9th International Workshop

NEURAL CODING 2010

Limassol, Cyprus
29 October – 3 November 2010

ABSTRACT BOOK

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`http://www.cs.ucy.ac.cy/nc2010/`

Front cover

Left: *Petra tou Romiou*, ("The rock of the Greek"),
Aphrodite's legendary birthplace in Paphos, Cyprus.
Centre: Aphrodite, Greek Godess of Love, Archeological Museum, Nicosia, Cyprus.
Right: Curium amphitheatre, Limassol, Cyprus.

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Contents

History of Neural Coding Workshops and aim of NC2010

Neural Coding Workshops are traditionally biennial symposia each lasting 5-6 days. They are relatively small in size, inter- and trans- disciplinary with major emphasis on the search for common principles in neural coding , without neglecting functionally relevant differences between different systems and across system levels.

NC2010, which is to be held in the sunny resort of Limassol, Cyprus, is the 9th of this international workshop series. As in the previous workshops in Prague (1995), Versailles (1997), Osaka (1999), Plymouth (2001), Aulla (2003), Marburg (2005), Montevideo (2007) and Tainan (2009), this will be a single track multi-disciplinary event bringing together experimental and computational neuroscientists with ample time for informal discussions in a convivial atmosphere. Attendees of the workshop should thus be prepared to cross the borders of their own disciplines.

NC2010 will have the honour of having Professor Jose Pedro (Pepe) Segundo marking the opening of its scientific programme. The appreciation and respect of everyone is offered to Professor Segundo, an important and leading member of the pioneering Neurosciences Research Program "neural coding" workshop in 1968 and a keen and active participant in this series of workshops since their inception.

In total, there will be 70 presentations at NC2010 divided into 44 oral and 26 poster ones, with the poster sessions preceded by poster trailer oral sessions. Main emphasis will be given on the exchange of ideas, which would hopefully continue during the various social events (see Programme Schedule), that are integrated into the symposium. Moreover, this will be an excellent opportunity to establish contacts between the international experts and a very small but valuable and growing community of Greek Cypriot computational neuroscientists and to foster international collaboration.

Neural Coding 2010 – Programme Schedule

Friday, 29 October 2010

19:00-19:30	Registration	
19:30-	Welcoming Reception – Venue: Mediterranean Beach Hotel	

Saturday, 30 October 2010

Venue: Mediterranean Beach Hotel

08:30-09:00	Registration	
09:00-09:05	Welcoming and practical information *Chris Christodoulou*	
09:05-09:15	A few words a propos of Neural Coding *Jose Segundo*	

Session IA
Chair: Jose Segundo

09:15-09:35	The Encoding of Information by Neurons in the Temporal Visual Cortical Areas, the Hippocampus, and the Orbitofrontal Cortex *Edmund T Rolls*	Page 099
09:35-09:55	Neural Latching Dynamics: A Salutatory Code for Sustained Cognition *Alessandro Treves and Eleonora Russo*	Page 129
09:55-10:15	Spatio-Temporal Filtering of the Distributed Temporal Information in Spike Trains Through a Diverging/Converging Neural Network *Yoshiyuki Asai and Alessandro E. P. Villa*	Page 001
10:15-10:35	Using Classical Ablations and Modern Molecular Biology to Study Neural Codes *Barry Richmond*	Page 097
10:35-11:05	Coffee Break	

Session IB
Chair: Petr Lansky

11:05-11:25	Emergence of Bayesian Computation and Neural Codes for Hidden Causes through STDP in Generic Cortical Microcircuits *Wolfgang Maass*	Page 067

11:25-11:45	Biologically Realistic Model of Neural Connections of the Tadpole Spinal Cord Generates Swimming Activity *Roman Borisyuk and Abul Kalam al Azad*	Page 007
11:45-12:05	On the Dependencies Between Spiking Times of a Couple of Neurons *Laura Sacerdote*	Page 103
12:05-12:25	Neural Coding in Graphs of BAMs *Guenther Palm and David Bouchain*	Page 091
12:25-12:45	High Firing Irregularity Enhances Learning *Chris Christodoulou and Aristodemos Cleanthous*	Page 019
12:45-14:30	Lunch - Venue: Franx Bar & Restaurant http://www.franxbar.com/ (right opposite the entrance to the Mediterranean Beach Hotel)	
14:30-14:45	Hanging of Posters for Poster Session I	

Poster Trailer Oral Session I
Chair: Jean-Pierre Rospars

14:45-15:55	Poster trailer Oral sessions (5 mins each - 14 poster presentations)	
	PI.1: Electric Images of a Fish With a Distributed Electric Organ *Ruben Budelli, Federico Pedraja, Juan Ignacio Sanguinetti, Adriana Migliaro, Leonel Gomez, Esteban Cilleruelo, Pedro Aguilera and Angel Caputi*	Page 011
	PI.2: Multiple Spike Trains Observed in a Short-Time Window *Zbynek Pawlas and Petr Lansky*	Page 093
	PI.3: An Information Theoretic Approach to Inferring the Optimal Number of Electrodes for Future Cochlear Implants *Alexey S. Moroz and Mark D. McDonnell*	Page 077
	PI.4: Inverse Suprathreshold Stochastic Resonance in a Network of Hodgkin-Huxley Model Neurons *Sean S. C. Wong and Mark D. McDonnell*	Page 135
	PI.5: Information Capacity in the Weak Signal Approximation *Lubomir Kostal*	Page 055
	PI.6: Spike-Frequency-Adaptation Benefits Neural Population Coding *Martin Paul Nawrot, Eilif Mueller and Farzad Farkhooi*	Page 083

	PI.7: Analysis of the Signal Transformation From First- to Second-order Neurons in the Moth Sex-Pheromone Olfactory System *A. Gremiaux, D. Jarriault, A. Chaffiol, S. Anton, D. Martinez and J. P. Rospars*	Page 041
	PI.8: Temporal Modulation of the Input Parameters Can be Deduced From Intracellular Recordings in the Ornstein-Uhlenbeck Neuronal Model *Ryota Kobayashi, Shigeru Shinomoto and Petr Lansky*	Page 053
	PI.9: A Neurocomputational Model of Deviance Detection in Stimulus-Specific Adaptation *Robert Mill, Martin Coath, Thomas Wennekers and Susan L. Denham*	Page 073
	PI.10: Cortico-Thalamic Modulation and Emergent Feature Preferences in a Model of Auditory Cortex *Martin Coath, Robert Mill, Susan L. Denham and Thomas Wennekers*	Page 021
	PI.11: Synchronized Activity in the Subthalamic Nucleus *Alessandra Lintas, Izabella Silkis, Olga Chibirova, Tatyana Aksyonova, Lavinia Alberi, Alessandro E. P. Villa*	Page 061
	PI.12: Effect of Feedback Projections Between Networks in Evolvable Hierarchically Organized Neural Circuits *Vladyslav Shaposhnyk and Alessandro E. P. Villa*	Page 115
	PI.13: Deterministic Bias in Spike-Train Similarity Measures Used for Fitting *Richard Naud, Felipe Gerhard, Skander Mensi and Wulfram Gerstner*	Page 081
	PI.14: Distinguishing the Causes of Firing with the Membrane Potential Slope *Achilleas Koutsou, Chris Christodoulou, Guido Bugmann and Jacob Kanev*	Page 057
16:00-18:15 (approx)	Poster Session I (14 Posters) (combined with Coffee Break served at 16:00)	
19:00-	Dinner - Venue: Music Ark, Stavros Greek Tavern (opposite the east side of the Mediterranean Beach Hotel)	

NC2010 Schedule

Sunday, 31 October 2010

Please note that at 04:00 am on Sunday, 31 October 2010, the daylight saving time (summer time) ends in Cyprus and clocks turn back one hour

Venue: Mediterranean Beach Hotel

Session IIA

Chair: Ruben Budelli

08:30-08:50	Stimulus Coding by Populations of First- and Second-Order Olfactory Neurons *Jean-Pierre Rospars, Petr Lansky, Pavel Sanda and Patricia Duchamp-Viret*	Page 101
08:50-09:10	Neural Coding in the Olfactory System of Insects *Christopher L. Buckley, Andrei Zavada and Thomas Nowotny*	Page 139
09:10-09:30	Extending the Critical Brain Hypothesis to the Rate Domain: A Case Study of the Pheromone System of the Moth *Christopher L. Buckley and Thomas Nowotny*	Page 009
09:30-09:50	Multiple Subtypes of Local Interneurons Suggest Distinct Tasks During Odor Processing in the Antennal Lobe *Debora Fusca, Andreas Husch, Lars Paeger, Moritz Paehler, Andreas Pippow and Peter Kloppenburg*	Page 037
09:50-10:10	Coffee Break	

Session IIB

Chair: Alessandro E. P. Villa

10:10-10:30	Coincidence Detection vs. Temporal Integration in Insect Olfaction *Maxim Bazhenov*	Page 003
10:30-10:50	Spontaneous and Evoked Responses of Olfactory Receptor Neurons Determine the Properties of Follower Neurons *Mark Stopfer*	Page 123
10:50-11:10	Electric Scene Segmentation by the Electric Fish *Leonel Gomez-Sena, Juan Ignacio Sanguinetti and Ruben Budelli*	Page 039
11:10-11:30	Coding of Electric Images in Electric Fish with Distributed Electric Organs *Angel Ariel Caputi, Esteban Cilleruelo and Carolina Pereira*	Page 015

11:30-14:45 (approx)	Excursion and Cultural Bus Tour to Ancient Curium Amphitheatre/City passing from Kolossi Castle (packed lunch - to be consumed after arrival at Curium and not in the bus) Group Photo in the Ancient Curium Amphitheatre Return to the Cyprus University of Technology, Limassol	

Venue: Cyprus University of Technology, Limassol

Session IIC
Chair: Barry Richmond

15:00-15:20	Spike Surrogates Based on Operational Time *Markus Diesmann, Sebastien Louis, George L. Gerstein and Sonja Gruen*	Page 025
15:20-15:40	Signatures of Spiking Neuronal Assemblies in the Local Field Potential *Sonja Gruen, Michael Denker, Markus Diesmann, Sebastien Roux, Alexa Riehle and Henrik Linden*	Page 043
15:40-16:00	Neural Coding Clues From Early Brain Activity in Well-Circumscribed Areas Obtained With Tomographic Analysis of Magnetoencephalographic (MEG) Signals *Andreas A. Ioannides, Lichan Liu and Vahe Poghosyan*	Page 049
16:00-16:20	Neural Coding of Natural Vestibular Signals *Lars Schwabe, Youwei Zheng, Andre Hoffmeyer and Thomas Kirste*	Page 113
16:20-16:50	Coffee Break	

Session IID
Chair: Roman Borisyuk

16:50-17:10	Waves in Potassium Driven Neuronal Media *L. Schimansky-Geier, F. Mueller, N. Kouvaris and D. Postnov*	Page 109
17:10-17:30	Spontaneous Oscillations, Information Transmission and Signal Detection in Ampullary Electroreceptors *Alexander B. Neiman, Tatiana A. Engel, David F. Russell and Lutz Schimansky-Geier*	Page 085

17:30-17:50	Information-Optimal Neural Coding in Poisson Neurons *Alexander Nikitin, Nigel G. Stocks, Robert P. Morse and Mark D. McDonnell*	Page 087
17:50-18:10	Modulation of Gamma Oscillations in Simulations of Cortical Networks is Sensitive to Network Topology *Mark D. McDonnell and Lawrence M. Ward*	Page 071
18:10-18:30	Quantifying Neural Encoding of Event Timing *Demetris S Soteropoulos and Stuart N Baker*	Page 119
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19:00- (approx)	Dinner - Venue: Karatello Cyprus Tavern, http://www.carobmill-restaurants.com/article.php?id=53	

NC2010 Schedule

Monday, 1 November 2010

08:30-08:45	Departure for Nicosia
09:45-13:15 (approx)	Tour of Nicosia - Europe’s last divided capital
	Transfer to the University of Cyprus, Nicosia (New Campus)
13:30-14:45 (approx)	Lunch - Venue: University of Cyprus (New Campus)

