons that share similar functional response features. However, the extent to which rules for local cortical connection specificity shape visual responses, as well as full details relating structure and function both remain unknown. We considered whether complex responses to plaid stimuli in mouse V1 could be explained by one of two alternative connectivity schemes: whether local connections are aligned with simple feedforward visual properties, or whether local connections group across feedforward visual properties. Using a combined experimental and computational approach, we found that responses to plaid stimuli in mouse V1 were best explained by a connectivity scheme which binds multiple feedforward visual properties. Our results show that feature binding can occur through a recurrent mechanism not requiring feedforward convergence; such a mechanism is consistent with visual responses in mouse V1.

Synchrony measure for a neuron driven by excitatory and inhibitory inputs

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The neural code refers to the mechanisms with which a single neuron and networks of neurons exchange sequences of spike trains. Discovering and understanding these mechanisms and in particular, figuring out how cells encode, decode and process information is very important in our quest of deciphering the neural code. A key aspect of solving the neural encoding problem is to distinguish the operational mode of a neuron, i.e., whether it operates as a temporal integrator or as a coincidence detector. Researchers have proposed a number of methods for solving this problem like, the *coincidence advantage* [1], the *integration time window measure* [2] and the *neural mode and drive* [3] (see Kanev et al. [3] for a review of these methods). One other method is the *normalised pre-spike membrane potential slope* (NPSS) measure of Koutsou et al. [4]. The NPSS tries to solve the problem of distinguishing the operational mode of a neuron by observing the depolarisation of the membrane potential of a neuron prior to the moment of crossing the threshold, within a short period of time. These authors show how to identify the degree of synchrony that is responsible for firing spikes in a simple neuron model and describe how this measurement is equivalent to the operational mode. The measure calculates two bounds for the slope of the membrane potential: the upper bound which represents the slope of the membrane potential in the case where the neuron was firing as a result of purely synchronised inputs (coincidence detector), and the lower bound which represents the slope of the membrane potential in the case where the neuron was firing as a result of many, randomly distributed input spikes (temporal integrator). The final value is determined by linearly normalising the measured slope of the membrane potential prior to each spike fired by the neuron between the two calculated bounds. When developing the method, Koutsou et al. [4] used the Leaky Integrate-and-Fire neuron model driven only by excitatory inputs. The method itself relied on the assumption that there were no inhibitory inputs driving the neuron and this was stated as one of the limitations of the NPSS.

Given this limitation, in this work we adapt the NPSS of Koutsou et al. [4] so that it can be applied to models which are driven by both excitatory and inhibitory inputs. More specifically, we analyse the behaviour of a conductance-based neuron model that receives both kinds of inputs and studied the way in which the membrane potential fluctuates. Based on the behaviour of the trajectory of the membrane potential, we adjusted the calculation of the upper bound to accommodate for the higher possible slope values that result from the lower average and minimum membrane potential values, the latter being equal to the inhibitory reversal potential values.

Preliminary results indicate that the inclusion of strong inhibitory inputs cause the neuron to operate primarily as a temporal integrator. The neuron can operate as a coincident detector, but only when the ratio of excitatory to inhibitory inputs is very low. This could be attributed to the increased frequency and amplitude of the membrane potential fluctuations that happens in such cases, as shown by Christodoulou et al. [5]. It has to be noted that the strong

correlation, which was observed in general between the measure and the input synchrony in Koutsou et al. [4], becomes weaker to non-existent as the inhibition on concurrent excitation increases. The lack of correlation was also observed in cases where the strength of the excitatory synchronous inputs was on average below threshold (see Koutsou et al. [6]).

Keywords: neural operational modes, inhibition, synchrony

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Testing statistical significance of synaptic connectivity

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The brain consists of a large number of neurons that communicate each other by sending spikes through synaptic connections. It is essential to investigate the synaptic connectivity between neurons for analyzing the information processing in a neuronal circuit. Advances on experimental techniques, including Ca^{2+} imaging techniques and multiple electrode arrays, have enabled us to record spiking activity of hundreds or thousands of neurons.

Cross-correlation method [1] is a basic means to infer the synaptic connectivity from spike data of multiple neurons. The method has been applied to various experimental data because of its simplicity. Recently, the generalized linear model (GLM) [2] is becoming pervasive due to the advanced accuracy in the inference [3]; it has been reported that the GLM can recover the synaptic connectivity with an error rate of less than 1% under some ideal conditions [4]. One of the problems in the application of the GLM to experimental data is that the observation period is limited and there could be uncertainties in the estimator. Thus, it is desirable to develop a statistical method for testing the significance of the estimated synaptic connectivity.

In this study, we develop a method for testing whether there is a synaptic connection between two neurons or not. The method is validated using the synthetic spike data generated from a realistic computational model of a cortical circuit.

Keywords: synaptic connectivity estimation, generalized linear model, statistical testing

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Neural coding accuracy and stimulus information in variable frames of reference

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Any particular stimulus intensity, as a physical quantity, can be equivalently described in different unit systems. Researchers automatically expect the methodology and the insight obtained about the neural coding precision to be independent from such a subjective choice. We show, however, that one may obtain inconsistent inference about the ultimate neural coding accuracy just by re-evaluating the identical scenario in transformed units. On one hand, our results point to a potentially problematic aspect of certain popular information measures in neurosciences, such as the Fisher information. On the other hand, we speculate that the unwanted transformation covariance may be removed by considering the psychophysical scale based on the ideal observer paradigm. Finally, we discuss the impact of the reference frame choice on information measures derived from Shannon's theory.

Keywords: coding accuracy, mutual information, measurement scale

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Approximate methods for the inference of stochastic reaction networks

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Stochastic reaction networks provide a probabilistic description of the evolution of interacting species. They are used for modeling phenomena in a wide range of disciplines; those species may represent molecules in chemical reactions [1], RNA, DNA and proteins in gene regulatory networks [2, 3], animal species in ecology [4], susceptibles and infectives in epidemic models [5], and information packets in telecommunication networks [6].

The evolution of networks is modeled by a continuous-time Markov jump process, for which the probability distribution of the number of individuals of each species obeys the master equation [7, 8]. Here, we consider a situation in which only noisy and partial measurements of underlying reaction networks are available. Our objective is to infer the number of individuals of species from the observations obtained up to current time. In the literature on signal processing, this problem is called *filtering* [9].

The filtering equation, which governs the posterior distribution conditioned on the observations, is not analytically obtainable due to intractability of the master equation. It is possible to perform exact numerical simulation and obtain samples from Markov jump processes using stochastic simulation algorithm (SSA) [10]. By simulating many ‘particles’ with the SSA and sampling the weighted particles in favor of the observations, we could obtain samples from the posterior distribution; this technique is known as *sequential Monte Carlo methods* or *particle filtering* [11]. However, the SSA is often very slow, and moreover, particle filtering requires sufficiently many particles to obtain precise posterior expectations. Thus, particle filtering may not be efficient for performing online posterior inference.

An alternative approach is to consider suitable approximations of Markov jump processes. In the linear noise approximation (LNA), which is the most widely used, a Markov jump process is approximated by a Gaussian process, whose mean obeys the rate equation [8]. The LNA approximates the original Markov jump process well when the number of individuals of species is large [12]. Since the Gaussian process is tractable, the LNA enables us to derive an analytical expression of approximate filtering equation [13].

Here, we propose applying the projection method [14] to derive an approximate filter. In this method, the evolution of the probability distributions is constraint in a finite-dimensional family of densities through orthogonal projection on the tangent space with respect to the Fisher metric. By choosing the Gaussian distributions for a finite-dimensional manifold, we obtain another Gaussian process that approximate to the original Markov jump process. We label this approximation as ‘Gaussian projection (GP).’

We contrast the two approximate filters based on the LNA and the GP in terms of their derivations and filtering performance. It is demonstrated with numerical simulations that the approximate filter based on the GP outperforms that based on the LNA; the superiority of the

GP over the LNA stands out when the observation noise is increased.

Keywords: Reaction networks, linear noise approximation, Gaussian projection

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First passage time of leaky integrate-and-fire neuron driven by a jump process

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A single Leaky Integrate-and-Fire (LIF) neuron is considered. An attention is focused on the First Passage Time Problem. Namely, we wish to obtain the first passage time probability density function (p.d.f.) if input stimulation is known. Typically, the first passage time p.d.f. is found using diffusion approximation (assuming single EPSP to be infinitesimally small as compared to the threshold of a neuron), which is not suitable for all types of neurons, see e.g. [1, 2]. In this paper, we discard the diffusion approximation and allow the relation between neuron's threshold and the EPSP amplitude to take an arbitrary finite value. In this case, the time course of neuron's membrane voltage represents a jump stochastic process and not a diffusion one. A sequence of arrival times of input impulses is considered as a Poisson point process.

We develop a method, which allows to obtain exact mathematical expressions for the first passage time p.d.f. without any additional approximations. The expressions obtained will be different for different relations between the threshold of a neuron and the altitude of input impulse (an analogue of EPSP amplitude in the LIF model). The developed method is applied for a particular case of such relation, and exact formulas are obtained for this case. Also, we perform numerical Monte-Carlo simulations of a single LIF neuron with Poisson input stimulation and compare numerical results to those found analytically. Numerical and analytical results coincide perfectly. Therefore, we propose the developed method to be utilized by researches dealing with the First Passage Time Problem beyond diffusion approximation.

Keywords: first passage time, leaky integrate-and-fire neuron, jump process

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Principles underlying sensory map topography in primary visual cortex

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The primary visual cortex contains a detailed map of the visual scene, which is represented according to multiple stimulus dimensions including spatial location, ocular dominance and stimulus orientation. While it is known that the maps for spatial location and ocular dominance arise from the spatial arrangement of thalamic afferent axons in the cortex, the origin of the orientation map remain unclear. A possible anatomical substrate for orientation maps could be the axonal arrangement of ON and OFF thalamic afferents in the cortex just as the substrate for ocular dominance maps is the arrangement of thalamic afferents from the contralateral and ipsilateral eyes. To test this hypothesis we introduced 32-channel multielectrode arrays (inter-electrode separation: 0.1 mm, Neuronexus) horizontally into the cat primary visual cortex. We measured ON and OFF retinotopy with light and dark stimuli and orientation tuning with moving bars. These recordings allowed us to study the relationship between ON/OFF retinotopy and orientation preference in different regions of the orientation map, including regions in which orientation and direction preference changed abruptly and across ocular dominance columns.

Our results [1] show that the cortical maps for orientation, direction and retinal disparity in the cat are all strongly related to the organization of the map for spatial location of light (ON) and dark (OFF) stimuli. We show that this organization is OFF-dominated and OFF-centric, i.e. OFF retinotopy is more precise than ON retinotopy and OFF acts as the anchor of the cortical retinotopic map [2]. These unexpected results have now also been shown in tree shrew visual cortex [3], seem to be present in primate [1] and therefore are likely a common design principle in species with orientation maps. In this OFF-dominated and OFF-centric topography, changes in orientation and direction preference are determined by changes in ON/OFF retinotopy. Furthermore, we also show that the organization for ON/OFF runs orthogonal to the ocular dominance columns and that ON/OFF retinotopy is well matched at the ocular dominance border. This binocular match of ON/OFF retinotopy can explain why orientation preference shows a tendency to remain constant across the border of ocular dominance columns.

Because the ON/OFF organization originates from clustering of ON and OFF thalamic afferents in the cat visual cortex [4], we conclude that all main features of visual cortical topography, including orientation, direction and retinal disparity, follow a common organizing principle that arranges thalamic axons with similar retinotopy and ON–OFF polarity in neighbouring cortical regions.

Keywords: visual cortex, orientation maps, ON/OFF maps, OFF-dominance

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Neural correlates of flying insect navigation: from simulation to electro-physiology on a quadcopter

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Within the insect world, honeybees exhibit extraordinary navigational capabilities. Experimental evidence for different strategies, such as path integration and visual guidance using picture memories, have been put forward [1, 2]. However, it remains controversial how those components are combined and at which level of abstraction the different components are available to a navigating bee [3]. Studies using harmonic radar suggest that bees can robustly find their nest, even with an invalidated path or disturbed sun compass [3]. Another fascinating aspect of navigation is the waggle dance communication system with which foragers can direct nestmates to field locations [4]. After decoding a dance, honeybees have been shown to perform shortcut flights between known and dance-advertised sites over novel terrain, a behavior that indicates a geometrical relationship between memories is used [5]. However, analytical approaches to investigate the neural correlates face a technological dilemma: to this date, there is no lab-based protocol available to study all aspects of long-range navigation in flying honeybees, e.g. using virtual environments as shown in fruit flies (for a review see [6]). Recording units that can be carried by the honeybees themselves are not yet available. In our work, we follow both the synthetic and the analytic approach by implementing and testing neural models in silico and by developing a flying robotic platform for electrophysiological observations while the animal is navigating in the field.