Venue: University of Cyprus, Nicosia (New Campus)

Session IIIA

Chair: Laura Sacerdote

15:00-15:20	Individual Firing Frequencies Estimated From Superimposed Spike Trains *Ondrej Pokora and Petr Lansky*	Page 095
15:20-15:40	A Network Model of Learning Stimulus-Response Associations *Guido Bugmann*	Page 013
15:40-16:00	Layer-Specific Modification of Spontaneous Cortical State Dynamics by Sensory Stimulation *Simon R Schultz, E Phoka and M Barahona*	Page 111
16:00-16:20	Primary Visual Cortex Encodes Complementary Information About Naturalistic Movies at Different Temporal Scales *Alberto Mazzoni, Christoph Kayser, Yusuke Murayama, Juan Martinez, Rodrigo Q Quiroga, Nikos K. Logothetis and Stefano Panzeri*	Page 069
16:20-16:50	Coffee Break	

Session IIIB

Chair: Hans Braun

16:50-17:10	Single Neuron And Network Models in Force Control *Leonardo Abdala Elias and Andre Fabio Kohn*	Page 031
16:10-17:30	Modeling FM Responses of Midbrain Auditory Neurons – An Integrated Approach Based on STRF and PSTH *T.R. Chang, T.W. Chiu, X. Sun and Paul W.F. Poon*	Page 017

17:30-17:50	Sharpening Tuning Curves With Spike-Time Dependent Plasticity *Fabio Stefanini, Rahel Von Rohr, Giacomo Indiveri and Elisabetta Chicca*	Page 121
17:50-18:10	Sound Encoding in the Auditory Pathway: Auditory Brainstem and Beyond *Pavel Sanda and Petr Marsalek*	Page 107
18:10-18:30	Category Perception: From Efficient Coding to Reaction Times *Laurent Bonnasse-Gahot and Jean-Pierre Nadal*	Page 005
	Back towards Limassol and stop at Kalymnos Fish Tavern, Governor's Beach for dinner	
19:45-20:00 (approx)	Dinner - Venue: Kalymnos Fish Tavern, Governor's Beach	

NC2010 Schedule

Tuesday, 2 November 2010

Venue: Mediterranean Beach Hotel

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Chair: Guido Bugmann

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09:50-10:10	The Multiple Time Scales of Spike After-Effects *Richard Naud, Christian Pozzorini, Skander Mensi and Wulfram Gerstner*	Page 079
10:10-10:30	Dependencies Between Spike Times of a Couple of Neurons Modeled via a Two-Dimensional LIF Model *Laura Sacerdote, Massimiliano Tamborrino and Cristina Zucca*	Page 104
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Session IVB
Chair: Shigeru Shinomoto

11:00-11:20	The Morris-Lecar Neuron Model Embeds the Leaky Integrate-and-Fire Model *Susanne Ditlevsen and Priscilla Greenwood*	Page 027
11:20-11:40	Cooperative Effects of Noise and Nonlinear Dynamics in Hodgkin-Huxley-Type Model Neurons *Christian Finke, Ulrike Feudel, Jan A. Freund, Svetlana Postnova and Hans A. Braun*	Page 033
11:40-12:00	Evolution of Neural Networks under Unsupervised Learning *Tatyana Turova*	Page 131
12:00-12:20	Recursive Bayesian Algorithms for Real-Time Brain-Computer Interface *Shinsuke Koyama*	Page 059
12:20-12:40	Evaluation of Alternative Coding Strategies in Early Olfaction *Pawel Herman and Anders Lansner*	Page 045

12:40-14:15 Lunch - Venue: Franx Bar & Restaurant,
http://www.franxbar.com/
(right opposite the entrance to the Mediterranean Beach Hotel)

14:15-14:30 Hanging of Posters for Poster Session II

Poster Trailer Oral Session II
Chair: Paul Poon

14:30-15:30 Poster trailer Oral sessions (5 mins each - 12 poster presentations)

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Satoshi Yamauchi, Hideaki Kim and Shigeru Shinomoto

PII.2: Effects of Type 1 and Type 2 Synapses on Oscillations in Models of Recurrent Cortical Networks — Page 075
Ashutosh Mohan, Mark D. McDonnell and Christian Stricker

PII.3: Information Capacity and Robustness of Spatially Separated Dendritic Synapses — Page 047
Nicolangelo L. Iannella and Mark D. McDonnell

PII.4: Bayesian Analysis of the Single Cell Response in Mouse Olfactory Receptor Neurons — Page 029
Daniel P. Dougherty and Johannes Reisert

PII.5: Auditory Coding in the Inner Hair Cell Ribbon Synapse — Page 133
Daniela Woltmann and Nigel Stocks

PII.6: Stochastic Modelling of Neuron Activity — Page 035
Blazena Frcalova, Viktor Benes and Daniel Klement

PII.7: Estimation of Functional Connections in the Premotor Center of an Insect Brain — Page 089
Ikuko Nishikawa, Tanaka Taiga, Yoshiki Igarashi, Ryota Kobayashi, Hidetoshi Ikeno, Tomoki Kazawa and Kanzaki Ryohei

PII.8: Hebbian Plasticity Combined With Homeostasis Shows STDP-Like Behavior — Page 127
Christian Tetzlaff, Christoph Kolodziejski and Florentin Woergoetter

PII.9: Short-Term Potentiation in Pattern Recall Process of Sparsely Coded Neural Network — Page 125
Julius Stroffek and Petr Marsalek

	PII.10:	Anatomically Realistic Winner-Take-All Networks as Models of Cortical Computation *Markus Jehl and Giacomo Indiveri* (to be presented by *Fabio Stefanini*)	Page 051
	PII.11:	Neural Coding and Variability Measure via Cumulative Entropy *Antonio Di Crescenzo*	Page 023
	PII.12:	Multilevel Constraints on a Cortical Attractor Model *Mikael Lundqvist, Pawel Herman and Anders Lansner*	Page 063
15:30-18:00	Poster Session II (12 Posters) (combined with Coffee Break served at 15:30)		
18:00 (approx)	Workshop closing		
	Free Evening		

Wednesday, 3 November 2010

Optional Tour to Paphos – Departure 08:30-08:45
Please register for the tour at the registration desk

Abstracts

in alphabetical order by first author

Spatio-Temporal Filtering of the Distributed Temporal Information in Spike Trains Through a Diverging/Converging Neural Network

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ABSTRACT

It is well established and known for a long time that the temporal structure of the afferent spike trains plays a critical role for the integration of neural activity [1]. Experimental evidence in multiple spike trains recordings *in vivo* and in behaving animals revealed that the temporal information is preserved at high level of cortical processing [2]. Each one of multiple afferences may carry complex temporal information. A neuron can be considered as a dynamic filter of afferent spike trains characterized by highly nonlinear transfer functions [3] at the presence of the stochastic background activities which can mask the temporal information embedded in the spike trains. The filtering effect of spike trains by neurons remains unclear to which extent the precise afferent temporal information may be preserved throughout a neural network. This study investigates the ability of a diverging/converging neural network to transmit and integrate a complex temporally organized activity embedded in afferent spike trains.

Recurrent temporal patterns of spikes, often referred to as precise firing sequences, consist of occurrences of higher order spike intervals with high temporal accuracy of the order of milliseconds. We applied the Pattern Grouping Algorithm (PGA) [4] developed to detect all sequences of events recurring more often than expected by chance to examine the spatiotemporal precise firing pattern in a spike train [5]. In our previous studies based on a simple spiking neuron model, we investigated the spike filtering properties of a single neuron [6] mimicking the behavior of several archetypal neurons and of sequentially connected multiple neurons [7] using the PGA. It has been shown that the characteristic transfer function of a neuronal model and the statistical feature of the the background activity may affect the transmission of temporal information through synaptic links. We suggested that specific neuronal dynamics characteristic of certain brain areas or associated to specific functional neuronal states play an essential role in the efficacy of transmitting a temporal pattern in a neuronal network. This feature is critical to determine the encoding and decoding processing that might be carried out by a single neuron and by the network and the extent of a distributed population coding scheme.

In the current research we extend our previous analysis to diverging/converging feed-forward neuronal networks–synfire chains–which are supposed to represent the most appropriate circuits able to transmit information with the best temporal accuracy [8]. The temporal structure originated in a deterministic dynamical system embedded in stochastic background activity is dispersively given to the neural network composed of three neuron layers. We investigate the robustness and reliability of transmitting the precise afferent temporal structure through neural networks characterized by different neuronal models. We suggest that adaptive threshold neurons are more efficient in maintaining a specific temporal structure throughout the layers of a synfire chain.

Keywords: Spatio-temporal pattern, Spiking neuron, Reconstruction of spike train.

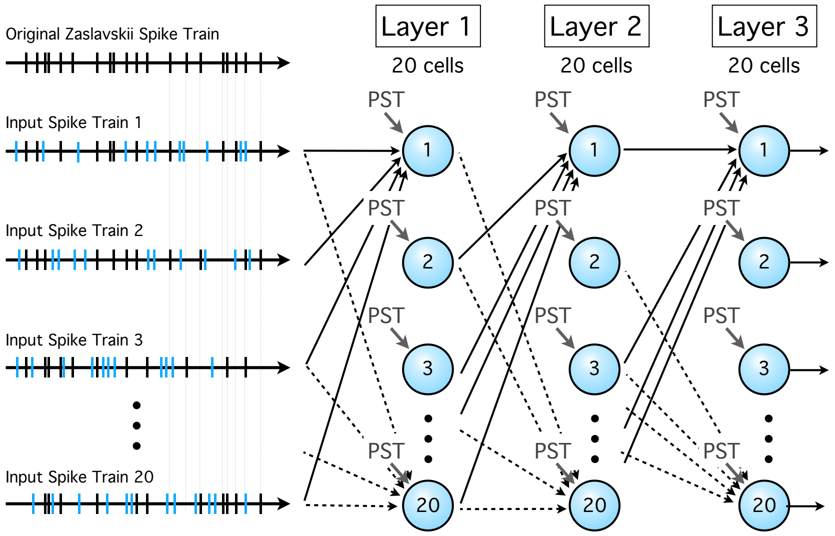

Figure 1: A three layer neural network model. Randomly selected fifteen neurons in a layer converge to one neuron. Each neuron also receives an independent stochastic background activity.

References

[1] Segundo, J. P. and Perkel, D. H. and Moore, G. P. (1966) Spike probability in neurones: Influence of temporal structure in the train of synaptic events. Kybernetik, 3: 67-82.

[2] Villa A. E. P. (2000) Empirical Evidence about Temporal Structure in Multi-unit Recordings, in: *Time and the Brain* (R. Miller, Ed.), Conceptual advances in brain research, vol. 2., Harwood Academic Publishers, pp. 1-51.

[3] Segundo, J. P. (2001) Nonlinear dynamics of point process systems and data. Int. J. of Bifurcation and Chaos, 13: 2035-2116.

[4] Tetko, I. V. and Villa, A. E. P. (2001) A pattern grouping algorithm for analysis of spatiotemporal patterns in neuronal spike trains. 1. Detection of repeated patterns. Journal of Neuroscience Methods, 105: 1-14.

[5] Asai, Y. and Villa, A. E. P. (2008) Reconstruction of Underlying Nonlinear Deterministic Dynamics Embedded in Noisy Spike Train. Journal of Biological Physics, 34, pp.325-340.

[6] Asai, Y., Yokoi, T. and Villa, A. E. P. (2007) Deterministic Nonlinear Spike Train Filtered by Spiking Neuron Model. Lecture Notes in Computer Science 4667, pp.924-933.

[7] Asai, Y., Guha, A. and Villa, A. E. P. (2008) Deterministic neural dynamics transmitted through neural networks. Neural Networks, vol.21:6, pp.799-809.