As a popular animal model in neuroscience, the honeybee's brain has thoroughly been investigated [7]. The mushroom body, previously shown to be involved in associative learning, might also play a role in storing and retrieving higher-order information such as used in navigation [8, 9]. A neural model of the mushroom body has recently been proposed as a visual matching unit that enables desert ants to robustly follow routes [10]. The network model maps the current view of the navigating agent to a familiarity value. By maximizing the familiarity with respect to the heading direction, a target location can be reached, without explicit knowledge of the field location and without other higher level representations of the world such as a mental map. We investigated whether this concept is applicable to flying insects such as the honeybee as well. To this end, we developed various 3D models of typical environments and implemented the proposed SNN model with slight adaptations to approximately match the honeybees' visual input. Additionally, we propose an extension to the model to represent different motivational contexts, such as outbound or inbound foraging flights. We find that the model can indeed be adapted to flying insects. In our experiments, simulated bees were able to correctly navigate along previously learned routes even with panoramic cues missing. However, the structure and information content of the environment play crucial role. Environments exhibiting medium landmark densities yield a better performance. Higher or lower densities yield worse results suggesting the network's capacity and the information content being insufficient, respectively. Salient structures, such as long

stretches of roads or field edges may serve as guiding structures but, in some cases, may outbalance the network such that the agent clings to these structures as long as they are in visual range, failing to follow the correct route. Given the complexity of natural behavior of bees, whose foraging lives span several weeks and comprise many different routes, it seems likely that the model mechanism is complemented by additional subsystems used for guidance and action selection while navigating in the field.

Electrophysiological data in navigating flying bees does not exist to this date, but would greatly drive the development of neural models that could reproduce the behavioral complexity. We therefore developed the first prototype of a flying platform for extracellular recordings. Our quadro-copter is based on the open “ArduCopter” system and carries an additional carbon fiber rod for holding payload as far away from disturbances as possible. This way, the bee has an almost unrestricted view of her surroundings. An amplifier and a digitizer are placed behind the animal to minimize additional noise reception. Spike data is recorded and saved to an embedded computer. In a first test we could record from mushroom body extrinsic neurons in flight yielding low noise levels and clearly separable spikes. In future experiments we will correlate spike data with the bee’s visual input and other implicit information to find candidate features represented and used by the navigating bee brain.

Keywords: insect navigation, spiking neural networks, electrophysiology

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Coding of faces by tensor components

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Neurons selectively responsive to faces exist in the ventral visual stream of both monkeys and humans [1-3]. However, the characteristics of face cell receptive fields are largely unknown. Here we use multiway tensor decompositions of faces to explore a range of possibilities for the neural coding of faces.

Multiway tensor decomposition is in some sense a generalization of principal component analysis (PCA) to higher dimensions [4]. PCA can only be used to decompose 2D inputs [5]. To analyze a population of N faces using PCA (or ICA), each face image must first be vectorized to a 1D array of pixels. Then a 2D matrix is formed with N columns, where each column is one vectorized face. This procedure has the disadvantage that the vectorization process causes face pixels to lose their spatial context. In contrast, tensor methods can decompose inputs with arbitrary dimensionality, so no vectorization is necessary and context is retained. For this study the input set was 4D, with two spatial dimensions, color the third dimension, and the population of different faces forming the fourth dimension.

Tensor decomposition of a population of face images produces a set of components. The tensor components can be used to reconstruct different face images by performing a weighted combination of the components. Different faces correspond to different weights. Tensor components (or “tensorfaces”) are 2D arrays that have face-like appearances, and conceptually correspond to receptive fields of biological face cells. The weights correspond to the response activations of the tensorfaces to stimuli. A set of tensorfaces therefore forms a population code for the representation of faces.

When doing a tensor decomposition of faces, we were able to specify the matrix rank of the resulting tensorfaces [6]. Tensorface rank is related to Kolmogorov complexity (algorithmic information), which is measured as bits/pixel required to represent a tensorface in compressed form. High-rank tensorfaces correspond to greater Kolmogorov complexity. High-rank tensorfaces have clear face-like appearances, while low-rank tensorfaces have blob-like appearances that crudely approximate faces. We were interested in comparing high-complexity versus low-complexity coding of faces. The range of tensorface ranks we examined was from 2 (low complexity) to 32 (high complexity), for tensorfaces with size 200x200 pixels.

To examine how accurately a population of tensorfaces could reconstruct faces, we used a set of test faces different from the set of training faces that created the components, but in which the test and training sets were similar. Reconstruction accuracy increased as tensorface rank

increased. However, when reconstructing a face that was very different from anything in the training set, accuracy decreased as tensorface rank increased. This suggests that in the coding of faces there is a trade-off between accurate representation for familiar stimuli (best with high-complexity receptive fields) and the ability to generalize for representing novel stimuli (best with low-complexity receptive fields). In that case, it may be optimal for face coding to use neurons with receptive fields having intermediate complexity, or alternatively for encoding populations to have a mixture of different complexities.

We also examined the sparseness of face representations by calculating the entropy of the weights (activations) for each tensorface across a set of stimulus faces. We found some tensorface responses had low sparseness, with similar activations for all faces, while other tensorfaces had high sparseness with strong activations only for certain faces. One hypothesis compatible with this observation is that low-sparseness tensorfaces build up a representation of an average face and are always active, while high-sparseness tensorfaces provide the details for individual faces.

Keywords: object recognition, Kolmogorov complexity, sparse coding

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Signal-enhancing effect of spontaneous activity in latency coding

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Many experimental studies provide evidence that the time between the stimulus onset and the first subsequent spike, the *first-spike latency*, varies with the stimulus intensity (e.g. [1, 2, 3]) and thus can be a possible form of the neural code. Intuitively, the detection of the stimulus intensity from the first-spike latency becomes complicated if the input to the neuron carrying the information about the stimulus is mixed with presynaptic spontaneous activity. The analytical results for very simple neuronal models of a spike train, such as the Poisson process and the renewal process, demonstrate that the accuracy of stimulus decoding deteriorates in the presence of spontaneous activity [4].

In our recent paper [5], we analyzed the accuracy of stimulus decoding and the role of spontaneous activity, assuming latency coding in the stochastic perfect integrate-and-fire model. We studied three possible scenarios how the stimulation changes the parameters of the underlying Wiener process (the drift of the membrane potential changes while the volatility is constant, excitatory and inhibitory inputs change proportionally, the excitatory input changes while the inhibitory input is constant). As a measure of decoding accuracy, we applied the Fisher information. Paradoxically, we found out that the best decoding performance is achieved with a non-zero level of spontaneous activity in two of the three studied scenarios. The cause of this phenomenon lies in the probability distribution of the membrane potential at the time of the stimulus onset and in the way how this distribution is influenced by spontaneous activity. The spontaneous activity stabilizes the membrane potential in the sense that the variability of the membrane potential decreases and its excursions to negative values are less likely to happen. Consequently, the better predictability of the membrane potential improves the estimation of the stimulus from the timing of the first spike. The described phenomenon represents a novel example of a noise-induced signal enhancement.

Keywords: latency coding, spontaneous activity, Fisher information

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Synchrony coding by neural populations - theory and experiment

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Neural populations carry information about time-dependent stimuli in their overall population activity. Specific features of the stimulus may also be encoded in the synchronous activity of a sizable fraction of the population. In my talk I review recent theoretical and experimental results on the conditions under which a synchrony code can act as an information filter.

Subthreshold oscillations facilitate memory of precise temporal spike trains: A computational approach

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It is an unsolved question how precise temporal patterns of neuronal spikes can reliably be stored and recalled. Here, I propose a simple mechanism to achieve this by means of intrinsic oscillations of the membrane potentials through varying frequencies and phases. Some supervised learning algorithms are reported, enabling neuronal networks to read out temporal spike trains as an answer to precise temporal input spike trains [1, 2, 3, 4]. They progressively approximate the first output to the temporal target spike train through many trials. The model proposed here describes a general tool for encoding precise temporal patterns in small neuronal circuits by a simple mechanism even through single trial. It enables encoding and recall. For this memorizing process subthreshold oscillations of membrane potentials are essential. Oscillatory activity in the brain has been widely observed. Already 1999 Desmaisons et al. [5] found that subthreshold oscillatory activity can precisely trigger the temporal occurrence of spikes. Oscillations can be generated by intrinsic processes of neurons [6] or by rhythmic inputs from excitatory and/or inhibitory connections. Oscillation frequencies and their phases can vary substantially between neuronal areas and locations, e.g. in the entorhinal cortex [7]. The presented model randomly varies frequencies as well as phases of oscillations within a group of neurons (N^{OS}). This leads to varying times of membrane potential peaks in the neurons of N^{OS} . If an input into N^{OS} can generate spikes at these peaks only, different times of input spikes lead to spikes in different neurons. The time pattern of the spiking of the input neuron thereby is transformed into a spatial pattern in N^{OS} . This spatial pattern can be stored by strengthening the synaptic connections from the input neuron to the individual neurons of N^{OS} via spike-timing dependent plasticity (STDP). The input spike times need to be built through a certain basic frequency pulse but can contain a varying number of spikes. To allow for discrimination between the encoding and the recalling process, an additional input from a supporting neuron to all neurons of N^{OS} accompanies the encoding. This supporting neuron fires with the basic frequency pulse and is necessary for exceeding the firing threshold of the neurons in N^{OS} during the peaks of intrinsic oscillations. Firing of neurons in N^{OS} strengthens their synaptic weights from the input neuron by STDP. During recall the supporting neuron remains inactive whereas the input neuron keeps firing persistently with the basic frequency. This way the spatial version of the stored spike train in N^{OS} is reactivated. The persistent firing produces an answer above threshold in the continuing oscillating neurons of N^{OS} at the initially learned precise time points only. If the neurons of N^{OS} are connected to a single output neuron it will be activated at the points in time of the original input train. Therefore the persistent firing input neuron enables the recall of the formerly learnt precise temporal spike train. The model was implemented by dendritic connections from the input neuron to N^{OS} and by somatic connections from the supporting neuron to N^{OS} . Only the synaptic weights to dendrites are varied by STDP. All neurons of N^{OS} were somatically connected to an output neuron. The input trains lasted for 200 ms with 1 to 8 randomly set spikes by a 50 Hz scheme. The oscillation frequencies in N^{OS} neurons were randomly set between 5 and 8 Hz, the phase shifting of N^{OS} neurons was randomly set between 0 to 200 ms, the amplitude of oscillations was constantly set at 8 mV.

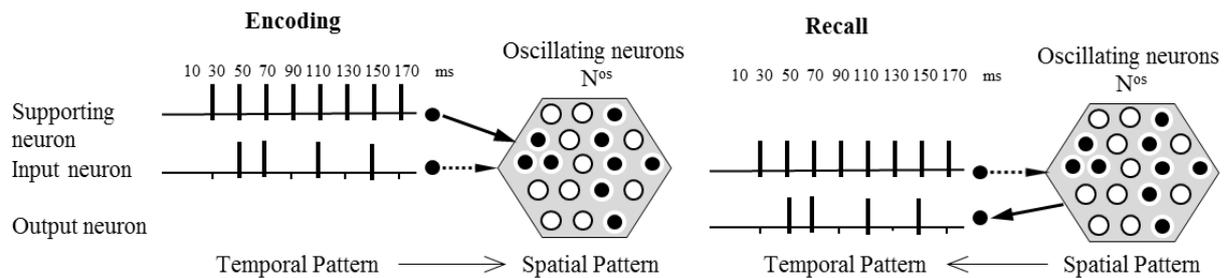


Fig.1: From temporal to spatial to temporal interactions. Encoding: A precise temporal spike train from the input neuron leads to a spatial pattern triggered by subthreshold oscillations in N^{os} and by an additional 50 Hz input spike train from the supporting neuron. Individual input spikes activate different neurons in N^{os} (black dots in N^{os}) at different points in time. The synaptic weights from the input neuron to the dendrites of activated neurons in N^{os} are strengthened by STDP (Dotted arrows: excitatory connections to dendrites, full arrows: excitatory connections to the soma of neurons). Recall: Once strengthened a sustaining 50 Hz spike train from the input neuron activates the encoded spatial pattern in N^{os} even if the supporting neuron does not fire. The continuing oscillations in N^{os} generate spikes exactly and only at the points in time of the original input train.

The model was tested by ‘Neurexcell’ a yet unpublished spiking neural net simulation code executed in VBA for Microsoft Excel 2010, developed by the author and consistent with the spike response model of Gerstner and Kistler [8], but complimented by branch-specific processes. A set of 20 randomly generated spike trains was presented by a single trial. By a further activation of the input neuron through a continuous spike train the output neuron always produced the formerly encoded precise spike train.

Keywords: precise temporal spike trains, subthreshold oscillations, memory

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Predicting arm movement direction with spiking neural networks and neuromorphic hardware

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Brain-computer interfacing aims to restore interaction capabilities to patients who are paralysed or unable to speak by directly coupling brain activity to external devices, such as prosthetic limbs. Previous approaches typically required reformatting the neuronal code into a time-averaged, continuous representation (e.g. firing rates) that can be analysed with conventional computers. We present here a novel method that uses neuromorphic hardware to predict movement intentions, based on single unit activity recorded from the motor cortex of a monkey performing an arm-reaching task. The advantage of the neuromorphic platform over conventional computers is its reduced size, low-power consumption and the inherent spike-based computation mode which makes it suitable for direct interfacing with biological neurons. Our study uses spike trains from 12 cortical neurons as input to a spiking network, trained in a supervised fashion to predict the direction of movement before any action is performed. The network implements lateral inhibition and comprises 176 neurons in total. All computations are performed on the Spikey neuromorphic chip, which operates in a brain-inspired, parallel fashion. Due to the spike-based nature of the neuromorphic platform, the artificial neural network works directly on spikes emitted by the cortical neurons, without the need for prior processing. After only 100 training trials we are able to predict movement direction with an accuracy of around 90%, as shown in Figure 1. This study serves as proof-of-concept for the use of a neuromorphic device in a brain-computer interfacing setting.

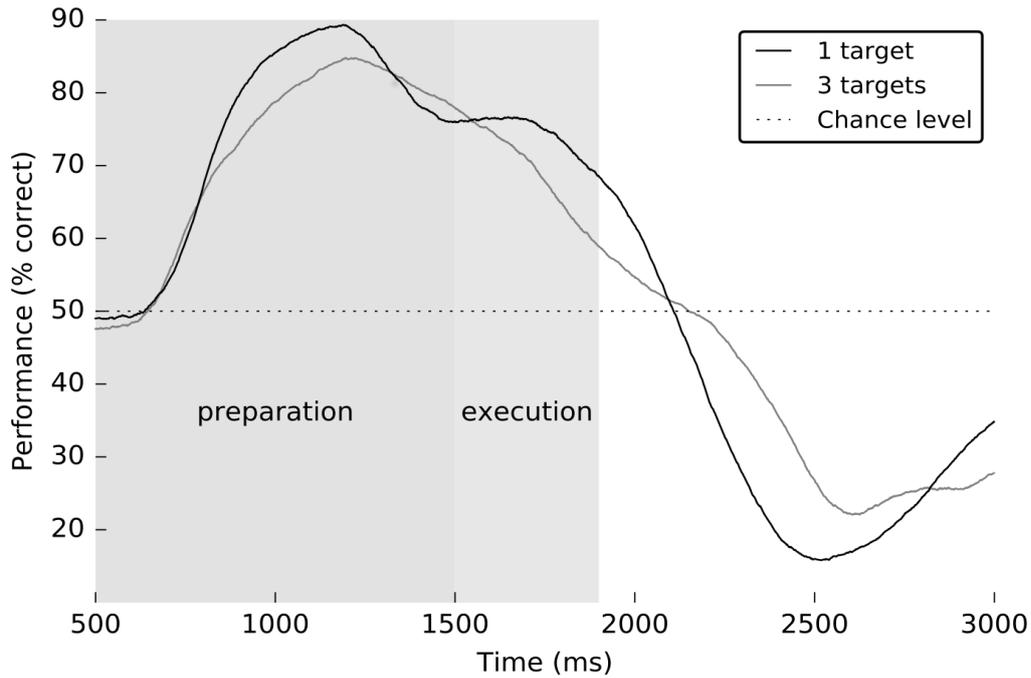


Figure 1: Time-resolved decoding performance of the spiking classifier for predicting the correct (left- or rightward) arm movement from an initial starting point to a left or right target point. The classifier was trained on the period 650 ms to 1400 ms, during which the monkey was not allowed to move. The prediction was evaluated in a sliding window of 500 ms duration. The movement was executed in the execution period. The inverse performance in the late phase of the trial refers to the backward movement from the target to the initial starting point.

Keywords: brain-machine interfacing, neuromorphic hardware, spiking neural network

Quantitative description of neural computations in the auditory brainstem using the ergodic hypothesis

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The ergodic hypothesis in statistical physics states that averages taken over smaller set of particles (or just one particle) and longer period of time should equal to averages over larger set of particles and shorter period of time. Unitary events studied here are action potentials in individual neurons. They form spike trains and their firing rates can be averaged both over time and over sets of neurons.

We studied spike timing precision in systems with different levels of complexity. We compared standard deviation of spike timing with more elaborated measures of statistical dispersion [3]. We also compared single neuron codes and population codes [4]. Next we studied time and population summation of synaptic interactions. We used inversion formula of probability density to study parameters of spike timing in the auditory brainstem [5]. To describe time averages, Bures [1] described spike counting processes in relaying neurons of the auditory periphery. This description was applied to comparison of time averaging versus population averaging in auditory brainstem [2]. Number of neurons necessary to signal input variable (like sound azimuth) with given precision in time period was compared with sensory latencies.

All the models mentioned above share the application of the ergodic hypothesis to neuronal signaling. We therefore present the ergodic hypothesis as a framework useful for description of psychophysical and neural signaling in the auditory system. Our conclusion is that the ergodic hypothesis can be utilized in studies of sensory stimulation and in particular to estimate computational complexity realized by small populations of sensory neurons in higher animals.

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Keywords: auditory brainstem, ergodic hypothesis, spike train, spike timing, population coding

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Clique topology and dynamics in neuronal network simulations

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We study the dynamical evolution of a simulated neuronal network in relation to its topological structure by considering the directed clique topology of the network. Directed cliques, or completely connected sub-graphs, [1] are a topological construction (Figure 1), which encodes the directed structure of connections of a network in the form of a simplicial complex. Such an object can be studied mathematically to obtain network invariants.

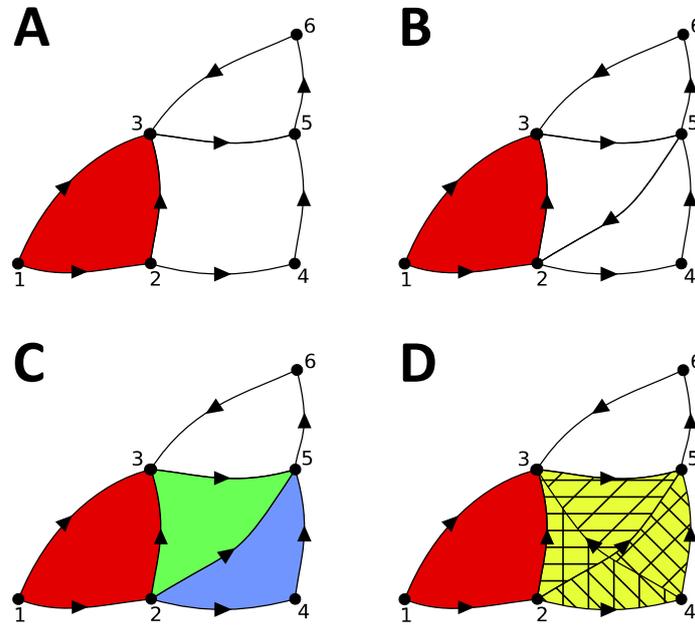


Figure 1: The directed clique complex. (A) The directed clique complex of the represented graph consists of a 0-simplex for each vertex and a 1-simplex for each edge. There is only one 2-simplex (123). Note that '2453' does not form a 3-simplex because it is not fully connected. '356' does not form a simplex either, because the edges are not oriented correctly. (B) The addition of the edge (52) to the graph in (A) does not contribute to creating any new 2-simplex, because of its orientation. The edges connecting the vertices 2, 3 and 5 (respectively 2, 4 and 5) are oriented cyclically, and therefore they do not follow the conditions of the definition of directed clique complex. (C) By reversing the orientation of the new edge (25), we obtain two new 2-simplices: (235) and (245). Note that we do not have any 3-simplex. (D) We added a new edge (43), thus the sub-graph (2435) becomes fully connected and is oriented correctly to be a 3-simplex in the directed clique complex. In addition this construction gives two other 2-simplices: (243) and (435).

The networks we study are simulated using JNet [2], which is a highly expandable and flexible framework aimed at simulating hierarchical neural systems implemented in Java. The simulator is designed to efficiently emulate neural network models with emphasis on facilities for model reconfiguration and adjustment and on functionally rich possibilities for detailed network state acquisition. The neural simulation consists in a set of processes run over a set of neurons.

The biologically-plausible simulations that we run show in their preliminary results a correlation between the invariants based on the network's clique topology and its activation level and activation patterns observed during its dynamical evolution.

Keywords: clique topology, network dynamics, synaptic plasticity

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Effects of electric fields on cognitive functions

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The influence of exposure to the external electric field (EF) generated by production, transmission, and use of electrical energy is under more and more intense scrutiny. Most of the efforts are usually focused on studying the possible risks for biological damage or permanent malfunctions of cells and, more generally, for human health. Cognitive and behavioral effects have also been experimentally studied, but the results have been so far inconsistent or contradictory [1, 2]: the main problem is that cognitive processes are the end result of cellular and network properties and interactions that are almost impossible to figure out or control experimentally *in vivo*. In this work we highlight, in single neurons, a few of those interactions that may be relevant at higher levels [3].

Using a morphologically and biophysically realistic three-dimensional model of CA1 pyramidal neurons, we investigate how, why and to what extent external perturbations of the intrinsic neuronal activity, such as those that can be caused by external Electrical Fields (EFs) at power line frequency can affect neuronal activity during cognitive processes. The simulation findings suggest that EFs at environmentally measured strength, can significantly alter both the average firing rate and temporal spike distribution properties of a hippocampal CA1 pyramidal neuron. This effect strongly depends on the specific and instantaneous relative spatial location of the neuron with respect to the field, and on the synaptic input properties. The model makes experimentally testable predictions on the possible functional consequences for normal hippocampal functions such as object recognition and spatial navigation. Our results suggest that, although EF effects on cognitive processes may be difficult to occur in everyday life, their functional consequences deserve some consideration, especially when they constitute a systematic presence in living environments.

Keywords: CA1 pyramidal neurons, external electric field, cognitive functions

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Accelerated information transmission with stable sparse code in strongly divergent-convergent feedforward networks

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A minimal number of higher-order neurons provide the coding basis for decision making and survival [1]. However, sensory information travels through several neural layers before converging onto a smaller number of neurons in a decision layer [2]. Indeed, accurate pattern recognition and reliable codification require sequences of neural layers to filter and extract useful information from raw sensory stimuli. Thus, multi-layered architectures induce a time lag between peripheral input and behavioral response, which is inconsistent with the need for reaction speed. We propose that the divergent-convergent synaptic organizations, often occurring in multilayered neuropils, enhance processing speed while guaranteeing accurate stimulus representation. Specifically, insect olfactory processing is a good model for investigating perceptual timing [3], where effective classification in the 4th layer 'anticipates' classification in input layers by 50ms [4].

Here we show that this anticipation emerges from a feedforward divergent-convergent connectivity and the relative sizes of each layer, which rapidly amplifies subtle input signals and improves precision. We consider Projection Neurons (PNs) from the Antennal Lobe that connect to Kenyon Cells (KCs) at the Mushroom Bodies. KCs then converge into the Mushroom Body Output Neurons (MBONs), where reward-based classification takes place. Because KC population is more than 100 times larger than MBON and PN populations, we set our network in a robust gain-control condition provided by GABAergic feedback neurons in the Protocerebro-Calycal Tract (PCTs). Our model reproduces experimental results of peak classification in MBONs anticipating PNs by 50ms on average. This becomes more pronounced as the KC layer grows, although for an oversized KC layer this anticipation becomes lower and the signal is eventually destroyed by the emphasized noise.

The key feature to this anticipation is the ratio between KCs to PNs, showing that larger brains may balance these populations to achieve jointly higher pattern recognition capabilities and fast discrimination times. However small this anticipation may seem, 50ms is comparable to the timescale that is needed for behavioral response in many insects. Thus, our contribution improves our understanding of the role of divergent-convergent networks, ubiquitous in many brains, on the stability of fast and accurate decision-making.

Keywords: feedforward, sparse code, Mushroom Bodies

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Thalamocortical mechanisms controlling motor timing in behaving primates

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The timing of actions is considered to be dictated by cerebellar output that is relayed to the motor cortex via the motor thalamus [1]. This hypothesis is consistent with the finding that cerebellar patients exhibit poorly timed and uncoordinated actions [2, 3]. We investigated the mechanisms by which the cerebellar-thalamo-cortical (CTC) system dictates temporal properties of motor cortical activity and the events that emerge when information flow through this pathway is temporarily interrupted.

Monkeys were trained to perform a 2-D reaching task that required tight control of motor timing. A cortical chamber was implanted above the motor cortex and stimulating electrodes were chronically implanted in the ipsilateral superior cerebellar peduncle (SCP). Neural activity was recorded from primary motor (M1, n=252) and premotor areas (PM, n=131).

Single pulse SCP stimuli efficiently recruited neurons in both M1 and PM (77% and 68% respectively) producing an early excitation followed by a prolonged inhibition. Cortical response in M1 occurred earlier than in premotor cortex (2.9 vs. 3.6 ms, $p < 0.01$) and had a shorter duration, whereas the subsequent inhibition was significantly longer (34.6 vs. 26.5 ms, $p < 0.01$).

Persistent high frequency SCP stimulation (HFS) led to a significant increase in reaction time (RT; -144ms vs. -189.3ms in control; $p < 0.005$) and movement time (MT; 447.2ms vs. 369.6ms in control; $p < 0.001$). In addition, the path travelled from center position to the peripheral target became more variable and generally longer (3.8cm vs. 3.5cm in control; $p < 0.001$). Finally, these changes were more prominent for targets that required a coordinated elbow-shoulder movement.

These behavioral changes were accompanied by changes in neural activity. We computed the preferred direction (PD) of single cortical cells and their phasic-tonic index (PTI) which measured their tendency to fire in a tonic vs. phasic manner. Single cortical cells maintained their PD during HFS trials but their PTI decreased significantly ($p < 0.005$), consistent with a shift from a phasic to tonic response pattern.

These results suggest that the CTC evokes an extensive excitatory-inhibitory motor cortical

volley that is temporally organized across M1 and PM areas. Interfering with the flow of information in this pathway produces motor deficits similar to those found in cerebellar ataxia. The neural correlate of these behavioral changes is the loss of phasic firing at movement onset. It is thus suggested that CTC system controls the timing and coordination of voluntary movements by shaping the response pattern of single cortical cells independently of their spatial properties.