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Coincidence Detection vs. Temporal Integration in Insect Olfaction

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ABSTRACT

Ideally, a coding strategy used by a sensory system should provide an optimal representation across the full possible range of stimulation conditions. For the olfactory system, this task involves optimally encoding odors at different concentrations, an ability critical in many species for survival. How successive layers of neural circuits in the olfactory system regulate sensory input to maintain stable odor representations across broad ranges of concentration remains a mystery. Drawing on results obtained with biophysical network models of insect olfaction, I will discuss intrinsic and circuit properties that contribute to encoding olfactory information at different levels of odor processing, and the role of the intrinsic dynamics of the olfactory system in optimizing odor representations. I will present a hypothesis how circuit properties of the olfactory system allow adopting an optimal strategy of information processing, shifting from coincidence detection to temporal integration as the odor concentration changes. The ability to shift operational modes can be achieved readily by a combination of environmental contingencies and network interactions.

Category Perception: From Efficient Coding to Reaction Times

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ABSTRACT

When dealing with a categorization task, the brain has to face two different sources of uncertainty: categorization uncertainty and neuronal uncertainty. The latter stems from neuronal noise, whereas the former is intrinsic to the category structure: categories like phonemes or colors typically overlap in stimulus space, so that a given stimulus might corresponds to different categories. Here, we propose a general neural theory of category coding, in which these two sources of uncertainty are quantified by means of information theoretic tools. We analytically show [1, 2] how these two quantities combine at both coding and decoding stages of the information process. From the hypothesis of optimal information processing, we derive formulae which capture different psychophysical consequences of category learning – namely, a better discrimination between categories, and longer reaction times to identify the category of a stimulus lying at the category boundary. Finally, we model experimental data, in the present work taken from the psycholinguistic literature. A major contribution of this work is thus to exhibit, in both quantitative and qualitative terms, the interplay between discrimination and identification.

Keywords: categorization, reaction times, optimal coding

References

[1] Laurent Bonnasse-Gahot and Jean-Pierre Nadal (2008), Neural Coding of Categories: Information Efficiency and Optimal Population Codes *Journal of Computational Neuroscience* 25:1, pp. 169-187

[2] Laurent Bonnasse-Gahot and Jean-Pierre Nadal (2010), Perception of Categories: from Coding Efficiency to Reaction Times, *Submitted*

Biologically Realistic Model of Neural Connections of the Tadpole Spinal Cord Generates Swimming Activity

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ABSTRACT

Although computational neuroscience provides a variety of biologically realistic models of a single neuron, modelling of a neural network activity is still an open problem. A crucial question is to define an appropriate architecture of neural connections which provides a proper dynamical pattern of neural activity corresponding to a function of this neural network. Thus, to address the classical structure-function problem we model anatomy and electrophysiology of the tadpole spinal cord. Our approach to modelling of neural connectivity is based on developmental processes of axon growth. A simple mathematical model of axon growths allows us to reconstruct a complete biologically realistic architecture of neuronal connectivity of the tadpole spinal cord ([1], [2]). In this project we collaborate with neurobiologists from Prof. Alan Roberts Lab at the University of Bristol.

In the reconstruction model, both cell bodies and dendrites are randomly distributed along the spinal cord on the left and right sides of the body in correspondence with the experimental measurements provided by A. Roberts Lab. The growing axon makes a synaptic contact with some probability if the axon passes through the dendrite of some neuron. The total neural network contains 1680 neurons of six cell types (280 neurons of each cell type) and the total number of connections is about 100,000. The anatomical model contains random components; therefore, each repetition of the reconstruction procedure generates a neural network which differs from others. However, there are some common features of all these networks. For example, statistical characteristics of distributions of cell bodies, dendrites and axons are the same for all generated connection architectures.

A study of connection architecture reveals a complex structure of the connectivity graph with many interesting specific features. Some features are similar to connectivity graphs of other animals. For example, the distribution of connection lengths (without taken into account cell types and direction of the connection) is similar to the distribution of connection lengths in the global neuronal network of C. elegans (see this distribution in Fig. 2D of paper [3]). Analysis of specific connections between cells of different types in ascending (towards head) and descending (towards tail) directions shows a broad variety of distributions. Figure 1 shows two distributions of lengths for incoming connections from neurons of dlc type. The histogram in Figure A (left) corresponds to incoming connections to descending interneurons of dIN type. This distribution shows that there are many connections between neurons of these types, the total number of connections is about 6500, the mean number of incoming connections to the neuron is about 23. Although there are many short-range connections, the distribution is bimodal with peaks corresponding to distance of about 300 microns in each direction. The histogram in Figure B (right) corresponds to incoming connections between neurons of dlc type (connection from dlc

cell to dlc cell). The total number of connections is relatively small (about 450) and the mean number of incoming connections per neuron is about 1.6. The distribution is asymmetrical: more connections arrive from the tail than from the head side. Also, this distribution shows that there are no local connections in the vicinity of 100 microns from the dlc cell.

To model neural activity we use the Morris-Lecar neuron with post-inhibitory rebound. Coupling between these neurons is arranged in accordance with the reconstruction connectivity. Simulation of the neural network shows that the model demonstrates a pattern of neural activity corresponding to swimming. It means that any two cells of the same type allocated near the same rostro-caudal position but on opposite sides of the body (one cell on the right and one cell on the left) will generate spikes in anti-phase and the metachronal wave of spiking activity will propagate from head to tail.

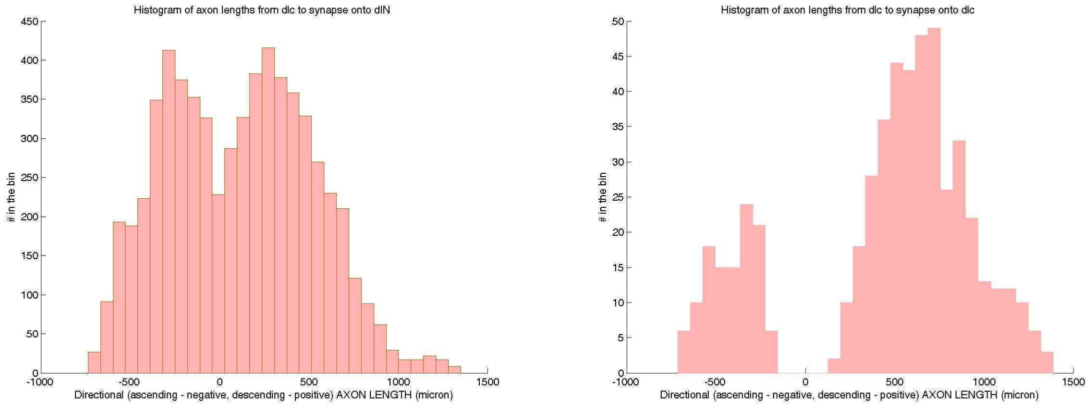

Figure 1: Figure. Distribution of connection lengths for different cell types in different directions (negative (positive) values correspond to ascending (descending) direction). A (left) Histogram of connection lengths for connections from neurons of dlc type to neurons of dIN type. B (right) Histogram of connection lengths connections from neurons of dlc type to neurons of dlc type.

Keywords: Connectivity, tadpole, swimming pattern

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Extending the Critical Brain Hypothesis to the Rate Domain: A Case Study of the Pheromone System of the Moth

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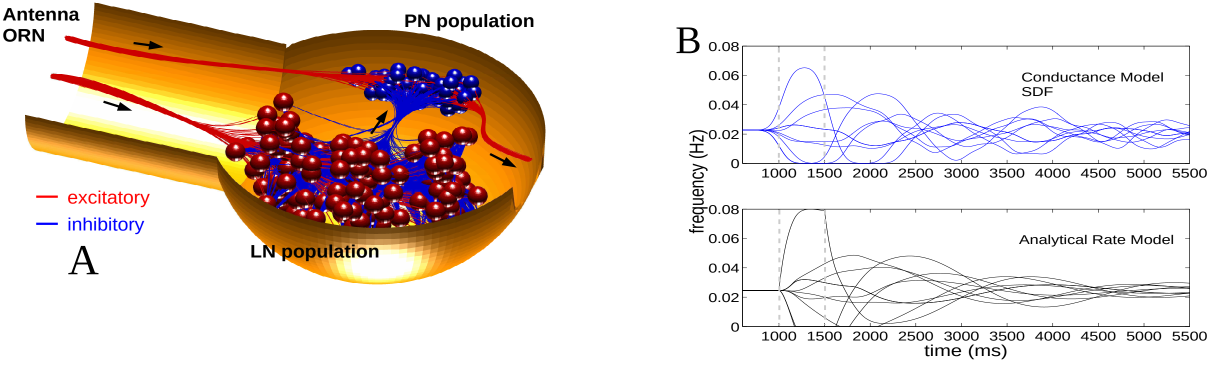
ABSTRACT

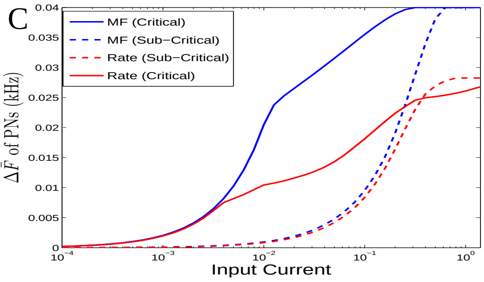
The critical brain hypothesis has been receiving an increasing amount of attention in the neuroscience literature [1, 2, 3, 4]. The idea goes that the dynamics of the brain are analogous with a system poised at the critical point of a phase transition [1]. Such dynamics afford the brain a suite of computational properties including optimal information storage [2], signal transmission [3] and dynamic range [4]. The conceptual and formal framework that has been used to scaffold this idea draws heavily on phase transitions in Ising spin or more generally stick slip models. Consequently, neural models have tended to comprise of discrete states (firing or quiescence) non-leaky integrate a fire neurons interacting via excitatory synapses. The dynamics of these model is generally sparse and characterised by periods of silence followed by transient period of activity called avalanches. Such models are reminiscent of the dynamics of cortex and have been used with a degree of effectiveness to account for several observed experimental properties [1]. To date it is not clear if, or how, the critical brain hypothesis could be applied to wider range of neural systems which are not well described by avalanche dynamics. For example, can a notion of criticality be developed in systems interacting through slow synapses which perhaps sustain significant information processing through a rate based code?



Recently Kinouchi et. al. [4] have suggested that critical dynamics can account for the dynamic range of the mammalian olfactory system . They demonstrated that the sensitivity and dynamic range of a network of excitable elements, is maximised near the critical point of a phase transition. They suggest such a system is underpinned by the dynamics of gap junctions within the olfactory bulb (OB). However, the level of involvement of gap junctions in the dynamics of the OB has yet to be established. Further the presence of gap junction has not been experimentally established in antennal lobe AL (the invertebrate equivalent of the OB) which also exhibits a large dynamic range. Perhaps more importantly the dynamics of both the OB and AL are not consistent with an excitable system. These systems are dominated by both fast and slow inhibitory synapses that mediate slow rate patterning dynamics. In this work we propose an account of the dynamic range of the AL which draws in spirit from the critical brain hypothesis

but develop an alternate notion of criticality in terms of the rate interactions between neurons. We ground this idea in a model of the Macro Glomerular Complex (MGC), a core subsytem of the AL of the male moth devoted to the detection of pheromones. The pheromone subsystem of the olfactory system of MGC comprises a set of specialized olfactory receptor neurons (ORNs) on the antennae that project to a recurrent network of GABA$_B$ inhibitory local interneurons (LNs) in the MGC. These in turn synapse on a set of projection neurons (PNs) that arbourise outside the AL and relay information to higher brain areas, see figure A.

We model the MGC systems as a large random, recurrent network of slow inhibitory neurons. We employ Hodgkin Huxley neurons with an m-current and ("$\alpha - \beta$") synapses. Leveraging the fact that GABA$_B$ synapses act at a much slower timescale than the membrane dynamics we reduce our conductance based model to a formally equivalent rate model, see figure B. We model the rate dynamics of the LNs as transient excursions from their stable baseline rates which are formally described as a globally asymptotically stable fixed point attractor. We then show how even a randomly connected network of LNs constrained to show these transient dynamics can account for the slow rate patterning and strong disinhibition of the PNs observed in experiment.