Keywords: Thalamocortical, ataxia, motor control

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The early olfactory code in bees

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The transduction and coding process of odorants has many common features across phyla and in the early stages consists of a shallow, feed-forward network that performs the initial odour coding. In bees, odours bind to roughly 160 different olfactory receptor types. Receptors are expressed in the membrane of olfactory receptor neurons (ORNs) and each ORN expresses only one receptor type. The ORNs that express the same receptor type all project to the same, spherical regions, so-called glomeruli, in the antennal lobe. This is presumably where the first lateral interactions between signals from different receptors, and hence the first non-trivial coding transformations, take place.

Experimentally, the olfactory code in bees has been investigated with electro-physiological recordings but predominantly with calcium imaging methods. In electrophysiological recordings, observations are limited to single cells (intra-cellular recording) or a few cells (extra-cellular recordings), while in calcium imaging a wider field of the antennal lobe can be observed, albeit with much lower time resolution. In none of the methods do we obtain a full set of responses from all 160 glomeruli. Imaging, e.g., routinely only provides data from about 30 glomeruli [1, 2], Figure 1A.

Here we report a model of the early olfactory system in bees that attempts to give a likely account of the full 160-dimensional response profile of the bee antennal lobe. To guide the construction of the model we utilized a number of complimentary experimental data sets and observations:

- We used data from bath applied calcium imaging of 26 identified glomeruli at a single, high concentration, which reflect the receptor neuron responses at saturation [1].
- We extract first and second order statistics from the data and augment response patterns so that these statistics are preserved.
- We use the insights on concentration dependence of olfactory responses in moths [3] to extend the model to lower concentrations.

The resulting olfactory receptor activation patterns were translated into rates and implemented into a leaky-integrate-and-fire (LIF) neuron network, in which ORNs project to both, local neurons (LNs) and projection neurons (PNs) in the antennal lobe. LNs inhibit each other and the PNs of all other glomeruli (see Figure 1B).

Our model is consistent with results of other experiments that were not directly used for building it. An example is displayed in Figure 2. Bees were exposed to short 2ms pulses of odors at different frequencies to observe the bees' ability to track high frequency inputs [4]. As in the real bees, the model tracks slower input well, albeit already with some integration, and then increasingly integrates input at high frequencies. Note however, that the time scales between experiment and model are not matched perfectly due to some simplifications in the model.

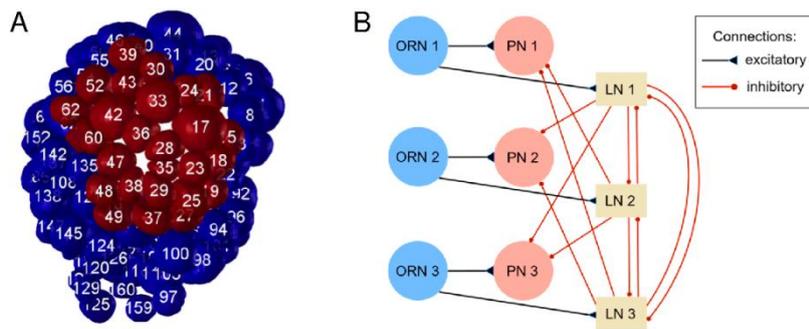


Figure 1: A Bee antennal lobe with identified glomeruli [2]. Only the glomeruli in red can be routinely observed. B Simple antennal lobe model.

Other results include reproducing the correlation profile between ORN and PN activity patterns with a strong peak at 0.7 [5] and the trends in dose response and correlations in ORNs versus those in PNs [6].

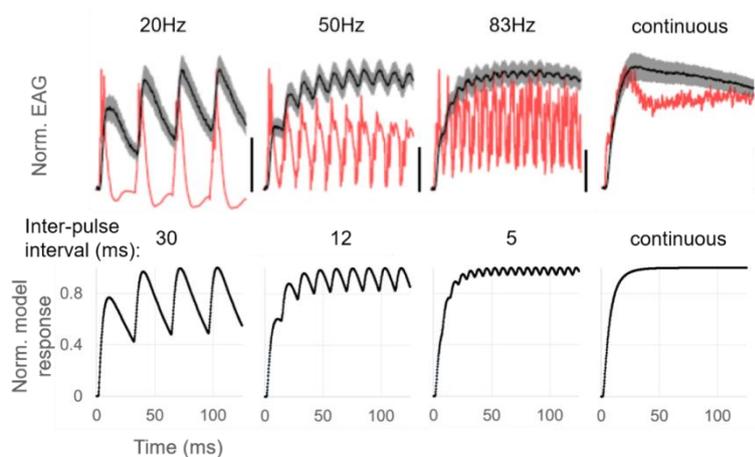


Figure 2: Pulse tracking in experiments (top) [4] and the model. Pulses are well-tracked for lower frequencies and responses become more integrating for higher ones. The qualitative behaviour is captured well in the model even though the exact time scales differ slightly.

Keywords: Insect olfaction, odour coding, chemical senses

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Criticality in the emergence of spontaneous fluctuations in spiking neuron networks

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Spontaneous fluctuations in neuronal firing activity are widely observed in neural networks *in vivo* as well as *in vitro* [1]. In recent studies, it is proposed that spontaneous fluctuations in neural networks can be utilized for generating motion or storing memory because of a rich variety of temporal dynamics [2, 3]. Thus it is important to comprehend the mechanism by which spontaneous fluctuations appear. When considering an isolated network of neurons, the firing rates remains constant for weak interactions among neurons, while the firing rates may exhibit non-stationary fluctuations even in the absence of external inputs for strong interactions. The critical interaction strength for the emergence of fluctuations may depend greatly on the network structure in which neurons are connected. Furthermore, we develop a method of reallocating connections among neurons so that fluctuations may be either impeded or impelled in a network. Accordingly we found that reciprocal connections and clustering tends to facilitate spontaneous fluctuations in the firing activity.

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The dopamine signal under sensory and temporal uncertainty

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Animals live in uncertain environments where they have to make decisions based on noisy sensory information to maximize possible rewards. Ideas from the field of reinforcement learning have played an important role in neurobiological theories of reward-motivated behavior [1]. Although reinforcement learning successfully explained dopaminergic activity in classical and operant conditioning, its potential in understanding the role of dopamine in decision-making tasks with uncertain temporal and sensory information has not been investigated.

I will first review our previous modeling work about how the cortex could detect weak stimuli arriving at unknown times [2-4]. Later I will use the belief about the presence of these stimuli in a reinforcement learning model [5] to describe the dopamine signal recorded in the same task [6]. The model correctly predicts that dopamine neurons are phasically activated by the subjective perception of the relevant stimulus. The tonic activity is affected by the temporal uncertainty in the task. In correct rejection trials this activity results from the variable duration of the trial. In hit trials it comes mainly from the finite resolution in the estimation of time intervals. It represents a form of negative reward prediction error generated by the temporal expectation of an event that fails to occur.

This study shows that reinforcement learning procedures can be a powerful tool to study decision-making tasks with sensory and temporal uncertainties.

Keywords: decision-making, reinforcement learning, dopaminergic activity

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Towards modeling of stochastic correlated inputs and adaptation in neuronal firing

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The phenomenon of adaptation in the spike-frequency in the central nervous system has a role in the neural information processing. In literature there are several different approaches to investigate and model the observed decrease in the firing rate after intensive spiking periods and under the effects of applied inputs, see [9, 10] and references therein. Spike-frequency adaptation is often explained as a consequence of the dynamics of membrane neuronal gates or of the action of given ionic currents, as those related to voltage-dependent potassium channel or those related to the slow calcium dependent potassium channels. In the stochastic modeling the behavior of the membrane potential is thus connected to the stochastic dynamics of varying in time input currents generated by the variations of ionic species, but the understanding of the adaptation and of its generating mechanism is still not completed.

The theory of Gauss-Markov (GM) processes [1] and the First Passage Time (FPT) problem through specified boundaries turns out especially useful in the stochastic modeling of neuronal firing [2-5]. Starting from a Leaky Integrate-and-Fire (LIF) model including time-dependent features of the neuronal dynamics, the usefulness of theoretical and numerical results related to a time-inhomogeneous Ornstein-Uhlenbeck (OU) process has been properly exploited. The use of the corresponding GM process allowed to obtain reliable estimations of the neuronal firing activity and some satisfactory approximations of results as those highlighted, for instance, in [6]. Then, the need of describing several phenomena, such as interactions between neurons [7], effects of input currents [8], a particular adaptation of the firing activity [9, 10], occurrence of spike trains [11, 12] have led us to design specialized neuronal models and consequently to construct suitable GM processes.

In order to understand why and what can generate the adaptation phenomenon, here we construct a neuronal stochastic model considering a time-inhomogeneous LIF model including specified time correlated inputs, similarly as suggested in [13]. This inclusion can affect the characteristic times and resting levels in time and originate the adaptation. By including stochastic correlated inputs we aim to model not only the ionic currents but also the effect of eventual inhibitory synaptic currents. Theoretical approximations by GM processes and their FPTs densities will be derived to provide estimations of firing activity of such a neuron. The investigation will be also centered on how and how much the correlated inputs and their correlation times affect the firing dynamics. Different time-scale parameters can be considered. How the GM approach can be useful to predict the highlighted aspects of the above neuronal firing activity can be shown by comparing numerical and simulation results.

Keywords: generalized stochastic LIF models, integral approach, correlation time

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Functional data analysis of the recordings of auditory evoked potentials

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We study the drug-induced tinnitus animal model where rats receive daily overdoses of salicylate to induce reversible episodes of tinnitus [3]. Following salicylate injections, auditory evoked potentials (AEPs) were recorded from awake animals in response to either narrow-band signal (tone burst) or a wide-band signal (click) presented at different intensities. Single-trial AEPs were then extracted. In the previous study [4], the data were fitted parametrically using nonlinear regression and the Fisher information of the AEPs was finally calculated over a range of sound intensities to represent intensity coding in the pre- and post-drug conditions. The flexibility of such modelling is limited.

We continue to analyse the data using the methods of the functional data analysis (FDA, [1]). Nonparametric ideas have been adapted to the functional variable settings, providing much more flexible models. In the concept of FDA, the single-trial AEPs are considered to be (smooth) curves. The statistical tools of FDA include kernel smoothing, functional principal component analysis, functional kernel regression [2] or classification. The challenges with functional data lie in the infinite-dimensional nature of the data, among others. Using FDA, we expect to gain more information from the AEPs than by using the classical regression technique.

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Keywords: single trial auditory evoked potential, functional data analysis, kernel regression.

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Excitation-inhibition interplay controls timing and coordination of motor actions

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Proper performance of voluntary movements requires the integration of both spatial and temporal information about the ensuing movements. The timing of actions is often considered to be dictated by cerebellar output that is relayed to the motor cortex via the motor thalamus. We investigated the mechanisms by which the cerebellar-thalamo-cortical (CTC) system controls temporal properties of motor cortical activity.

We found that in primates the CTC pathway efficiently recruits motor cortical neurons in primary motor and premotor areas. Cortical responses to CTC activation were dominated by prolonged inhibition mediated by a feedforward mechanism. We further found that cortical cells that integrated CTC input fired transiently and synchronously at movement onset, when the timing of action is dictated. Moreover, when preventing the flow of information in the pathway the phasic firing at movement onset was reduced, but the preferred direction of the cells remained unchanged. These changes in neural firing were correlated with altered motor behavior: the monkeys were able to perform the task but with increased reaction and movement times.

These results suggest that the CTC system affects cortical firing by changing the excitation-inhibition balance at movement onset in an extensive network of TC-activated motor cortical neurons. In this manner, the temporal pattern of neural firing is shaped, and firing across groups of neurons is synchronized to generate transiently enhanced firing.

Variability in neural spike trains

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While exploring the neural code, a very important question arises what is the character and purpose of the variability observed in the spike firing. There are various possibilities leading to various concepts of coding [1]. The simplest one, the rate coding, supposes that the variability is just a noise, and that only the rate of the spikes plays the role. On the other hand, the exact spiking times could code the information. Another concept, the variability coding, which is between these two extremes, assumes that directly an amount of the variability contains some information. The true mechanism of coding performed by neurons is still not clear, however, understanding the variability is a step to its clarification. Therefore, recently, we have been interested in the variability measures and their estimation, as correct quantification is the first step to its study and understanding.

In this contribution, we present an overview of our results in this field. Four main topics are concerned – (i) estimation of Fano factor, which is a common used variability measure of neural spike trains [2], (ii) its generalization by incorporating an in-time decreasing influence of the incoming spikes [3], (iii) a study of influence of the input variability on the output of a neuron described by the Stein's model [4] and (iv) a proposal of a new measure of randomness.

Keywords: Variability coding, neural spike train, Fano factor

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Modeling of EEG time-series by conditional probability neural networks.

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Electroencephalography (EEG) is a popular method to record voltage fluctuations on the surface of the brain. Although it is often used to assess brain dysfunction like epileptic seizures in clinical contexts, the origins of the EEG signal are still poorly understood, and only very few generative models (see e.g. [1]) exist. Here we introduce Conditional Probability Neural Networks (CPNN) as a new means of modeling EEG, or similar neurophysiological data. We train the CPNN to EEG time series recorded from epileptic dogs [2]. We demonstrate that the trained CPNN outperforms standard time series models, such as the autoregressive process or multilayer perceptron regression in generating signals that match the power spectrum and other statistics of the recorded EEG.

By our method, which we adapted from particle physics [3], a neural network is trained to represent the conditional probability density function of the future values of a stochastic process, given a set of samples from its past. Once the CPNN is trained, samples drawn from the trained model have very similar statistics to samples of the original process. Moreover, the CPNN can be used as a predictive model if generated samples are presented as inputs to the CPNN iteratively. Such a model may then be used for forecasting and generation of time-series [4, 5], in order to predict brain dysfunctions, like epileptic seizures or other neurological events.

In contrast to common machine learning approaches which learn to predict the most likely future value from presented samples, the CPNN provides an estimate of the conditional probability density function (or posterior distribution), and thus has an intrinsic representation of the process' stochasticity. This aspect might be crucial for modeling highly variable neurophysiological time series such as EEG.

Keywords: conditional probability density estimation, artificial neural networks, stochastic process modeling

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Variability of motor cortical spiking activity is modulated by the behavioral context

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Exploring the nature and origin of neuronal variability is essential for our understanding of information processing in cortical networks. We hypothesize that the variability of spiking activity varies as a function of the behavioral context. We analyzed a large set of spike trains recorded in motor cortex of two monkeys during the execution of an instructed-delay reach-to-grasp task (for details see [1]). We exploited two measures for variability: (i) the Fano factor (FF) which measures the spike count variability across trials, and (ii) the local measure of the coefficient of variation $CV2$ [2] measuring the interspike interval variability. We performed the analysis of the variability within two different behavioral contexts: a) during the instructed delay (*wait*) when no movement was allowed, and b) during the subsequent movement execution (*movement*).

Our data show that, first, FF significantly decreases from *wait* to *movement*. This is in agreement with our former studies [3] and a large meta-study [4]. At the same time, $CV2$ significantly increases from *wait* to *movement*. A reason for this may be the tendency of spikes to lock to LFP beta oscillations [5], which have been shown to be prominent during *wait* but absent during movement [6].

Second, in stationary and renewal processes, a widely used model for spiking activity [7,8], the two variability measures are related as $FF \approx CV2$. In our data, however, we find that the relation of $CV2$ to FF depends considerably on the behavioral context (see Fig. 1). Whereas

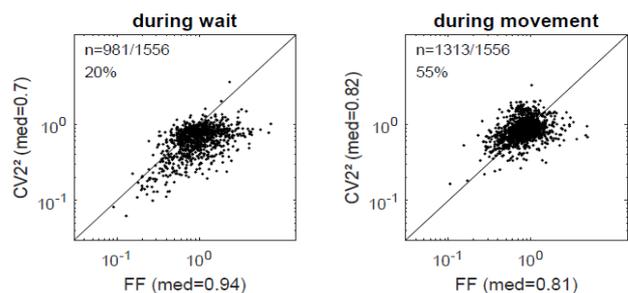


Figure 1: Log-log representation of scatter diagrams of the $CV2^2$ vs FF during *wait* (left) and *movement* (right) for the spiking data of one of the two monkeys. In the left upper corner of each plot, the percentage of neurons is indicated whose ratio $FF/CV2^2$ was smaller than 1.

during *movement* the renewal prediction is fulfilled (at the right), it is not during *wait* (at the left), where the spike count variability across trials is much larger than the spike time irregularity within spike trains ($FF \gg CV^2$). Thus, our results suggest that during movement preparation (*wait*), ongoing brain processes [9] dominate and thereby result in spike trains that are highly variable across trials, as identified by the increased FF. During *movement*, the task-related activity increases at the expense of ongoing processes, and therefore the FF decreases. We conclude that ongoing processes in cortical networks provide a major source of count variability that is not task-related, but suppressed during movement execution.

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Keywords: monkey motor cortex, spike trains, variability

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Differences in movement-related, inter-regional phase-locking in young and elderly healthy subjects

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The vast majority of motor actions, including their preparation and execution, is the result of a complex interplay of various brain regions. Novel methods in computational neuroscience allow us to assess interregional interactions from time series acquired with in-vivo techniques like electro-encephalography (EEG). These methods provide different neuronal representations of movement (e.g. ERD, ERS, PLI). However, our knowledge of the functional changes in neural networks during non-pathological aging is relatively poor.

To advance our knowledge on this topic, we recorded EEG (64 channel system) from 18 right-handed healthy young participants (22-35 years, 10 female) and 24 right-handed healthy old participants (60-79 years, 12 female) during a simple motor task. The participants had to execute voluntary low frequency left or right index finger tapping movements.

We used the relative phase-locking value (rPLV) computed from the phases obtained by Morlet wavelet transformation of the Laplacian-referenced EEG data to identify the functional coupling of brain regions during the motor task. We analyzed the connectivity for electrodes lying above the left and right premotor areas (lPM: F3, FC3 and rPM: F4, FC4), supplementary motor area (SMA: Cz, FCz) and the left and right primary motor cortex (lM1: C3, CP3 and rM1: C4, CP4). We compared the resulting networks of significant phase-locking increase in time-intervals prior, during and after the movement.

Our analysis revealed an underlying coupling structure around the movement onset in the delta-theta frequency band (2-7 Hz), only. For young subjects, the connection from SMA to M1 contralateral to the moving hand showed a significant rPLV increase already in the preparatory phase of the movement. This synchronization remained significant during the movement and in a time interval after it. In elderly subjects, however, the change in rPLV between SMA and contralateral M1 was significant only during the execution of the movement. We furthermore monitored the behavioral performance of the two age groups and observed a lower movement speed in the elderly subjects. We therefore suggest that a lateralized rPLV between SMA and M1 prior the movement is needed to accurately initiate and perform the finger movements.

Keywords: network, connectivity, ageing

Variability dynamics in balanced networks with clustered inhibitory and excitatory connectivity

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The high trial-to-trial variability of the spike count of neurons in the mammalian neocortex, as measured by the Fano Factor (FF), can be significantly reduced by stimulus presentation or movement onset [1, 2]. In extracellular recordings from Macaque motor cortex taken during a delayed reaching task [3] we analyse time resolved spike count and inter-spike-interval statistics. While count statistics (FF) are temporally modulated, the interval variability as quantified by different measures (squared coefficient of variation (CV^2), local coefficient of variation (CV_2) and local variation (L_V)) shows comparatively weak modulations (Fig 1. upper panel, see also companion abstract [4]).

Recently, a series of studies have shown that the stimulus induced reduction in FF can be captured by balanced network models of integrate and fire neurons with clusters of stronger connectivity in the excitatory population [5, 6, 7]. In these networks, individual clusters cycle between states of high and low activity. This introduces firing rate variations which increase the FF to values above unity. When a stimulus in the form of an increased current injection is applied to one or more of the clusters, these clusters are clamped to the high activity state and others are suppressed through lateral inhibition. This mechanism quenches the rate variations and the FF is reduced to that of an unstructured balanced network. In these clustered network models, neurons in the active clusters fire at rates close to saturation and produce very regular spike trains. Such high rate, regular spike firing, is however inconsistent with findings in physiological recordings from the neocortex.

Using a mean field description of networks of binary neurons [8], we analyse the stable rate configurations of networks with clustered connectivity and show that the firing rates in the active states can be reduced by the additional introduction of inhibitory clusters. We then show that this result can be transferred to networks of spiking leaky integrate-and-fire (LIF) neurons where the inhibitory clusters preserve the balance of excitatory and inhibitory input currents in the high activity states. This leads to variable spike trains at moderate firing rates in agreement with our findings in the cortical data set (fig. 1, lower panel). The range of parameters over which cycling between clusters is achieved is thereby greatly increased, reducing the need for fine tuning of network parameters

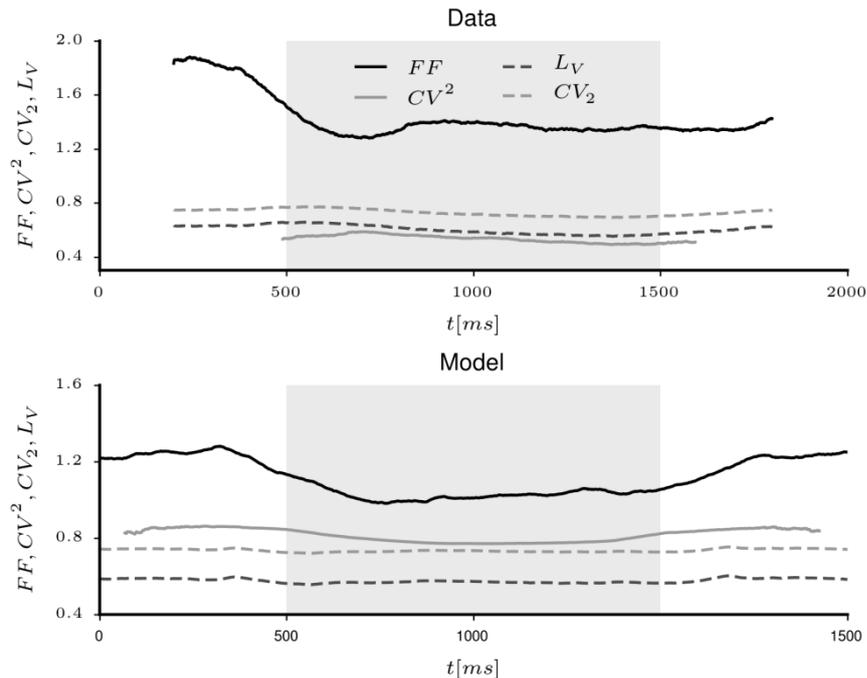


Figure 1: Time resolved variability statistics in monkey motor cortex (top) and balanced network model of LIF neurons (bottom). Shaded area represents interval of cue presentation (top) or application of stimulation current (bottom).

Keywords: Cortical Variability, Balanced Networks, Clustered Connectivity

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Integrate and fire like models with stable distribution for the interspike intervals

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In 1964, Gernstein and Mandelbrot [1] proposed the Integrate and Fire model to account for the observed stable behavior of the Interspike Interval distribution. Their study of histograms of ISIs revealed the stable property and they suggested modeling the membrane potential through a Wiener process in order to get the inverse Gaussian as first passage time distribution, i.e. a stable distribution.

Later many variants of the original model appeared with the aim to improve its realism but meanwhile researches forgot the initial clue for the model. The Leaky Integrate and Fire model that has not stable FPT distribution gives an example. The same holds for many other variants of this model.

Holden [2] observed that stable distributions determine a simple transmission pathway. Signals from different neurons are summed up during the elaboration. Different ISIs distributions would determine an incredible variety of firing distributions as the information progresses in the network. Furthermore, the stable ISIs paradigm gives rise to a more robust transmission algorithm since a possible lack of detection of some spike from the surrounding neurons does not change the nature of the final distribution.

Here we rethink to the problem, taking advantage of the mathematical progresses on Levy processes [3]. Hence, we propose to start the model formulation from the main property, i.e. the stable nature of the ISIs distribution.

This is a preliminary contribution in this direction and we limit ourselves to some aspects of the modelling proposal but we are conscious that these are preliminary examples and some further mathematical study will be necessary and some further effort is necessary to make realistic some of our assumptions.

In this framework we present a model that exhibits tempered [4] stable distributed ISIs, that is stable behavior with finite moments. We model the supremum of the membrane potential through an inverse tempered stable subordinator, and the ISIs according with the Integrate and Fire paradigm. Special cases include Gamma or Inverse Gaussian distributed ISIs.

Keywords: stable distribution; Integrate and Fire Model; ISIs distribution

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Adaptive motor control: task-specificity of movement feedback processing during the generation of steps in a curve walking insect

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Animals need to move flexibly to adapt to environmental demands. This becomes immediately clear from observing complex motor tasks, like climbing, but it also holds for rather simple motor tasks, like changing walking direction, e.g. during curve walking, when the legs of the animal have to generate different kinematics in order to successfully generate a turn. During curve walking, a middle outside leg generates large amplitude, longitudinally directed stance movements, whereas the inside leg generates small amplitude stance movements with marked tibial flexion [1]. Recently we have shown, that three specific descending influences from stepping rostral legs modify the processing of movement and load feedback as well as the activity of central pattern generating networks in caudal segments. This contributes to the task-specific changes in motor activity during the generation of curve steps in the middle legs [2, 3]. For example, flexion signals from the Femur-Tibia (FTi-) joint, reported by the femoral chordotonal organ (fCO), induce reinforcement of the *Flexor tibiae* activity more often on the inside than on the outside.

In the present study, we tested whether this task-specificity arises from the fact that parameters of tibial movement are processed differently between inside or outside steps, and whether the same parameters of tibial movement are processed differently during directional stepping. For this purpose, we stimulated the middle leg fCO with a broad range of stimulus velocities (150-750deg/s), varying amplitudes of FTi-joint movement (40-100deg), and at varying starting angles (70-150deg). Simultaneously, we recorded the activity of tibial motoneurons and muscles while animals generated curve stepping on a slippery surface with the remaining legs.

With increasing starting angles and decreasing stimulus velocities [4] the frequency of occurrence of reinforcement of tibial motoneuron activity increased for the inside and outside leg, while it was unaffected by the amplitude of the FTi-joint excursion. The likelihood for reinforcement of movement for all three modalities was significantly higher during inside compared to outside steps. The highest probability was found to be 70% for the inside leg condition with an FTi-joint movement amplitude of 100deg, a movement velocity of 150deg/s and a starting angle of 150deg (N=11, n=132).

Our results show that the occurrence of movement reinforcement caused by fCO elongation during inside and outside steps on both sides markedly depends on starting angle and velocity of movement. However, thresholds for eliciting the motor response are drastically lower for the inside leg. To explore the mechanisms behind this response, we currently perform intracellular recordings from tibial motoneurons and premotor interneurons [5].

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Stochastic mean-field theory for finite-size populations of spiking neurons

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Bridging the scales from single neurons to mesoscopic populations of neurons is fundamental for multi-scale modeling of the brain. However, to establish a quantitative map from experimentally verified spiking neuron dynamics to the dynamics of mesoscopic populations remains a largely unsolved theoretical problem.