The dynamic range of the male moths response to pheromone has been found to manifest in the PN's initial excitatory response. Correspondingly we demonstrate that if the fixed point attractor describing the rate dynamics of the LN network is barely stable the disinhibition of the PNs will be highly sensitive to input (formally we show the effective gain of the system tends to infinity as the largest real eigenvalue of the Jacobian of the fixed point tends to zero). Furthermore by employing a population mean field approach we show if the baseline rate of the LNs are sufficiently inhomogeneous then the dynamic range of the PN responses is maximised at this critical point, see figure C.

We finish by arguing that this idea of critical rate dynamics is a much more appealing account of the dynamic range of the AL and OB. We also claim that the notion of neural criticality as a bifurcation in a higher level quantity (here the rate dynamics) is much more general than the "stick slip" framework prevalent in the neuroscience literature. In future work we hope to show how this idea can be applied more widely to biological systems. For example there is a striking similarity between the ideas outlined here and an account of the dynamic range of the mammalian auditory system, which is thought to be mediated by a Hopf bifurcation in the dynamics of the inner ear's mechanoreceptive hair cells [5].

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Electric Images of a Fish With a Distributed Electric Organ

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ABSTRACT

The active electroreception of *Gymnotus omarorum* is a complex sensory modality that allows this specie to create its own electric field in a pulse like manner and sense it by measuring transepidermal voltage or current density [2]. Differently than mormyriform electric fish, gymnotiforms have an electric organ distributed along the body, which does not fire synchronically. As a consequence, the shape of the electric field generated and the images of the objects change in time. To study how *G. omarorum* composes a perceptual representation, we developed a computational model [3] that allows the determination of the evolution of the field generated by the fish and the electric image.

We have found a correlation between in vivo measures and our model's predictions for the basal discharge, the relation to the conductance of the water of the environment and the electric images of metal objects. The image of resistive objects, in rostral regions, varies in amplitude, but the shape remains constant. This feature is important to detect capacitive properties of the object, since they will distort the shape of the local electric organ discharge that can be detected for the three types of electroreceptors present in rostral regions. To study these distortions, we propose ways to characterize the electric images, when they change along the electric pulse, allowing the definition of electric color [1].

Electrosensory afferents inform the brain about the local value of the image using a latency code and the brain structures involved are well suited to process smooth changes in the transepithelial currents. So, sudden changes of the image, as those occurring when the object is close to the region where the electric potential generated by the electric organ is close to zero, will be distorted by the brain. The objects positions where this occurs are caudal, where the density of receptors is low. Consequently, these changes of the image could be used mainly to detect the position of the object rather than its shape.

Keywords: electrolocation, image, active sense.

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A Network Model of Learning Stimulus-Response Associations

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ABSTRACT

Humans are able to learn Stimulus-Response (S-R) association in a very short time, e.g. following verbal instructions such as If that red light turns ON, then press that left button. This involves establishing rapidly a link between the cortical representation of the stimulus and the cortical representation of the response. It is known that verbal actions and objects descriptions activate motor preparation areas in the posterior parietal cortex (PPC) and representation areas of the visual stream [1,2]. There are also data showing that an area of the PPC becomes responsive to the stimulus after instruction [3] but that is about all we know on the process of linking S and R areas during instruction.

The work presented here explores a possible neural network architecture that enables one-shot learning of S-R associations in a biologically plausible way. Given the lack of physiological data on the process, some elements of the model are necessarily speculative.

The architecture design is guided by following considerations: We assume a layered organization of brain areas. Given that neurons have a limited receptive field in the previous layer, several layers will be needed to ensure a complete representation of the stimulus. We also assume that each layer has the same number of neurons. More speculatively, we assume that each neuron is capable of self-sustained firing and that is projects inhibitory feedback to its inputs in the previous layer. This ensures information propagation, while minimizing the neuronal activity.

The representation is of all-or-none type. This minimizes the number of neurons involved in representing any stimulus and reflects the selective response of neurons in the visual system.

The proposed learning mechanism is designed to automatically generate a sparse pyramid of nodes representing completely the stimulus S. This implements a representational push. At the same time, the response R is given the power to guide the growth of the pyramid towards activating the desired neurons in the

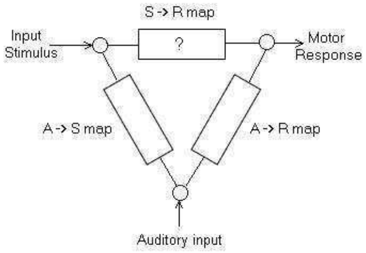

Figure 1: The S-R map is the focus of this work. It is assumed that the mapping between speech input and stimulus imagery is available, as well as the mapping between speech input and motor imagery.

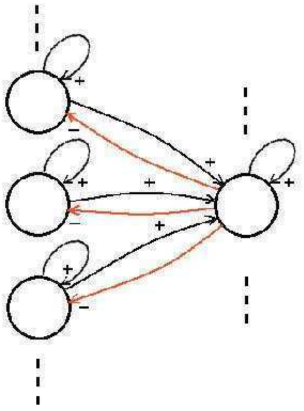

Figure 2: Neuronal connectivity assumed in the model.

response layer (Activity pull).

This model has been initially implemented using binary neurons, demonstrating fast learning of binary S-R pairs. Its implementation with spiking neurons will be discussed at the workshop, including effects of the limited selectivity of spiking neurons, the required synaptic learning rules and the trade-off between speed of learning and capacity.

Overall, this work addresses the problem of fast S-R learning across several neural layers, using a representation and code guided by considerations of energy consumption minimization.

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Coding of Electric Images in Electric Fish with Distributed Electric Organs

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ABSTRACT

Some fish generate weakly electric discharges (EOD) by activating an electric organ derived either from muscular or neural tissue. The polarization of objects by such electric field creates an electric image sensed by electroreceptor organs distributed on the skin of the fish. This sensory modality is called active electroreception because it is based on the sensing of an electric field ultimately caused by the activity of the fish own electric organ. While some fish have a localized electric organ generating a brief EOD, others have an electric organ distributed all along the body.

Since discovering of active electroreception it has been an important incognita on how electrosensory images generated by fish with distributed electric organs are coded at the skin of these fish.

In order address this problem we have studied the electric images of objects by measuring the local field along the fishs lateral surface and constructed the first neural image (i.e. the pattern of discharge of primary afferents) by modeling the transduction and coding mechanisms at the level of each receptor type.

We found that different regions of the electric organ generate dissimilar waveforms that summate to form the whole electric field polarizing the surrounding objects. Thus, objects having equal material but unlike shapes accentuate or attenuate differently the frequency components of the illuminating field depending on their relative position and orientation respect to the fish (Fig 1).

Taking into account that the electro-sensory organs respond with and dumped oscillation, we modeled sensory transduction as a second order linear system in which gain and resonant frequency can be tuned to match biological data obtained by recording local receptor potentials (Fig. 1A). Sensory cells converge synaptically onto a single primary afferent which integrates these signals. We model the generator potential and the spike train using a leaky-integrate-and-fire model. Because of the synapse there is a rectification and because of membrane properties there is low pass filtering. This causes that the spike train depends on the envelope of the receptor damped oscillation (Fig. 1B).

As expected latency and number of spikes may vary according the model parameters. Then,

we tuned the model parameters to match the three types of afferent tuning curves that can be obtained experimentally. In this way, taking into account the local EOD profiles obtained in the presence of various objects we were able to construct and compare their neural images.

Our main finding is that extensive attributes of an object as for example shape could be coded in a parallel by the activity of different receptor types. Because of the action of the object on different electrogenic sources the limits of the image of an object having edges are sharper than as those of a sphere. Since local sources have different power spectra, receptors with different tuning curves code differently the image. As shown in the example of Fig 1C and 1D low frequency waveforms mainly generated at the rostral region of the fish's body are better sensed by low pass receptors located in front of the rostral limit of the object and high frequency waveforms mainly generated at the caudal region of the fish's body are better sensed by narrow band receptors located in front of the caudal limit of the object.

We conclude that if the three types of receptors are represented on the side of the fish, object's shape might be coded by the combination of activities of multiple receptor types. Ongoing experiments are in progress to test such hypothesis.

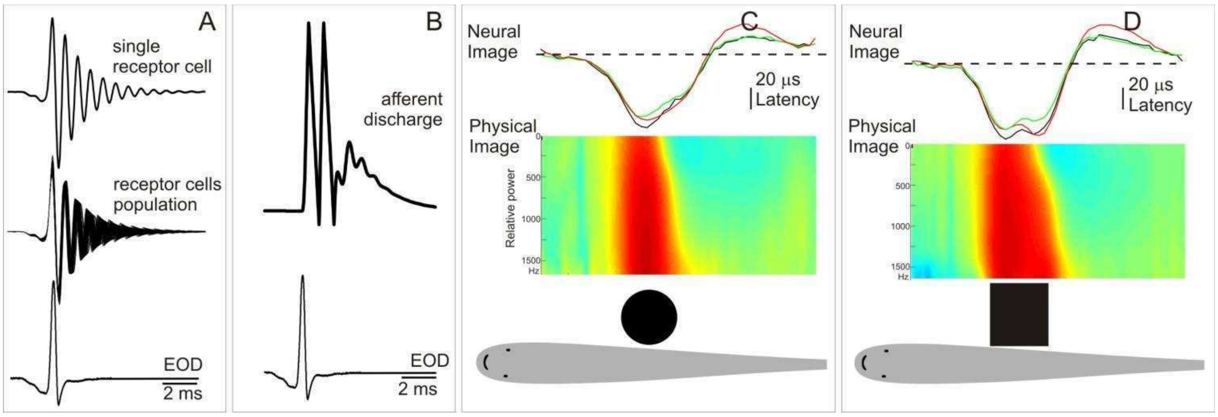

Figure 1

Keywords: Electric images, receptor transduction, afferent coding.

Modeling FM Responses of Midbrain Auditory Neurons – An Integrated Approach Based on STRF and PSTH

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ABSTRACT

In linear modeling single auditory neuron's response to complex sounds, less success is found at the higher brain centers when compared to primary auditory afferents. The difficulty has commonly been attributed to greater nonlinear property at higher levels of the brain. The auditory midbrain is an important center along the ascending pathways where neurons sensitive to frequency modulation (FM) but not steady tones first emerge [1]. The exact neural mechanism of FM coding remains elusive. Spectrotemporal receptive field (STRF) is a powerful way to characterize the input-output relationship particularly of FM-sensitive cells. In these STRFs, spike-averaging the preceding spectral sound energy typically displays the putative FM-trigger features which have been used to model neural response to other sounds. Previous studies on STRFs of FM cells in the rat midbrain suggested the presence of multiple trigger features, separable into main and partial components [2]. We speculated that such trigger features could reflect synaptic events likely taking place over dendrites of the FM-sensitive cells. Here we developed and tested a method to answer the following question: how effective it is to predict a cell's response by integrating information in its STRF and peri-stimulus time histogram (PSTH) to FM sounds using artificial neural networks that involve mainly linear elements.

Single unit responses of auditory midbrain neurons to sounds were first recorded extracellularly in urethane-anesthetized rats using glass microelectrode. Two sets of sound stimuli were presented: (a) random FM: a family of random FM tone that varied across 60 trials, and (b) frozen FM: a member of the random FM tone that was repeated as identical stimulus across 60 trials. Spike responses to random FM were used to generate STRF and those to frozen FM generated PSTH. STRF was generated by adding in the spectro-temporal plane the instantaneous frequency time profiles within 40 msec preceding the spikes, followed by de-jittering to enhance the trigger features. PSTH was generated by computing spike counts at 0.4 msec time bins, followed by low-pass filtering to obtain the probability of firing. A novel method of data analysis was developed that integrated results obtained with both stimuli. First we separated STRF trigger features, using a progressive thresholding method, into two categories: main and partial. A

similar thresholding method was used to separate peaks in the PSTH into strong and weak responses. An artificial neural network was trained to model separately the strong and weak responses based on spectro-temporal characteristics of the preceding modulating signal. This approach in time series prediction involves constructing an underlying model that best produces the observed neural events. A finite impulse response neural network (FIRNN) which models synapses as FIR linear filters was used in the form of autoregressive time series. The performance of the model was finally assessed in terms of probability of spike firing (or PSTH fidelity) against a new frozen FM sound in comparison with empirical data obtained from the modeled neuron. Furthermore, the part of pre-spike stimulus critical for the modeling the cell response was determined by artificially lesioning portions of the modulating waveform in a systematic manner using a sliding time window. The effect of lesioning was again assessed based on the model performance.

With this integrated approach we found a highly satisfactory performance of our model in predicting the spike occurrence to FM sounds. Over 90% success was attained particularly with the strong responses. Furthermore, the critical segments of the pre-spike modulating time waveform coincided well in time with the trigger features as determined in the STRF. Results were also taken to indicate that it is not strictly necessary to rely on non-linear property of the system to model FM responses at the auditory midbrain if spike responses were treated as heterogeneous populations.

When the strong responses were compared with the preceding modulating signal, the main trigger feature often corresponded with an FM tone sweeping through a restricted spectral range and mostly at a fixed rate. Often we found two or more temporal segments of the pre-spike signal particularly critical for successful modeling. These results are consistent with the STRF reported for midbrain auditory neurons that are sensitive to FM sounds and could reflect interacting synaptic events taking place on the cells dendrites. On the other hand, the partial trigger feature that associated with weak response appeared less obvious in the STRF and appeared more variable across neurons. For example, partial trigger feature could fall close to main trigger features in one cell, but lie distant to the main trigger feature in another. The exact nature of partial trigger features cannot be fully determined in the present study which assumed that trigger features are primarily excitatory events. The auditory midbrain is well known to be rich in inhibitory mechanisms (including post-inhibitory rebound) as shown by immunohistochemistry and in vivo as well as in vitro electrophysiological studies [3]. In relation to this, it is not clear to what extent such inhibition-related phenomenon could underlie the weak responses. We suggest that testing responses of these auditory neurons to sounds with multiple spectral components and other complex sounds (e.g., dynamic ripples) would be useful to answer this question.

Keywords: complex sound coding, frequency modulation, neural modeling, artificial neural network.

Acknowledgment: Supported by Taiwan National Science Council, NSC99-2221-E-218-007

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High Firing Irregularity Enhances Learning

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ABSTRACT

Softky and Koch [8, 9] analysed spike train recordings from cortical neurons and demonstrated that these cells in vivo fire irregularly at high rates. They also showed that the Leaky Integrate-and-Fire (LIF) neuron model, which temporally integrates excitatory postsynaptic potentials generated by independent stochastic input spike trains, failed in reproducing this observed high firing irregularity. While many methods were proposed to reproduce Softky and Koch's findings (see [2, 3] for a brief review), we have shown that a LIF neuron model with partial somatic reset is a very good candidate for reproducing the observed highly irregular firing at high rates by cortical neurons [1, 3]. In this paper, we are investigating whether the high firing irregularity produced by LIF neurons with the partial somatic reset mechanism, when used in spiking neural networks in the benchmark problem of XOR and in a general-sum game, enhances reward-modulated Spike Timing-Dependent Plasticity (STDP) with eligibility trace [5]. More specifically, in the case of the general-sum game, we have a multiagent Reinforcement Learning (RL) task with spiking neural networks as agents in the iterated version of Prisoner's Dilemma (PD) [7] (systems architecture same as the one we designed and used in [4], but with learning based on modulation of STDP with eligibility trace [6]) and we are examining whether its cooperative outcome could be enhanced if the LIF neurons of the networks comprising the agents are equipped with the partial somatic reset mechanism. According to the results, the increased firing irregularity at high rates does indeed enhance learning for both systems investigated [5].

Keywords: High firing irregularity, partial somatic reset, reward-modulated Spike Timing-Dependent Plasticity

Acknowledgments: We gratefully acknowledge the support of the Cyprus Research Promotion Foundation as well as the European Union Structural Funds for grant PENEK/ENISX/0308/82.

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Cortico-Thalamic Modulation and Emergent Feature Preferences in a Model of Auditory Cortex

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ABSTRACT

Since Hubel and Wiesel [3] showed that there were ‘preferred stimuli’ which evoked a more vigorous response in cortical neurons it has become commonplace to think of discrete neural units as having stimulus preferences. Although it is widely believed that auditory perception is based on the responses of cortical neurons that are tuned to spectro-temporal ‘features’ [7] it is not clear what these features are or how they might come in to existence. There is, however, evidence that cortical responses develop to reflect the nature of stimuli experienced in the early post-natal period, and that the development of these responses can be disrupted by exposure to impoverished or noisy auditory environments (for a review see [4]).

It has been reported recently [1, 2] that a recurrently connected cortical model exhibiting spike timing dependent plasticity (STDP) will, when exposed to a range of formative stimuli, develop responses with varying temporal properties and exhibiting a range of heterotopic integration.

Here we extend previous results by characterizing the responses of a large number of model neurons exposed to synthetic, parametric stimuli and arguing that the responses of the trained network can be understood as ‘feature preferences’. We also show that these feature preferences can, in the first instance, be demonstrated in terms of the observed firing rate. However it is not clear whether the rates of firing fully characterize the differences between neurons. To investigate this we construct difference matrices in terms of the van Rossum spike metric [6] using a range of values for the time variable (λ) and show that the discrimination between two stimuli, as evident in the distance between pairs of neurons, depends on timing as well as rate of firing.

In addition we show that both before and after training, the neurons exhibit simple receptive fields when these are characterized with simple, ‘tonal’ stimuli despite exhibiting more complex spectro-temporal preferences. This can be understood in terms of cortico-fugal activity which exerts modulatory rather than driving influence on the thalamus and provides insight into how areas “might interact to compute features of the auditory scene” [5].

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Neural Coding and Variability Measure via Cumulative Entropy

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ABSTRACT

Information coding and transmission play a relevant role in understanding and describing the behavior of biological and engineering systems. Entropy, as a baseline concept in the field of information theory, was introduced by Shannon [4] and Wiener [5], and it is, for instance, also invoked to deal with information in the context of theoretical neurobiology (see for instance Johnson and Glantz [3]).

The classical approach to the description of information related to a non-negative absolutely continuous random variable X is based on the differential entropy of X, or Shannon information measure. Other measures of uncertainty as suitable generalizations or modifications of the classical entropy have been proposed in the recent literature such as the weighted entropy or the cumulative residual entropy.

Here we consider the cumulative entropy of a non-negative random variable X, defined as (see Di Crescenzo and Longobardi [1])

$$\mathcal{CE}(X) = -\int_0^{+\infty} F(x)\,\log F(x)\,\mathrm{d}x,$$

where $F(x) = P(X \leq x)$ is the distribution function of X. We present various properties of such information measure. Furthermore, we recall the empirical cumulative entropy, which is a suitable estimate of $\mathcal{CE}(X)$ (see, for instance, Di Crescenzo and Longobardi [2]). We discuss the role of the empirical cumulative entropy to describe the information content and the variability in neuronal data sets.

Keywords: Information coding, Cumulative entropy, Variability measure.

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Spike Surrogates Based on Operational Time

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ABSTRACT

Detecting the excess of spike synchrony and testing its significance can not be done analytically for many types of spike trains and relies on adequate surrogate methods. The main challenge for these methods is to conserve certain features of the spike trains, the two most important being the firing rate and the inter-spike interval statistics. In this study we make use of operational time to introduce generalizations to spike dithering and propose two novel surrogate methods which conserve both features with high accuracy. Compared to earlier approaches, the methods show an improved robustness in detecting excess synchrony between spike trains.

The Morris-Lecar Neuron Model Embeds the Leaky Integrate-and-Fire Model

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ABSTRACT

We analyze the stochastic-dynamical process produced by the Morris-Lecar neuron model, where the randomness arises from channel noise. Using stochastic averaging, we show that in a neighborhood of the stable point, representing subthreshold fluctuations of the neuron, this two-dimensional stochastic process can be approximated by a two-dimensional Ornstein-Uhlenbeck modulation of a constant circular motion. The firing of the Morris-Lecar neuron corresponds to this Ornstein-Uhlenbeck process crossing a boundary, which is equivalent to the crossing of a one-dimensional leaky integrate-and-fire model with state dependent noise. This model is the Feller neuron model where an inhibitory reversal potential is accounted for. The result justifies the large amount of attention paid to the stochastic leaky integrate-and fire models. A more detailed picture emerges from simulation studies.

Keywords: Ornstein-Uhlenbeck process, Feller model, Separate time scales.

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Bayesian Analysis of the Single Cell Response in Mouse Olfactory Receptor Neurons

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ABSTRACT

In this talk, we develop a Bayesian Markov Chain Monte-Carlo (MCMC) estimation scheme for the parameters of a computational model of the olfactory receptor neuron (ORN) in mouse. Our approach is a Bayesian extension of the method of Ramsay et al. [1] and involves conditioning the model likelihood on specific pivotal feature statistics [2] identified in the neuronal outputs. We invoke a specific intrinsic property of locally weighted polynomial regression to develop a novel adaptive likelihood penalty term. We explore through high-dimensional visualization the penalty's optimality properties. Nonparametric kernel densities are used in formulating the likelihood of spike trains. The resulting model is a multi-scale extension of the transduction cascade model of Dougherty et al. [3] able to predict both the slow transduction current emanating from the cilia and the fast spike train emanating from the axon. We analyze recordings obtained from a mouse line which lack olfactory marker protein (OMP). OMP is a protein of unknown function, which is ubiquitous and selectively expressed in vertebrate ORNs. $\mathrm{OMP}^{-/-}$ ORNs display a 10-fold slowed olfactory response making them particularly interesting for our modeling approach [4]. Principle components analysis of the estimated model parameters provides some meaningful insights into the role of OMP within ORNs.

Keywords: Bayesian, Mouse, Receptor, Neuron, OMP

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Single Neuron And Network Models in Force Control

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ABSTRACT

The single neuron study had the goal of comparing the frequency response functions of two motoneuron (MN) models having similar soma dynamics but different dendritic dynamics: one had a passive dendrite and the other an active dendrite. Motoneurons with active dendrites have been described in decerebrate cats [7] in relation to the generation of a persistent inward current (PIC), bistability and plateau potentials, and are believed to occur also in humans [4]. The chosen passive-dendrite MN model was a two-compartment soma-dendrite model described in [2]. The active-dendrite MN model was based on the passive-dendrite model with the inclusion of a voltage-dependent L-type Ca++ channel in the dendritic compartment so that it could generate a PIC. The two models (the passive and active) were made to discharge at the same mean rate around 30/s, driven by a frequency-modulated presynaptic spike train (the input) of mean rate 4000/s (passive-dendrite) and 2000/s (active-dendrite) acting on the dendritic compartment. These presynaptic mean firing rates were different because in the active model the PIC that is generated in response to the synaptic drive contributes to the firing rate. Each cycle histogram obtained from the instantaneous firing rate of each of the simulated MN models (the output) was fitted by a sine function and the gain and phase shift were computed with respect to the input modulating sine function. Note that the force generated by a motor unit associated with the motoneuron would follow the modulating frequency with no attenuation at least up to 1 Hz [1]. The frequency responses in absolute value (gain) were quite different in the two models: the passive-dendrite MN showed an increasing gain up to about 13 Hz and then decayed while the active-dendrite MN showed a monotonic decreasing gain of lowpass nature, with a -1 dB cutoff frequency around 0.5 Hz. The tentative functional role ascribed to a potential PIC in human motoneurons is related to the maintenance of a standing posture [6] because the resulting bistability would require very little control from the descending pathways during quiet standing. Simplistically, these pathways would be required to turn on the MN (make it discharge regularly) by a burst of excitatory activity, therefore, freeing the upper centers from detailed control of the motoneuron pool. On the other hand, human postural sway has about 74% of the power concentrated at low frequencies up to 0.25 Hz [8], which are due to oscillations of the center of pressure [3]. Hence, for the task of controlling quiet standing, the lowpass feature of the active-dendrite MN model seems to be well-suited, as it would attenuate higher-frequency perturbations that could increase the postural sway. At the same time, the MN would pass the low frequencies needed for the feedback to correct displacements of the center of gravity. If human motoneurons do indeed exhibit such a lowpass feature during quiet standing is an open question which suggests new directions for future research.