Here, we derive stochastic mean-field equations for the population activities of interacting, finite-size populations of generalized integrate-and-fire neurons [1] that are randomly connected. The class of neuron models accounts for various spike-history effects like refractoriness, adaptation and bursting. Importantly, its parameters can be efficiently extracted from experiments [2] yielding faithful models of real cortical cells. The derived mesoscopic dynamics captures nonlinear emergent dynamics as well as finite-size effects, such as noisy limit-cycle oscillations and stochastic transitions in multistable networks. Realizations generated by the mesoscopic model have the same statistics as the original microscopic model to a high degree of accuracy, even for low numbers of neurons (e.g. $N = 100$). Our theory establishes a general framework for modeling finite-size, neural population dynamics based on single cell and synaptic parameters and offers an efficient way to analyze cortical circuits and computations.

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Keywords: multi-scale modeling, finite-size networks, mean-field theory, spiking neurons

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Comparative study of chemical neuroanatomy of the olfactory neuropil in mouse, honey bee and human

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In the honey bee, the antennal lobe (AL) is the first olfactory neuropil where axons from olfactory sensory neurons from the antenna converge into glomeruli, where they synapse onto dendrites of projection neurons. The glomerulus is a 'computational unit' that relays information about odors to higher odor centers such as the mushroom body and the lateral horn. The honey bee AL is a highly organized containing 160 glomeruli as well as an aglomerular neuropil where axons of AL neurons extend without synaptic connection. Each glomerulus contains an outer 'cortex' area and an inner 'core'. Axons from the olfactory receptors terminate into the glomerular cortex where they synapse onto dendrites of projection neurons and at least two types of local inhibitory interneurons. Synaptic contacts in the core serve to make lateral connections with other glomeruli through local interneurons, GABAergic multi-glomerular projection neurons and aminergic projection neurons. The latter connect regions such as the gustatory neuropils with the AL and higher odor neuropils. The AL is functionally analogous to the olfactory bulb (OB) in mammals. In this neuroanatomical study, we summarized the important similarities in the neuroanatomy of biogenic amine distributions in the AL and olfactory bulb in honey bee, mouse and human. Serotonergic fibers are similarly distributed among all glomeruli in honey bee and mouse, while octopaminergic/tyraminergetic fibers in the honey bee have a similar distribution, and possibly a similar function, to noradrenergic fibers in glomeruli of the mouse OB. Differences were observed in the distribution of dopaminergic neurons in glomeruli of honey bee as compared to mice. Each glomerulus in the mouse and human has a stereotypical group of dopaminergic neurons in each glomerulus. In the honey bee, the dopaminergic fibers are absent in glomeruli. Instead they innervate the neuropil just outside of and surrounding the glomerulus. The present data show that the honey bee and mouse olfactory centers (AL and OB) can be readily compared at the level of the glomerulus. The human OB has relatively less structural organization. We will present speculation on the reasons for the similarities and differences across these three species.

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Keywords: biogenic amines, olfactory bulb, neuroanatomy

Ito excursion theory: an application to the firing paradigm in stochastic neuronal models

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Integrate and Fire (IF) models are among the most used descriptions of the single neuron membrane potential dynamics.

However, in many instances, data are not consistent with a relevant feature of such models. We refer to the absorbing assumption imposed to the membrane potential at the threshold level, i.e. the firing condition. The presence of the absorbing boundary is often disregarded, introducing important errors in the estimation procedure [1, 2].

Mainly motivated by statistical purposes, we propose here a new definition of the firing time of a neuron. The new model relaxes the absorption condition and allows crossing of the threshold without firing.

We assume that a spike is generated as the membrane potential reaches a fixed threshold level and remains above it for a sufficiently long time interval. The firing time is defined as

$$H = \inf\{t \geq 0 \mid (t - g_t) \cdot 1_{V_t \geq S} \geq \Delta\}$$

where V_t is the neuron membrane potential, 1_A is the indicator function of the set A , Δ is the time window that the process has to spend above the threshold S and $\forall t$,

$$g_t = \inf\{s \leq t, V_s = S\}$$

In order to derive the Laplace transform of H for a general diffusion process V_t , we study H in the framework of Ito excursion theory [3]. In particular, we review the question of the first excursion of a diffusion process V_t above a certain level S with length strictly greater than Δ . Main references related to this problem are [4] and [5].

Finally, we specialize our results for the three diffusion processes that appear in (Leaky) Integrate and Fire neuronal models: Wiener, Ornstein-Uhlenbeck and Feller processes.

The results discussed in this paper are seminal to approach the estimation of the parameters for this new family of neural models.

Keywords: Ito Excursion theory, Leaky Integrate and Fire model, firing time.

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Bringing high performance neural simulation to the desktop with BrainGrid

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Neuroscience has benefitted as much as any scientific endeavor from becoming a computational science. Of course, computers have played a major role in neuroscience for decades (such as in [1]), but modern hardware now presents researchers with access to inexpensive desktop high-performance computing capabilities that rival that of recent-vintage supercomputers (for example, the NVIDIA Tesla K80 graphics processor has almost 5,000 processors with an aggregate performance of nearly 9 teraflops) for costs that range from the hundreds to a few thousand dollars.

Taking advantage of this computing power, however, is problematic. General-purpose simulation environments, such as Neuron [2] and GENESIS [3], focus primarily on supporting high-level, physiological descriptions of cells and networks and, as such, target single-processor platforms (whose performance characteristics have been flattening out in recent years) or networked clusters (which are expensive, difficult to maintain, and unlikely in general to provide significant performance increase). Other, special-purpose simulators targeting graphics processing units (GPUs), such as [4], have limited flexibility and would require significant GPU-oriented software development for most computational neuroscience investigations. Generally speaking, developing non-trivial GPU programs can take weeks to months. Moreover, while validation of simulation software is difficult in general, it is even more so for parallel hardware.

The BrainGrid simulation framework [5] has been developed to help researchers take advantage of inexpensive, modern multiprocessor hardware to either significantly speed up large and long-duration simulations or enable simulations that are impractical on general-purpose hardware, either singly or as clusters. This framework targets three pain points in such work: (1) time and difficulty in developing GPU code, (2) difficulty in validating correctness of parallel code, and (3) difficulty in gaining significant performance increases from parallel hardware, especially given the idiosyncrasies of neural simulation algorithms.

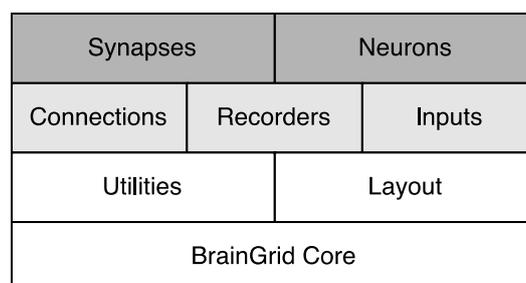


Figure 1: BrainGrid architecture. Dark grey: modules that require some coding to create new mathematical models; light grey may need additional code for specialized learning rules, stimulus protocols, or data collection.

Figure 1 shows this framework’s structure. We assume that investigators intend to write their

own simulation code. The BrainGrid framework isolates investigator code to the smallest possible context, often part of a single function, and provides coding patterns to further reduce the need to write code from scratch and simplify programming. It includes subsystems optimized for GPU-based neural simulations. Validation is facilitated by pre-structuring code so that patterns that are efficient on the GPU will run on an ordinary, single processor CPU. As a result, code can be written and validated first in a familiar CPU environment and then migrated to a GPU, with only minor changes, minimizing situations in which bugs can arise and maximizing performance. This framework inverts the usual approach to easing GPU software development, in which the GPU programming environment is made to look like the CPU environment. As a result, BrainGrid can achieve speedups in excess of 20X on six-year-old GPU technology [6] (more than 40X on current vintage hardware), as opposed to two to three times using others' methods. In addition, because the elements of the framework that optimize neural simulation algorithms on GPU hardware are part of the simulator core, existing models can take advantage of software and hardware performance improvements without need for modification.

BrainGrid's utility has been demonstrated in simulations of development and bursting in cortical cultures that involved 10,000 neurons, more than 450,000 synapses, and 600 million time steps [7], reducing what would have been impractically long 6-9 month simulations to 3-4 days' duration. BrainGrid is under active development by software engineers and is made available with an open source license. An extension to BrainGrid, the BrainGrid workbench, will use software engineering best practices to facilitate more rigorous testing and indicate when changes to software may invalidate the results of previous simulations.

Keywords: simulation, tools, high performance computing

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MantisBot is a robotic model of visually guided motion in the praying mantis

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Insects use highly distributed nervous systems to process exteroception from head sensors, compare that information with state-based goals, and direct posture or locomotion toward those goals. To study how descending commands from brain centers produce coordinated, goal-directed motion with a distributed nervous system, we have constructed a conductance-based neural system for our robot MantisBot, a 29 degree-of-freedom, 13.3:1 scale praying mantis robot [1]. Using the literature on mantis prey tracking and insect locomotion, we designed a hierarchical, distributed neural controller that establishes the goal, coordinates different joints, and executes prey-tracking motion.

In our controller, brain networks perceive the location of prey and predict its future location, store this location in memory, and formulate descending commands for ballistic saccades like those seen in the animal. The descending commands are simple, indicating only 1. whether the robot should walk or stand still, and 2. the intended direction of motion. Each joint's controller uses the descending commands differently to alter sensory-motor interactions, changing the sensory pathways that coordinate the joints' central pattern generators (CPGs) into one cohesive motion. Experiments with one leg of MantisBot show that visual input produces simple descending commands that alter walking kinematics, change the walking direction in a predictable manner, enact reflex reversals when necessary, and can control both static posture and locomotion with the same network. The resulting motion and reflex reversals are reminiscent of those observed in our recent work, in which stimulating specific populations in the central complex (CX) of the cockroach evoked the reflex reversals seen while the animal turns [2].

As in related models [3], each joint in our controller uses sensory feedback to affect both the timing and magnitude of motion. Descending commands encode desired body motion, which alter the processing of feedback differently at each joint to affect timing and magnitude simultaneously, producing foot motion in the intended direction. When the thorax-coxa (ThC) and femur-tibia (FTi) joints reach their posterior extreme position (PEP), the coxa-trochanter

(CTr) joint's CPG receives input to flex, causing the leg to enter swing phase. When the ThC and FTi joints reach their AEP, the CTr joint's CPG receives input to extend, causing the leg to enter stance phase.

Each joint possesses a network that maps the descending commands to the PEP, which is used to control the timing and magnitude of joint motion. To control joint timing, the network routes load information to the half of the CPG that will cause the proper stance phase motion. For instance, if the intended PEP is more extended than the resting posture, then a pathway from strain sensors in the leg to the extensor half of the CPG is disinhibited, causing joint extension in stance phase. Conversely, if the PEP is more flexed than the resting posture, then load information is routed to the flexion half of the CPG. To control magnitude, the network uses the angle between the PEP and resting posture to adjust the gain of the connection between the CPG and motoneurons (MNs), altering the joint's range of motion. A parallel network is used to control the anterior extreme position. This distributed structure enables the leg to walk in a continuum of directions while receiving descending commands that only encode the body's direction of motion.

Keywords: descending commands, praying mantis, robotics

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Neuronal response latency estimation in presence of a background signal

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Neuronal response latency is usually vaguely defined as the delay between the stimulus onset and the beginning of the response. It contains important information for the understanding of the temporal code. For this reason, the detection of the response latency has been extensively studied in the last twenty years, yielding different estimation methods [1]. If the response can only be observed on top of an indistinguishable background signal (in the form of ongoing spontaneous firing), the estimation of the time delay can be highly unreliable, unless the background signal is accounted for in the analysis [2]. Here we propose different parametric and non-parametric methods to investigate neuronal response latency based on detection of spikes evoked by the stimulation using interspike intervals and spike times. In particular, investigation from the first-spike latency in presence of excitatory inputs and/or inhibitory inputs is presented [3, 4, 5]. Poisson process, integrate-and-fire model (Wiener process) or Leaky integrate-and-fire model (Ornstein-Uhlenbeck) are considered for modeling the single neuron firing mechanisms, and the proposed methods are illustrated on both simulated and real data.

Keywords: extracellular recordings in neurons; spontaneous and evoked activity; maximum likelihood estimation.

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Numerical implementation of neural diversity

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No neuron reacts in the exactly same way as any other one, even if they are from the same population. Also neuronal network never consist of completely identical elements. This experimentally well-known diversity of neurons and synapses is in mathematical simulations mostly neglected.

We have implemented diversity in a HH-type model neuron which has been modified to directly represent experimentally observable membrane parameters [1] as used in the virtual “SimNeuron” laboratories (fully functioning demo versions available on www.virtual-physiology.com). All parameters of the membrane equations, from leak conductance and voltage to equilibrium potentials to voltage dependent conductances and membrane capacitance have been endowed with certain randomness (Fig. 1).

Besides of the membrane capacitance, however, these parameters were not directly randomized. Their distributions are results of simple uniform distributions of secondary parameters on which they are based. The equilibrium potentials are calculated from random distributions of intra- and extracellular ion concentrations using the Nernst equation. The leak conductance is the sum of single conductances which are individually randomized. The leak potential is the result of a combination of all these randomized parameters. Thereby an almost “normal” distribution is attained. However, in contrast to the Gauss distribution this one is limited.