The second study veryfied how the force variability, measured by the standard deviation of an isometric maintained force, depended on the mean force value. A network of 900 motoneurons (800 type S, 50 type FR and 50 thpe FF), representing the MN pool that drives the soleus muscle, was driven by 100 axons, each carrying a Poisson process with a specified intensity

and with an innervation ratio of 20% (meaning that each axon innervated a randomlychosen subset of the motoneurons containing 20% of the MN pool). If there was no limit set to the firing rates of the MNs in the pool, then the force standard deviation (std) showed a parabolic-like dependence on the mean force level, increasing with mean force and then decreasing as the mean force increased still further. However, if the firing rates of real MNs from humans are taken into account, then the valid part of the force std x force mean relationship is just a monotonic increasing function. This result suggests that for the soleus muscle the hypothesis of signal-dependent-noise [5] is applicable. A new investigation would be required to verify if the same is valid for the gastrocnemi muscles, as these are important synergists of the soleus in exerting plantarflexion but have a different motor unit type composition. A further step would be to study the influence of feedback from muscle spindles and Golgi tendon organs on force variability during isometric and nonisometric force and position control.

Keywords: persistent inward current, motoneuron models, force variability.

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Cooperative Effects of Noise and Nonlinear Dynamics in Hodgkin-Huxley-Type Model Neurons

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ABSTRACT

While simplistic (or reductionistic) approaches have their own merits in neuronal modeling (such as ease of analysis and efficiency of computation), models based on the Hodgkin-Huxley (HH) formalism are the physiologically more realistic alternative allowing a direct connection of theoretical and experimental studies. All state variables and parameters have a physiological meaning and can, at least in principle, be observed experimentally. Experimental biological data, however, are notoriously noisy. Accordingly, also model neurons should consider the effects of noise not only for physiologically realistic simulations. Also cooperative effects between noise and nonlinear dynamics can occur, e.g. stochastic resonance and coherence resonance phenomena, depending on the neurons' dynamic state.

For the examination of noise effects at different dynamic states we have used a four-dimensional HH-type model neuron, the Huber-Braun-model [1]. This model can generate a diversity of physiologically relevant impulse pattern, including impulse groups (bursts), chaotic impulse sequences as well as two different types of single-spike discharges (tonic firing). In such HH-type models, the membrane potential is given by the sum of ion currents that are charging or discharging the membrane capacitance (membrane equation) while the ion currents are determined by voltage- (or transmitter-) dependent activation and/or inactivation kinetics. Accordingly noise can be implemented at different levels and in different ways.

For simplicity, noise from different possible sources is often comprised in a single term of mostly Gaussian white noise that is added to the membrane equation (current noise). Another pos-

sibility is the addition of noise to the activation variables of the ionic currents (conductance noise). The effects on the impulse activity are in most situations principally the same. Both current and conductance noise smooth the deterministically abrupt transitions between different dynamic states. In the regular bursting regime, some random fluctuations of spike generation are induced and both types of noise can induce typical stochastic resonance effects when the neuron operate close to the threshold of spike generation [2,4,5].

However, when the neuron is operating in the pacemaker-like tonic firing regime, significant difference can be seen in comparison of current and conductance noise. While current noise essentially leads to random fluctuation of interspike-intervals the implementation of conductance noise can induce burst-like discharges in the previously tonic-firing state. This is apparently due to the propagation of conductance noise to the membrane equation where it enters as correlated noise with a correlation time according to the activation time-constants [2]. Accordingly, similar effects could be achieved with implementation of current noise with a correlation time corresponding to the activation time constants. Also in this case, such dramatic noise effects only appear in the deterrnistically pacemaker-like tonic firing regime [5]. State space analysis elucidates the functionally relevant dynamics in this regime: The trajectories show large excursions from the deterministic limit cycle towards an unstable saddle point [3]. We compare these particular phenomena with noise effects in other types of neurons and discuss whether the particular dynamics in this tonic-firing regime may also be responsible for the impairment of neuronal synchronization, for example in comparison to the bursting regime [5].

Keywords: impulse pattern, burst firing, pacemaker, conductance noise, correlated noise

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Stochastic Modelling of Neuron Activity

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ABSTRACT

Real data from a neurophysiology experiment are analysed. During the experiment, the spiking activity of a place cell of hippocampus of a rat moving in an arena together with the track of the rat was recorded. The action potentials (spikes) of the neuron are modelled as a Cox process on a curve. Also other approaches to such data are discussed. The first one is an estimation of a conditional intensity of the temporal process of spikes using recursive filtering. In the second one, the track of the rat together with the random driving intensity function of the process of the spikes is viewed as a random marked set.

Keywords: Cox point process, Spatio-temporal process, Random marked closed.

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Multiple Subtypes of Local Interneurons Suggest Distinct Tasks During Odor Processing in the Antennal Lobe

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ABSTRACT

The insect antennal lobe (AL) is the first synaptic relay that processes olfactory information and is the analog of the vertebrate olfactory bulb. The olfactory receptor neurons of the antennae, each expressing a single functional receptor gene, send their axons to the AL, where they collate by receptor type and converge into specific glomeruli. In the glomeruli they provide synaptic input to projection neurons and local interneurons (LNs). The projection neurons relay information to higher order neuropiles including the lateral lobe of the protocerebrum and the mushroom bodies. The LNs mediate complex inhibitory and excitatory interactions between glomeruli to structure the olfactory representation in the AL, which ultimately shapes the tuning profile of projection neurons.

In *Periplaneta americana* we characterized two main LN types with distinctive physiological properties: 1) type I LNs that generated Na^+ driven action potentials upon odor stimulation and exhibited GABA-like immunoreactivity (GLIR) and 2) type II LNs, in which odor stimulation evoked depolarizations, but no Na^+ driven action potentials. Type II LNs did not express voltage dependent transient Na^+ currents and accordingly would not trigger transmitter release by Na^+ driven action potentials. 90% of type II LNs did not exhibit GLIR. Type I LNs had arborizations in many, but not all glomeruli, while the density of neurites varied between glomeruli of a given neuron. Type II LNs had arborizations in all glomeruli, whereas the density and distribution of processes were similar in all glomeruli of a given neuron. In subsequent studies we identified two classes of non-spiking LNs (type IIa LNs and type IIb LNs) with distinct morphological features and distinct active membrane properties. The specific functional properties of I_{Ca} in both classes of non-spiking LNs correlated clearly with the active membrane properties of both LN types. Type IIa LNs with a large transient I_{Ca} component had stronger active membrane properties compared to type IIb LNs, in which this transient current component was significantly less pronounced.

The distinct intrinsic firing properties were reflected in functional parameters of their voltage-activated Ca^2+ currents (I_{Ca}). Consistent with graded synaptic release, we found a shift in the voltage for half-maximal activation of I_{Ca} to more hyperpolarized membrane potentials in the type II LNs. These marked physiological differences between the two LN types imply consequences for their computational capacity, synaptic output kinetics, and thus their function in the olfactory circuit: 1) The spiking, inhibitory, GABAergic type I LNs expressed different branching patterns in different glomeruli, suggesting a polar organization with defined input and output regions. Accordingly, the synaptic input from a defined receptive field (e.g. one or a few glomeruli) would be integrated at a local spike initiation zone into action potential firing that would spread to other innervated glomeruli, and provide a defined set of glomeruli with synaptic input. Glomeruli could interact independently of their distance: not only nearestneighbor glomeruli could interact, but also glomeruli that are distributed throughout the entire AL. 2) In contrast, type II LNs have very similar branching patterns in all glomeruli, suggesting that they can receive synaptic input from all innervated glomeruli. However, during odor stimulation, synaptic input from olfactory receptor neurons will be typically restricted to certain glomeruli, in which graded postsynaptic potentials will be generated. In type IIa LNs with strong active membrane properties, the transient I_{Ca} component might help to boost and shape dynamic signals such as EPSPs. Such mechanisms might help to shape functional compartments, for example for local integration or they might help to activate nearby output synapses. For non-spiking LNs with weakly active membrane properties, such as the type IIb LNs, interactions between glomeruli would be dependent of their (electrotonical) distance: potentials would spread only within the same glomerulus or to glomeruli that are electrotonically close to the stimulated glomerulus. These scenarios are testable with detailed structural, electrophysiological, and optophysiological studies together with structure and conductance based modeling.

Keywords: Antennal Lobe, Local Interneurons, Olfaction.

Electric Scene Segmentation by the Electric Fish

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ABSTRACT

Weakly electric fish (as *Gnathonemus petersii*, modeled here) use the distortions of the electric field, produced by its own electric organ, to perceive the world in close vicinity [4]. They have an arrangement of electric sensors distributed unevenly over the skin with the rostral zone having the highest density [2]. Pulse type fishes trigger the electric organ discharge (EOD) discontinuously in time, getting an "electric snapshot" of the nearby world, adapting the frequency of the discharge according to the requirement of perceptual information.

These animals can navigate successfully in complete darkness and can discriminate objects based on position, distance, shape and impedance [7, 8]. This implies that they can segment the electric scene using the information contained in the electric image. The electric sense peculiarities make it difficult to determine which elements of the physical electric image can be used as clues to segment the electric scene and how they are used to get unequivocal information about the objects in the scene. For example, objects that distort the electric field behave as a new source generating an image that is not the sum of the individual images [5].

Segmentation of an electrolocation image is a complex task. In vision the image of an object is projected to a region of the retina and does not superpose to the image of any other. By the contrary the images in electrolocation spread over the whole skin of the fish and the superposition of images is the rule. Nevertheless, for isolated objects or in the presence of a few objects projecting on widely separated regions of the skin, some clues can be used: the place on the skin where the image reach its peak signals the location of the object, distance is coded as a kind of blurriness given by the slope of the normalized image of the object, etc. But in complex scenes there is no one unequivocal simple parameter of the image that signals characteristics of the object. For example the size of the image is related with the size of the object but also with its distance. Active exploration could help to solve many of those ambiguities, since the change of perspective may be resourceful to estimate the parameters of the object in a three dimensional world from a two dimensional image. Composing images obtained from different positions, the fish could get additional information in the same way as we do using parallax in vision [1]. Consequently, this sense should, more appropriately, be included among the haptic senses that require the use of sequences of sensory and motor acts to solve perceptual ambiguities.

We developed a model using the boundary element method (BEM) [6], to explore this idea simulating the electric images generated on the skin of the fish in sequences of different spatial configurations. We define the "intensity" of an image as the square root of the addition of its square at each node on the surface. To compare images we defined a "intensity difference" as the square root of the addition of the square of each point to point difference between the images. This measure is 0 when images are equal and proportional to the information available to discriminate between them when they are different. In order to establish a realistic minimum of discriminability we relate this measure with behavioral experiments.

We show, for objects of the same size, that the intensity of the image produced decreases with distance to the fish. When we compare the intensity difference of a sphere (or rounded object) in a given position and another of the same shape but different size, the difference depends on

the distance of the second one, reaching a minimum (close to zero) for a given distance. Then, the size and relative distance of these objects cannot be clearly determined with only one image. In this case the exploratory swimming of the fish improves the capacity of discrimination of the size and position of these objects. Besides, the change of the position of the image on the skin surface, when the fish approaches and rotates around the object, provides more information about the object and its position.

Objects with edges generate sequences of images that change when the fish swims around them. The images of cubes, with edges perpendicular to the rostro-ventral direction, present different intensities as the fish moves around them, with a period of 90 degrees. Then, integrating information about the movement of its body and information provided by electrolocation, fish are able to determine the presence and position of the edges of the object. As before, this mechanism may work only for objects in close vicinity.

When the object is presented against a background, swimming may help to its segmentation, since the part of the scene image that changes as the fish moves corresponds to the image generated by the object. Besides, differences in impedance may also contribute to object discrimination if the shape of the objects image changes in a different way than that of the background [3].

Images, coded in the latency of spikes of primary afferents, reach the electrosensory lateral line lobe (ELL) as a somatotopically ordered pattern. From this temporal structure and the architecture and physiology of the ELL we can infer neurocomputational rules that extract object information from static and dynamic parameters of the electric images.

Keywords: electrolocation, image, active sense.

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Analysis of the Signal Transformation From First- to Second-order Neurons in the Moth Sex-Pheromone Olfactory System

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ABSTRACT

In the male moth, the sex pheromone plume emitted by females is detected by a population of specialized olfactory receptor neurons (ORNs) housed in antennal sensilla of conspecific males. A large number of these ORNs converge onto a few glomeruli in the brain antennal lobe, where they connect synaptically to a smaller number of projection neurons (PNs).

To study the transformation of the signal from ORNs to PNs, we recorded single ORNs [1] and PNs [2] in the Noctuid moth Agrotis ipsilon. Responses of these neurons to different concentrations of sex pheromone were characterized by their latency and firing rate. Mathematical functions were fitted to the concentration-response curves. To describe their variability across neurons, probability density functions of the fitting parameters were estimated [3]. Finally, the distributions obtained from ORNs and PNs were compared.

The results suggest that the ORNs with the lowest thresholds and shortest latencies in the population trigger the PN response; this may explain the higher sensitivity of the PNs at low concentrations of sex pheromone. They also show that the relatively variable ORN responses to a given pheromone stimulation are converted into less variable responses across PNs.

Keywords: olfaction, electrophysiology, quantitative analysis.

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Signatures of Spiking Neuronal Assemblies in the Local Field Potential

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ABSTRACT

The oscillatory nature of the cortical local field potential (LFP) is commonly interpreted as a reflection of synchronized network activity, but its relationship to observed transient coincident firing of neurons on the millisecond time-scale remains unclear. Here we present experimental evidence to reconcile the notions of synchrony at the level of neuronal spiking and at the mesoscopic scale. We demonstrate that only in time intervals of excess spike synchrony, coincident spikes are better entrained to the LFP than predicted by the locking of the individual spikes. This effect is enhanced in periods of large LFP amplitudes. A quantitative model explains the LFP dynamics by the orchestrated spiking activity in neuronal groups that contribute the observed surplus synchrony. From the correlation analysis, we infer that neurons participate in different constellations but contribute only a fraction of their spikes to temporally precise spike configurations, suggesting a dual coding scheme of rate and synchrony. This finding provides direct evidence for the hypothesized relation that precise spike synchrony constitutes a major temporally and spatially organized component of the LFP. Revealing that transient spike synchronization correlates not only with behavior, but with a mesoscopic brain signal corroborates its relevance in cortical processing.

Evaluation of Alternative Coding Strategies in Early Olfaction

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ABSTRACT

The sense of smell has attracted profound scientific interest and has been a source of fascination over the centuries. Yet, considerably less insight into the functionality and organization of olfactory system has been gained when compared to other sensory modalities in humans. One of the key challenges in the attempt to understand fundamental computational mechanisms underlying the functionality of the sense of smell is to elucidate the neural representation of key stimulus features. It still remains unclear how the olfactory system conveys the information about odor identity and intensity to facilitate robust recognition in natural environments. In this regard, the functional nature of the transformations in odor representation that take place in the so-called early stages of olfactory information processing, particularly in the olfactory bulb (OB) of vertebrates and the antennal lobe (AL) of insects, is of special importance [1].

The study outlined here deals with computational evaluation of different hypothetical early olfactory coding strategies from the perspective of the discriminative power of the resultant secondary representations. Specifically, it was aimed to examine a recently proposed concept of fuzzy interval coding of odor concentration [2][3] in comparison with concentration-saturating representations [4]. The simulated neural responses to single and mixed odorant stimuli at a wide range of concentration levels were generated using a reduced version of the computational model of olfactory processing in the layer of olfactory receptor neurons and the OB in vertebrates [2][3]. It should be mentioned that in this work the temporal characteristics of olfactory responses were not taken into account since the focus was on neural coding in terms of static activity patterns, similarly as in other modeling, e.g. [5], and experimental studies [6].

The separability of the induced patterns of neural activity at the OB output was analysed in the context of one of the most fundamental tasks that the sense of smell addresses - odor discrimination. To this end, a range of recognition scenarios were devised with two key variables - odor identity and intensity. The objective was to investigate to what extent the information about these target features is conveyed in the coding patterns under consideration. Their discriminative properties and the potential for relevant generalizations of one variable despite wide variations in the other one, as in concentration-invariant odor identification, were of special interest in this evaluation. Collectively, three groups of recognition tasks were tested. Firstly, concentration dependent setup assumed the assignment of the olfactory data to the classes of objects from the Cartesian product of odor labels and three concentration categories - low, medium and high. Secondly, concentration invariant odor recognition was verified using different intensity ranges for classification system's learning and recall. Thirdly, the odor recognition was performed separately for concentration and identity target variables.

The classification accuracy, obtained with support vector machines and connectionist neural network methods, was utilised as the criterion in the evaluation of the alternative olfactory coding strategies within the aforementioned odor recogntion framework. This quantification approach provided a link with artificial olfaction and the discussion of various learning and classification scenarios conveyed in this work should also be relevant to the development of modern electronic noses.

In conclusion, despite that no significant differences in the average performance of neural networks and support vector machines were reported, the latter classifiers produced the most consistent results and facilitated a fast model selection process. In terms of olfactory coding, the outcome of the extensive evaluation demonstrated that the fuzzy interval approach clearly favored concentration dependent odor recognition allowing for reliable classification of odor identity and detection of its concentration range. The specificity of this coding strategy though rendered the resultant representation less conducive to generalization. In this respect, conventional concentration-saturating codes had more universal characteristics in the tasks considered here. Finally, it should be emphasised that the approach adopted to examine the scope for concentration invariant odor classification by learning to recognize their identity at different intensity levels corresponds to biological scenarios where odorants appear in natural environments at rapidly fluctuating concentrations.

Keywords: Olfaction, Classification, Invariance.

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Information Capacity and Robustness of Spatially Separated Dendritic Synapses

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ABSTRACT

It is widely believed that it is the plastic properties of dendritic spines (synapses) that allows information to be learnt and stored in the brain, thus resulting in memory formation [1]. However, the interplay between synapse location, active membrane properties and processes mitigating synaptic plasticity remains largely unexplored. Recent experiments indicate that the synaptic strength within clustered—i.e. proximally located—synapses are synergistically strengthened through synaptic cross-talk. This suggests that clusters of nearby synapses may be the preferred physiological substrate underlying the learning and storage of new information.

In parallel, current experimental data supports the notion that synaptic strengths may have a limited number of discrete states, whose values are finitely bounded [2, 3, 4]. Such experiments have shown that when a single appropriately timed presynaptic input is paired with a large postsynaptic depolarization, then 'step' increases or decreases in synaptic strength occurs, switching between different stable discrete states. These all-or-none switching events result from increases in intracellular calcium concentration, which triggers the activation of different intracellular signalling cascades and ultimately leads to the insertion or removal of AMPA receptors from the postsynaptic density of the spine.

This experimental evidence is further supported by efforts in modelling biochemical signalling cascades, where such models naturally give rise to synapses with discrete multiple states [5]. One example is the binary synapse, where synaptic strength can be in one of two stable discrete states. Such synapses are known to have better robustness to noise than continuous synapses, despite an individual synapse's limited storage capacity.

Furthermore, synapses with discrete states are known to endow networks with the palimpsest property where old memories decay automatically as they are overwritten by new ones [6]. Network studies employing such synapses have further highlighted a higher degree of robustness to retain a memory trace in the face of ongoing plastic changes when compared to networks with continuous unbounded synapses [7].

Recent studies have further explored this issue in networks using multistate synapses, where such states differ in several degrees of freedom and not simply in their synaptic strength. These studies adopted the unifying principle where plasticity is combined with metaplasticity in a cascade of states increasingly resistant to plastic change and have illustrated superior ongoing storage, robustness, and memory retention capabilities [8, 3, 9].

Inspired by these recent experimental findings, we investigate the issue of information storage

capacity and robustness between spatially distributed synapses in a simplified neuron model, called the *clusteron* [10, 11]. For i synapses, and denoting w_i as the efficacy of synapse i, and x_i as its input, the clusteron model states that the synaptic response is given by

$$h = \sum_{i=1}^{n} w_i x_i \sum_{j \in D_i} x_j w_j,$$

where D_i is a set of neighbours of synapse i, including synapse i itself. Thus, this models the notion that the response depends on the spatial distribution of synapses.

Using this abstract model, we illustrate the dependence of storage capacity and robustness on various factors including the number of synapses in the cluster and the number of synaptic states. We provide analytical expressions for information capacity for such a neural system and compare our results to a recent study where the neuron is treated as an additive linear device and synapses were assumed to have binary states. Furthermore we propose a potential (information theoretical) role for cross-talk between synapses in dendrites.

Nicolangelo Iannella is the recipient of an ARC (Australian Research Council) Australian Postdoctoral Fellowship (project number DP1096083). Mark D. McDonnell is the recipient of an ARC Australian Research Fellowship (project number DP1093425).

Keywords: clusteron,synaptic plasticity,discrete synaptic efficacies.

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Neural Coding Clues From Early Brain Activity in Well-Circumscribed Areas Obtained With Tomographic Analysis of Magnetoencephalographic (MEG) Signals

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ABSTRACT

Our visual system has evolved to deal with stimuli that change instantaneously and unpredictably in the environment. Furthermore, even the ones that are significant for the system are often weak inducing a neural signature that represents only a tiny fraction of the neural activity elicited by other irrelevant stimuli. Yet, these small fraction of neural responses are the only clues available to humans for fleeting opportunities or deadly threads. It is therefore expected that evolution would have endowed the brain with mechanisms for fast and accurate recognition, emphasizing correct and fast recognition of biologically salient stimuli. It is not possible to wire in advance all different stimuli. In addition the objects in the external world are unlabeled, so early in life the brain has to invent its own categories and learn their significance through trial and error. The brain accomplishes the miracle of perception through neural activity. This neural activity contains only indirect imprints of real world objects as it is recorded at the sensory organs and tranformed into electrical changes in the brain. It is believed that the main, possibly only, way that the brain codes information is through the spikes that relay activity from one neuron to the next. Deciphering the neural code is thought to be equivalent to understanding how transformations between different representations is achieved through the organization in space and time of neural spikes. However, the neural code in the brain must not be equated with a dry information transfer in a static communication network. Instead, it has been proposed to view the various manifestations of neural spike signaling as adaptations that optimize ecological expected utility [1]. This leads to competing constraints for the way neural coding should be studied. On one hand, scientific rigor demands precise control of stimuli and using one sensory modality at the time creating conditions that are different from the ones encountered in the environment. On the other hand, ecological considerations demand natural stimuli often engaging more than one sensory modality with physical properties that vary in a non-systematic way.

It is not feasible to study collective activity elicited by complex stimuli with methods allowing mapping of localized neural responses in only one or few brain regions; it requires simultaneous mapping of activity over a wide range of brain areas. To satisfy this requirement we recorded magnetoencephgraphic (MEG) signals and used magnetic field tomography (MFT) [2, 3] to extract tomographic estimates of activity throughout the whole brain from each timeslice of data, i.e. with a millisecond temporal resolution. Moreover, we have resolved the competing requirements of rigorous stimulus control and ecological relevance by focusing on the visual modality and using visual stimuli that have well-defined physical properties and proven biological significance. Specifically we recorded the MEG signal from subjects while they participated in category/object detection, face affect recogntion and gender recognition tasks. We have focused on the visual system because we have a reasonably good understanding of how visual processing is organized and particularly how function is seggregated in different cortical areas. We have also contrasted the activity evoked by stimuli presented at the centre of the visual field or in one of the quadrants for two reasons. First, placing stimuli in specific parts of the visual field allowed

our precise tomographic analysis to capture the first arrival of the stimulus-evoked response in the primary visual cortex V1 and to follow the activity in each extrastriate area. Second, ecological considerations [4] and our own results showed that different neural circuits may be activated by stimuli in different parts of the visual field, at least in the early stages of processing.