The distributions of the voltage dependent conductances (Fig.1, lower left diagrams) are again based on uniformly randomized values, hereof slopes and half-potentials of Boltzmann functions and maximum conductances. These distributions are significantly different at different membrane potentials because of the voltage dependencies of the (in-) activation variables. Nevertheless, our randomization strategy guarantees that no negative values will appear. Finally, the typical lognormal distribution of the membrane capacitance, proportional to the membrane area, has been implemented using a newly developed algorithm that has been derived in the course of this study from the Nernst equation.

Such randomization generates a broad diversity of model neurons. When the mean values are taken from the “General Neuron” of the “SimNeuron” lab, most randomized neurons will likewise be in a steady state. Nevertheless, a certain percentage exhibits pacemaker activity (see Fig. 1, lower right diagram) with different firing rates. All these neurons will show significant differences of their coding properties [2].

Fig. 2 gives an example of the effects of diversity in neuronal networks. In this initially silent net, current injection to a single neuron induces spiking even leading to sustained activity propagating through the net in form of spiral waves which, however, only activate a part of

the network. Stimulating a different neuron will activate other parts of the net in a different form. In this way, neuronal diversity also enhances the variety of network responses.

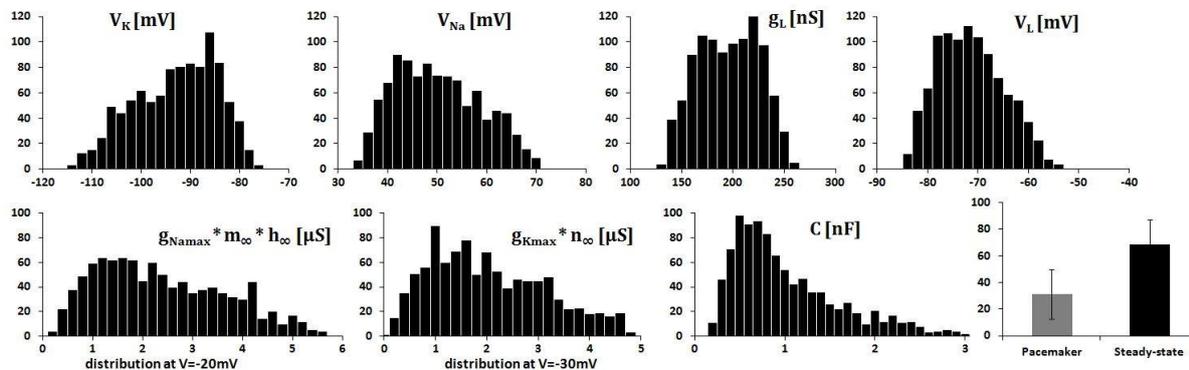


Figure 1: Randomized distribution of several neuron parameters.

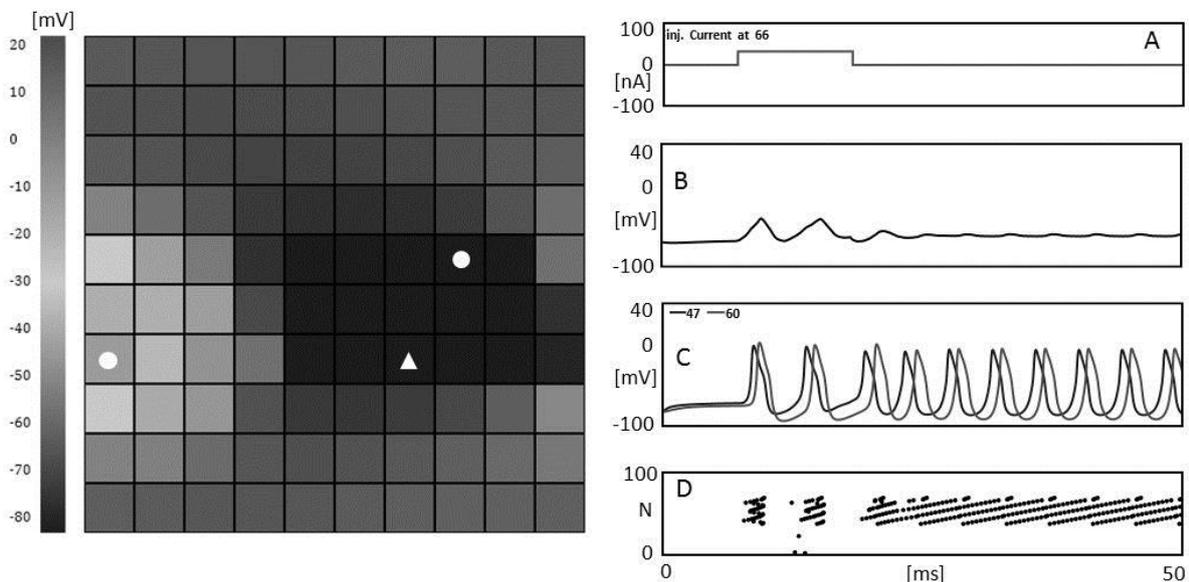


Figure 2: A network of 100 nearest neighbor gap-junction coupled neurons (coupling strength $0.01 \mu\text{S}$) with randomized parameter settings. Stimulating one of the neurons (no. 66: triangle dot in the raster plot) by an external current of 40nA (A) leads to the induction of action potentials and, after current offset, to sustained activity waves. However, only part of the network neurons is involved as also seen in the raster plot of spike times (D). Transient fluctuations in the global field potential (B), as observed during current injection, disappear with the appearance of ongoing waves, apparently also related to an increasing delay between subsequently activated neurons as indicated by the voltage traces of two randomly chosen neurons (white dots in the raster plot), here at position 47 and 60 (C).

Keywords: neural diversity, distribution, neural network

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Neural Decoding by Spike Train Factor Analysis Kernel

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Method:

The mixture kernel is introduced, which extends an arbitrary kernel for univariate spike trains to multivariate spike trains. Since it is defined in a general way, it can also be used for other data structures consisting of components. Mixture kernel k_p is a linear combination of symmetric positive-definite kernels on the components of the target data structure, in this case univariate spike trains. Let S be the set of all possible univariate spike trains, and let R be the set of real numbers. Let $k_e: S \times S \rightarrow R$ be a symmetric positive-definite kernel on univariate spike trains. Then the mixture kernel is defined by

$$k_p(x^{(i)}, x^{(j)}) = \sum_{m=1}^M \sum_{n=1}^M P_{mn} k_e(x_m^{(i)}, x_n^{(j)}), \quad (\text{Eq.1})$$

where P_{mn} is the (m,n) -th entry of a real matrix (coefficient matrix) P , and $x_m^{(i)}$ and $x_n^{(j)}$ are components of multivariate spike trains $x^{(i)}$ and $x^{(j)}$, respectively. $x_m^{(i)}$ is a univariate spike train observed at unit m . Note that $x^{(i)}$ indicates the i -th multivariate spike train in the sample set.

Theorem:

Mixture kernel k_p is symmetric positive-definite if P is a symmetric positive-semidefinite matrix.

The name "mixture kernel" derives from the common use of the word "mixture" to indicate a linear combination in physics and machine learning, for example in Gaussian mixture models.

Since the mixture kernel has a high degree of freedom which might make it difficult to optimize, a special class that has a lower degree of freedom is proposed. Rasmussen and Williams defined factor analysis matrix $M_{A,D}$ and proposed to use it as a precision matrix for the multivariate Gaussian kernel [1]. It is defined by

$$M_{A,D} = AA^T + D, \quad (\text{Eq.2})$$

where A is an arbitrary matrix and D is a diagonal matrix with non-negative diagonal entries. Its name is derived from its resemblance to a matrix used for factor analysis. Inspired by this definition, a special class of the mixture kernel is proposed in this work. Its coefficient matrix P is expressed as matrix $M_{A,D}$ in Eq. 2. Such a kernel will be called a factor analysis kernel (FA kernel). The rank of a factor analysis kernel is the number of columns of matrix A .

Corollary: The factor analysis kernel is symmetric positive-definite.

Experiments:

Rank-1 factor analysis kernel with a uniform eigenvector (i.e. all components have same values) was tested using a regression task of estimating visual stimuli (drifting bar directions) from observed multivariate spike trains. The PVC-3 data set, which is a 10-unit multivariate

spike trains available at the CRCNS (Collaborative Research in Computational Neuroscience) data sharing website, was used [2]. The data was recorded from area 17 (visual cortex) of an anesthetized cat using a polytrode, which is a 2 mm long silicon electrode array with 54 recording sites on its surface.

The values of the components of matrices A and D were optimized using training data. The resulting factor analysis kernel was compared to the population vector method, maximum likelihood decoding using a Poisson distribution, maximum likelihood decoding with time-varying rate (GLM with spline) [3], and the sum kernel [4]. The result is summarized in Table 1. It shows that kernel ridge regression with the factor analysis kernel performed better than other methods. For each data set, the left column is the result when all the conditions were used for training. The right column is the result when the conditions were thinned by a factor of 2, that is, when one out of every two conditions was removed from the training data. This was to evaluate the capability of decoding methods to interpolate directions that is not present in the training data set.

Table 1: RMSE (in degrees) for estimating the drifting bar directions

Conditions	All	Thinned
Population vector method	67.75	72.73
Maximum likelihood (Poisson)	68.88	64.72
GLM (spline) [3]	50.08	56.08
Sum kernel [4]	28.98	31.74
Rank-1 uniform factor analysis kernel	28.59	31.64

The factor analysis kernel proposed in this work extends the univariate spike train kernel in a systematic way. It consists of different classes having different numbers of parameters. Its specific example, the uniform factor analysis kernel, was tested for regression tasks using real data. The result showed that it performed better than commonly used neural decoding methods.

Keywords: Multivariate spike trains, positive definite kernel, kernel methods

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Random distance graphs on torus

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Random graphs are an important tool used to model structure and dynamics of real networks, in particular, neural networks [1, 2]. In general a network is a collection of objects connected to each other in some fashion. In neural network the nodes represent neurones, and the edges model the dendrites and axons which receive and transmit impulses. We studied the model introduced in [3], where given N^2 nodes in a torus T^2 , a connection between any two pair of nodes i, j , is defined with probability given by $p_{ij} = c/N\|i - j\|$, for different i, j , where $\|i - j\|$ is the graph distances between the vertices i and j . We want to investigate the degree distribution and the phase transition of the largest connected component.

Keywords: random graphs, neural networks, distance graphs

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MOD2, potential SMA modifier and much beyond?

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Previously being known as member of the Neuronal Calcium Sensor (NCS) family, MOD2 was first identified in our lab as a potential Spinal Muscular Atrophy (SMA) disease modifier. SMA a monogenic disorder, is characterized by functional loss of motor neurons in spinal cord, which eventually leads to motor disability in SMA patients. However, in certain individuals who carry the SMA genotype but do not show any SMA phenotype, we found MOD2 to be significantly downregulated. This finding implied the essential role of MOD2 in neuronal cells, which eventually rescues impaired neurons from SMA. Therefore, we are currently searching for the specific physiological role of Mod2 in and out of SMA context using a Mod2 knockout (KO) mouse model.

We observed that Mod2 KO mice are hyperactive and show anxiety like behavior, in line with data documented in International Mouse Phenotype Consortium. In order to understand the neurological mechanism behind these behavioral changes we characterized the brains of Mod2 KO mice at histological, cellular and molecular levels. Nissl staining of Mod2 KO brain sections revealed gross-morphological alterations in CA2, CA1 and Dentate gyrus regions of the hippocampus. These changes were accompanied by the ventriculomegaly and Corpus callosum atrophy. Altogether these phenotypes match various severe neurological conditions, such as Alzheimer's, Schizophrenia and Autism. Immunostainings of these brain sections revealed the specific expression pattern of NCALD in various regions of hippocampal formation like DG, CA1,2,3 and subiculum.

In addition to that, at cellular level the primary motor neurons derived from Mod2 KO/WT and Mod2 KO/KO mice spinal cord showed significant increase in axon length and axonal branching as compared to wildtype animals at early developmental stage i.e. 4 DIV. This finding supports the rescue of axonal degeneration on MOD2 reduction in SMA patients. However, it also implies that MOD2 has a role in maintaining the balance between neuronal differentiation and neurogenesis.

Moreover, at molecular level we investigated one of the hallmark of neuronal activity, the pERK/ MAP kinase pathway. Western blot of primary motor neurons show significantly upregulated pERK in Mod2 KO/WT compared to wildtype embryos. As high pERK level has been shown to increase the neuronal complexity these results may suggest a mechanism via which MOD2 affects the axonal length and branching in motor neurons.

Taken together, these results show various phenotypes and mechanisms which are affected by Mod2 knockout. An in depth analysis of these phenotypes and mechanism can potentially reveal the specific role of Mod2 in normal physiological condition as well as in SMA.

Nonlinear quantification of inter-hemispheric coupling in neocortical epilepsy in mice

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Epilepsy promotes rearrangements of neural circuitry leading to spontaneous seizures and little is known on how an epileptogenic focus impacts on neural activity in the contra-lateral hemisphere. Here, we analyze Local Field Potential (LFP) signals simultaneously recorded from both hemispheres of mice with unilateral epilepsy induced by injection of the synaptic blocker tetanus neurotoxin (TeNT) in the mouse primary visual cortex (V1). The recordings were performed in acute phase (peak of toxin action) and chronic condition (completion of TeNT effects). For the epileptic mice, the spectral analysis of LFP shown that the acute phase is characterized by a decrease in both hemispheres of the power content of the β (12- 30Hz) band, and an increase of that contained in the θ (4 - 8Hz) and δ (3 - 4Hz) bands. Moreover, the contra-lateral hemisphere exhibits a dampening of the power in the α (8 - 12Hz) band in both acute and chronic phases accompanied by an increase of that in the θ (4 - 8Hz) band in chronic condition. Next, the interdependence levels between LFP signals were quantified by several linear and nonlinear measures (i.e. Cross - Correlation, Spearman rank- order coefficient, Slope Phase Coherence and Mutual Information). All these measures agreed in indicating a reduction of the inter-hemispheric coupling in the acute phase, with partial or complete recovery in the chronic period. We also used Granger causality and Symbolic Transfer Entropy to investigate the coupling directionality between the two hemispheres. The chronic phase is characterized by an enhancement of the dominance of the TeNT-injected side, suggesting a greater driving influence of the epileptogenic focus on activity in the contra-lateral hemisphere. To better understand the neurobiological mechanisms underlying our results, also artificial LFP signals were generated and analyzed too. Altogether, our findings highlight the importance of robust plasticity phenomena and transcallosal interactions in neocortical epilepsy.

Keywords: neural recordings, nonlinear time series analysis, neural models

Fast Cl-type inhibitory neuron with delayed feedback has non-Markov output statistics

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Spiking statistics of various neuronal models under a random stimulation has been studied in the framework of two main approaches. The first one is named in [1] as "Gaussian", because it describes random stimulation by means of Gaussian noise, see e.g. [2]. This approach has developed into the well-known diffusion approximation methodology, see [3]. The second approach is named in [1] as "quantal", because it takes into account the discrete nature of the influence any input impulse may have on its target neuron.

We study here mathematically rigorously, in the framework of quantal approach, spiking statistics of *inhibitory* neuron model belonging to a class of models (the leaky integrate-and-fire model included) with fast Cl-type inhibitory delayed feedback. This construction is stimulated with Poisson stream of excitatory input impulses. For this configuration it was proven in [4] for a concrete neuronal model — the binding neuron with threshold 2 —, that statistics of its interspike intervals (ISI) is essentially non-Markov. In paper [5], it was proven for a wide class of *excitatory* neuronal models that the delayed feedback presence makes their activity non-Markov. In this paper, we extend the approach developed in [5] making it applicable to any *inhibitory* neuron with fast Cl-type inhibition satisfying a number of simple and natural conditions. Under those conditions, we prove rigorously that statistics of output ISIs of a neuron with delayed fast Cl-type inhibitory feedback stimulated with Poisson stream of input impulses cannot be presented as a Markov chain of any finite order. This is done by calculation of conditional probabilities $p(t_{n+1}|t_n, \dots, t_0)$ for ISIs t_0, \dots, t_{n+1} based on the output probability density function $p^0(t)$ of that same neuron with feedback line removed. The $p^0(t)$ is considered as given. The conditional probability is presented in the following form:

$$p(t_{n+1}|t_n, \dots, t_0) = p^w(t_{n+1}|t_n, \dots, t_0) + Z(t_{n+1}, t_n, \dots, t_0) \chi(\Delta - \sum_{i=0}^{n+1} t_i),$$

which proves that the t_0 -dependence cannot be eliminated in the $p(t_{n+1}|t_n, \dots, t_0)$ for any n .

Keywords: delayed feedback; fast Cl-type inhibition; non-Markov stochastic process

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Role of neuronal firing in reduction of dynamical states set in reverberating neuronal network

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Information about external world is delivered from sensory periphery to the brain in the form of structured in time spike trains. During further processing in higher brain areas, information is subjected to a certain condensation process [1], which results in formation of abstract conceptual images of external world entities, or discrete symbols in terminology of [1]. A possible physical mechanism of this process was proposed in [2] as convergence of some sets

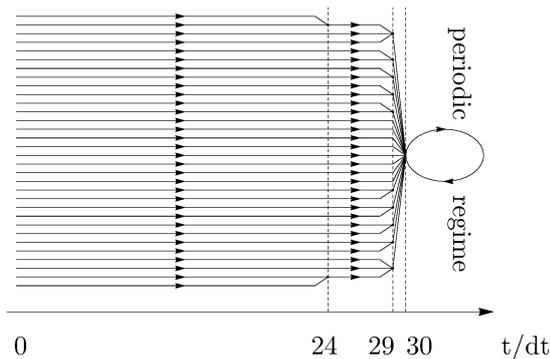


Figure 1: Illustration : Example of trajectories set belonging to a single attractor, merging moments and final periodic state.

of trajectories of reverberating neuronal network to a single periodic regime (attractor), which is treated as mentioned above discrete symbol. In this paper, we study a physical mechanism underlying the convergence itself. For this purpose, we run a computer model of fully connected neural net of 9 leaky integrate-and-fire neurons. The net is stimulated by various input spike trains similarly to [2]. As a result, different attractors are figured out together with corresponding sets of stimuli. For some sets we write down complete dynamical trajectories of the net. A set of trajectories corresponding to a single periodic state is then analyzed in order to find the moments when several different trajectories meet each other and progress further as a single trajectory. Usually, there are several such moments, see the Illustration 1. We then inspected the trajectory files in order to elucidate what happens just before two trajectories merge into a single one. We found that, exactly before each merging, a neuron, or several neurons should fire a spike. This suggests that condensation of information in a network may happen due to condensation of information in single neurons due to mechanism described in Sec. 2.1.1 of [2]. Additionally, we calculated the time course of dispersion in the whole set of trajectories belonging to a single attractor. It was found the dispersion monotonously decreases with time if neuronal firing takes place at the same moments for all trajectories. In some cases the firing moments are slightly different for different trajectories, and the dispersion increases dramatically during such periods of time.

Keywords: reverberating neural network; periodic attractor; condensation of information

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Nonparametric Granger causality of parkinsonian tremor

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Tremor is one of the characteristic movement disorders of patients with Parkinson's disease and is usually observed with a frequency of around 5 Hz. Intra-cranial measurements of local field potentials (LFP) within the subthalamic nucleus (STN) of patients with Parkinson's disease revealed several tremor associated sub-loops specific to certain muscle activity and different topographies of tremor clusters for postural and rest tremor [1]. An analysis of the causal relation between muscle activity and LFP [2] found more afferent input to the STN, i.e. information flow from the muscle to the STN, for the tremor-dominant subtype of Parkinson and more efferent inputs for the akinetic-rigid subtype. Here, we analyze a data set of 14 patients with Parkinson's disease using a combination of wavelet based methods to identify coherent tremor episodes and to determine the causal relation between muscle activity and STN and between different regions within the STN. We apply a nonparametric Granger causality method based on spectral factorization of the time-frequency resolved wavelet spectra [3]. The advantage of the nonparametric approach is that it does not depend on autoregressive modeling, which makes it also suitable for spike train analyses [4]. We further refined the method to be applicable to non-trial based data.

Keywords: wavelets, granger causality, Parkinson's disease

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Goal-directed behavior of a cultured neuron robot through reservoir computing

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A cultured neuronal network shows chaotic but orchestrated activity. We previously demonstrated that cultured neurons exhibit a repertoire of spatiotemporal patterns, which emerge from subpopulation-based state-dependent propagation [1]. Such robust and diverse activities in the cultured neuronal networks could be utilized as a pattern generator, serving as a potential source of biological intelligence.

Here, we hypothesize that the source of biological intelligence is a coherent output from a chaotic pattern generator, e.g., cultured neuronal network. To test this hypothesis, we attempt an embodiment experiment, in which the scheme of reservoir computing extracts a coherent output from cultured neurons and operates a moving robot. In this experiment, we demonstrate that complex goal-directed behaviors emerge from a cultured neuronal network.

Approximately 200,000 cortical neurons derived from E18 Wistar rats were plated on microelectrode arrays (Standard MEA 60MEA200/30iR-Ti-gr; Multi channel systems, Germany) and cultured for three weeks or more. Neural signals were band-pass (1-3k Hz) filtered and amplified (x1100) on MEA interface (MEA 1060-Up-BC-PA, Multi channel systems, Germany), and then captured through MEA bench software on a desktop computer. Spikes were detected from processed signals by LimAda algorithm. To convert spiking events into continuous firing rate, Gaussian kernel was convoluted to each spike event.

To extract coherent activity from cultured neurons, FORCE (first order reduced and controlled error learning) learning [2] was adopted in the system. FORCE learning is originally a reservoir-computing scheme in recurrent neural networks. In FORCE learning, the output of a linear weighted summation of neurons' activities becomes any arbitrary coherent temporal signal by optimizing the weights with recursive least-square (RLS) algorithm, and with a feedback of output itself to a network.

Feedback to cultured neurons was implemented with caged-glutamate and photostimulation. Rubi-glutamate (Abcam, UK) was supplemented so that the culture media contain 100 μ M Rubi-glutamate. Optical beam was generated from DPSS laser (473 nm; Ciel, UK) and controlled by digital micro mirror device (DMD; Discovery 1100, Texas Instruments, USA).

In our experiments, FORCE learning was used to produce a constant function. Then, the system was connected to a mobile vehicle robot (E-puck, AAI Japan, Japan). Robot control depended on the deviation of the output signal from the target constant function: if the actual output signal is above the target constant function, the robot turns right, and vice versa. When the weights were successfully optimized, the robot went straight forward with slight fluctuation.

The robot was then placed on the maze, where the robot moved toward the goal. Electrical stimulation pulses were provided when the robot hit against obstacles or wall of the maze or when the head of the robot deviated from the goal direction by 45 degrees or more. Experiments were tested in four different maze configurations, in all of which the robot could reach the goal.

Our experiments demonstrated that embodiment of cultured neuron exhibits a goal-directed behavior, i.e., maze solving ability. Previous embodiment experiments placed an emphasis on adaptation of neuronal networks [3], assuming that sensori-motor coupling through Hebbian learning shapes intelligent behaviors. Our experiments are totally different from these previous studies in that when cultured neurons with diverse but robust activity interact with an environment, goal-directed behavior could emerge without any adaptive change of neuronal networks. Our experiments thus offer an additional insight into a biologically plausible mechanism of biological intelligence.

Keywords: cultured neurons, neuro-robotics, reservoir computing.

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Correlating pre-synaptic synchrony with experimentally recorded intracellular membrane potential

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The operational mode of a neuron has recently attracted a lot of interest in neural coding research. Even though in recent years there seems to be a consensus that it lies in a continuum of temporal integration and coincidence detection [1-2], a way to infer it is still an open problem. Several studies have shown that presynaptic synchrony is highly correlated with the neuron's operational mode and the derivative of the postsynaptic membrane potential [3-6]. Koutsou et al. [2] proposed a measure that maps postsynaptic membrane potential to presynaptic input synchrony, and in the current work we examine this metric and propose a procedure for adapting it to experimentally recorded data.

Using the Leaky Integrate and Fire neuron model, Koutsou et al. [2, 7] demonstrated that the level of their developed normalised pre-spike slope (NPSS) of the membrane potential is highly correlated to the degree of the presynaptic synchrony responsible for firing. A very rapid mean potential change within a window prior to firing implies coincidence detection of highly synchronized inputs, while a smooth mean potential change implies temporal integration of random inputs. Alternatively, firing could be caused by a varying degree of contributions from both modes which would be signified by an intermediate rate of change in the potential. For this measure to be applied to experimental recordings, we need to define the slopes for the two extreme cases of the operational mode continuum: completely synchronous inputs and completely random inputs. In addition, the coincidence window that defines the period in which all input spikes are regarded as coincident needs to be readjusted accordingly.

The experimental data used for this article comes from the auditory thalamic neurons of anaesthetised guinea pigs, where the intracellular potential trace and the stimulus were available for the same experiment [8]. This data were also analysed in other theoretical studies (see [9-12]). The availability of both the membrane potential trace and the stimulus of the said data allows us to infer the degree of response-relevant synchrony.

The calculation of the bounds in the original NPSS, which depends on the analytical treatment of the underlying neuron model, is not possible in the case of analysis of real data. We therefore rely on empirical observations of the slope of depolarisation under different experimental conditions in order to estimate the bounds for the range of inter-spike interval (ISIs) lengths observed. We further show that the coincidence window size depends on the membrane leak time constant of the neuron under observation. We propose two possible methods for the empirical estimation of the bounds, that follow the theoretical reasoning and take into consideration the differences between the model neuron and the real one. One method relies on estimates of the minimum and maximum membrane potential slope values for an ISI length, and the other on the minimum and maximum membrane potential during individual ISIs. The resulting adapted versions of the NPSS measure support that the neuron under observation acts both as a temporal integrator and a coincidence detector in the absence of input stimulus and as a coincidence detector in the presence of input stimulus. These results

are compatible with the observation by Kobayashi et al. [12] when studying the same neuron. In particular, spikes that were known to be caused by higher degrees of input synchrony resulted in higher NPSS values. This shows that our methodology can capture the correlation between the input synchrony and the intracellular membrane potential slope of real cells. Additional evidence of the correlation between the NPSS and the operational mode continuum is given when we examine the results of identical ISI lengths, giving different normalised slopes in spontaneous activity than in the stimulated one.

Concluding, we note that our contribution was a methodology that estimates correctly the response-relevant input synchrony in a real neuron's firing activity. This methodology can easily be applied to a neuron for which only the membrane potential and input synchrony are known. In addition, our results validate the findings of Koutsou et al. [2] in practice, suggesting that it is possible to estimate the operational mode of real neurons using an adapted version of the NPSS.

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Keywords: neural operational modes, intracellular membrane potential, synchrony

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