Our results demonstrate that neural mechanisms underlying visual information processing in the brain are ultra-fast: attentional selection based on object location or category, and differentiation of facial expressions of emotion are completed well within 100 milliseconds post-stimulus and they depend on where the stimuli appear in the visual field. Moreover, our findings show that this fast neural processing is organized into stages of processing, each lasting about 30 ms, and involving cooperative activity of widely distributed brain areas (e.g. amygdala, V1 and fusiform gyrus). Within each stage of processing, activity from many areas converges into one hub. Then, the “processed information spreads from the hub to many other areas. Although the early processing, well within 100 ms post-stimulus, is below awareness, it is particularly refined: it is influenced by attention [5] and it distinguishes facial expressions [6]. The information flow is not fixed, but rather it depends on how difficult the task is [7] and where the stimulus appears in the visual field [8].

The features of visual processing highlighted by our results must be linked to attempts to deciper neural coding. At present our results can put only general constraints on possible neural codes, but more detailed results are expected from future experiments expoiting recently developed capabilities to identify contributions from specific cytoarchitectonic areas [9] and the use of stimuli and tasks designed to probe specific aspects of neural coding.

Keywords: Magnetoencephalography (MEG), magnetic field tomography (MFT), visual system, stages of processing, early attention, face, emotion.

Acknowledgement: Part of the work was supported by grants upgrade/info/0308/02 and human/sociol/0308(BE)/16 from the Cyprus Research Promotion Foundation.

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Anatomically Realistic Winner-Take-All Networks as Models of Cortical Computation

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ABSTRACT

Many neurons in the primary visual cortex of mammals are selective to visual stimuli of specific orientations. Although the specific details of how orientation tuning emerges in this area are still being debated, it is widely accepted that the neural response is driven through a combination of both feed-forward and recurrent feedback connections.

Many computational models have been proposed to understand and explain orientation selectivity in visual cortex, using these assumptions [5, 4, 6]. In particular models based on soft winner-take-all (WTA) networks have been shown to explain orientation tuning and describe many of the observed computational tasks the brain continuously performs [2, 3].

However it is still not clear if and how WTA is realized in the cortex. While most soft WTA and competitive-cooperative models of cortical circuits assume broad inhibition and local recurrent excitation (*e.g.*, which give rise to Mexican-hat like response profiles), the connectivity of neurons in the upper cortical layers, suggests a different network architecture, with local inhibition and broad excitation [1]. This is especially true in layers 2/3 of the visual cortex, where the WTA microcircuits are believed to be located.

While most of the previously proposed models were built from a top-down, functional point of view (with broad inhibition and narrow recurrent excitation), we approached the modeling task from the bottom-up: we started with anatomically realistic connectivity profiles [1] and determined the conditions under which visual cortical properties, and in particular soft-WTA behaviors, are reproduced. We first carried out theoretical analysis and parameter sweeps on networks of linear threshold units (LTUs) and then performed numerical simulations of networks of spiking neurons, using biophysically realistic parameters and anatomically consistent connectivity profiles.

Our findings suggest that the lateral non-isotropic, orientation-specific connectivity patches of the cortical network are critical for the emergence of competitive computation such as cross-orientation suppression. Surround inhibition is mediated by isotropic, local connections, while strong stimuli are recurrently amplified by orientation-specific lateral connections of excitatory cortical neurons.

Our network simulations are based on three anatomical assumptions:

1. Orientation-specific excitatory synapses connect preferably to excitatory neurons.
2. About 30% of the excitatory synapses are orientation-specific.

3. Orientation-specific lateral clusters have a smaller diameter than the local, isotropic connectivity region.

If these anatomical assumptions are correct, the performance of the simulated spiking network model can explain the electrophysiological findings in the primary visual cortex of cats. Cooperative-competitive behaviors and soft WTA competition is observed for inputs of significant strength differences, while inputs of similar strengths are equally represented by the neuronal activity. Furthermore, an analysis of the spike timing properties of the neural network revealed strong spike correlations of nearby neurons. These correlations come from the all-to-all connectivity applied in this model and reduce the soft-WTA effect of the network especially at high spike rates.

Keywords: soft WTA, orientation tuning, area V1, spiking neuron.

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Temporal Modulation of the Input Parameters Can be Deduced From Intracellular Recordings in the Ornstein-Uhlenbeck Neuronal Model

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ABSTRACT

The membrane voltage, in most of neuronal models, depends on two kinds of parameters, the input parameters and the intrinsic parameters. The input parameters are characterized by the mean and variance of the input signal. The intrinsic parameters characterize the membrane properties, such as the membrane capacitance or the ionic conductances.

We consider an estimation problem of input parameters from a single voltage trace obtained by intracellular recordings. Several methods for this estimation problem have been developed recently, [1, 2]. All these methods are based on the assumption that the input parameters are constant in time. However, it is natural to expect that neuronal activity *in vivo* is time-variable, reflecting the variable external conditions, [3]. We propose a Bayesian method to estimate the time-varying input parameters in absence of the firing. The proposed method is applied to the Ornstein-Uhlenbeck neuronal model and its estimation performance is evaluated.

Keywords: Ornstein-Uhlenbeck process, Statistical inference, Empirical Bayes method

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Information Capacity in the Weak Signal Approximation

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ABSTRACT

Theoretical approach to the problem of information processing in neuronal systems has received significant attention over the past few decades, with information theory providing the fundamental framework. Of particular interest are the optimality conditions under which the information between stimuli and responses is maximized, leading to the idea of *efficient coding*.

We derive an approximate expression for mutual information in a broad class of discrete-time stationary channels with continuous input, under the constraint of vanishing input amplitude or power. The approximation describes the input by its covariance matrix, while the channel properties are described by the Fisher information matrix. This separation of input and channel properties allows us to analyze the optimality conditions in a convenient way [1].

We provide illustration of the method on a simple model of electro-sensory neuron [2]. Our general results apply also to the study of information transfer in single neurons subject to weak stimulation, with implications to the problem of coding efficiency in biological systems.

Keywords: information capacity, neuronal coding.

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Distinguishing the Causes of Firing with the Membrane Potential Slope

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ABSTRACT

We present a metric for measuring the level of synchrony between spike trains at a neuron's input that were relevant to the firing of response spikes. The metric is calculated using the normalised slope of the membrane potential prior to the spikes fired by a neuron and we show that it is able to distinguish between the two operational modes that neurons are thought to be employing: temporal integration or coincidence detection [1]. The importance of this distinction lies in the fact that each mode implies a corresponding encoding mechanism; temporal integration suggests that information is encoded on the average firing rate, while coincidence detection indicates the importance of timing of individual spikes [2].

Our metric is inspired by the work of Kisley & Gerstein [3], which shows how higher levels of input synchrony result in higher pre-spike membrane potential slopes. These authors demonstrated how coincidence detection, enforced by high levels of input synchrony, resulted in higher pre-spike slopes than temporal integration. We expand on this by defining the bounds of the pre-spike membrane potential slope associated with each operational mode quantitatively, which in turn allows us to define an exact measure of the relative contribution of each mode to the firing of the neuron. The upper bound of the metric, which corresponds to coincidence detection, is defined as the slope of the membrane potential resulting from the arrival of synchronous input spikes, while the lower bound, which corresponds to temporal integration, requires defining the expected slope of the membrane potential of a neuron driven by random spike trains (i.e., no synchrony). More specifically, the upper bound is calculated as the slope of the membrane potential that rises from the resting potential to the threshold within a very short time period w. The parameter w is the duration of the "coincidence" window and its value is determined by what we consider to be the maximum difference between the arrival of two (or more) spikes that are still considered to be coincident. Coincident spikes may arrive from different inputs or from the same one, since no refractory period is used at the inputs. Any pre-spike membrane potential slopes with values higher than the upper bound, are regarded as equivalent to the bound. On the other hand, the lower bound of the membrane potential slope is calculated separately for each response spike and requires calculating the slope of the membrane potential that rises from the resting potential to threshold during the current inter-spike interval (ISI). This is based on the assumption that in the absence of any significant synchrony at the input, the membrane potential rises steadily towards the threshold during each ISI. Any lower slope values are considered to be equivalent to the bound. The calculation of the bounds may be generalised to account for arbitrary post-spike membrane potential reset values. For the upper

bound, this is done by calculating the potential of the membrane after it has decayed towards the resting potential (which assumes that no input is present during a given ISI) and measuring the slope of the theoretical membrane potential that rises from the decayed state towards the threshold within the time interval specified by the coincidence window (w) just preceding the end of the ISI. The bounds are used to linearly normalise the slope of the pre-spike membrane potential of each spike during a trial. Since the time course of the pre-spike membrane potential is a curve, we use the slope of the secant line that intersects the membrane potential curve at the beginning and at the end of the coincidence window (i.e., average rate of change). The result is a value between 0 and 1, where values closer to 0 denote dominance of temporal integration and values closer to 1 indicate coincidence detection. The metric has so far been applied to the membrane potential time course of a leaky integrate-and-fire (LIF) neuron model driven by inputs with varying levels of synchrony. The results indicate that the normalised pre-spike membrane potential slope can reliably measure input synchrony. We have also measured the normalised pre-spike membrane potential slope of a model neuron exhibiting highly irregular firing at high rates. This requires the use of a variant of the LIF model that employs a partial somatic reset mechanism, which has been shown to be the most likely candidate to reflect the mechanism used in the brain for producing the irregular firing of cortical neurons at high rates [4, 5]. This is the reason for deriving bounds for the normalisation for arbitrary reset values, explained above. The results suggest that neurons firing highly irregularly at high rates operate mainly as temporal integrators and coincidence detection is not necessary for producing the observed irregularity at high rates, as was suggested by Softky & Koch [6, 7].

While similar work exists on measuring spike train correlations and synchrony, either by directly observing the spikes fired from a population of neurons [8, 9], or by identifying synchronous activity in local field potentials [10], our proposed metric differs in that it only responds to the correlations between spike trains converging into a single neuron, when they are responsible for the triggering of response spikes. In this way, the metric is only concerned with the input statistics that affect the neuron's own spiking. It is this particular feature which links our metric's estimation of spike train synchrony to the underlying operational mode. The operational mode of a neuron is not defined solely by the synchrony of the spike trains it receives, but also by whether or not that synchronous activity causes firing. Our intent is to apply the metric to membrane potential data generated by increasingly complex neuron models and eventually from experimental intracellular recordings, in order to determine the operational mode of real neurons.

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Recursive Bayesian Algorithms for Real-Time Brain-Computer Interface

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ABSTRACT

A number of important data analysis problems in neuroscience can be solved using state-space models [1]. The optimal estimate of the state is its conditional expectation given the observation histories, but this expectation is computationally demanding when nonlinearities are present. Various authors have therefore used Gaussian approximations to posterior densities that appear in the formulation.

In the first part of the presentation, we investigate this approach, showing that the errors introduced by the approximation are not compounded across time. We then consider second-order expansions, and show that they can provide second-order accuracy in state estimates – but that no additional accuracy is possible by higher-order approximations [2]. We discuss implementation of these methods and illustrate by decoding multielectrode motor cortical data.

In the second part of the presentation, we have developed real-time software which implements our decoding methods in conjunction with a brain-computer interface. We show results from a monkey using these methods to control a cursor on a computer screen, and compare the performance of our decoding methods to that of the population vector algorithm and the optimal linear estimator. We also discuss the difference between off-line and on-line analysis [3].

Part of this works have been done in collaboration with R. E. Kass (CMU) and A. B. Schwartz (Univ. of Pittsburgh).

Keywords: State-space model, Approximate probabilistic inference, Brain-computer interface.

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Synchronized Activity in the Subthalamic Nucleus

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ABSTRACT

The subthalamic nucleus (STN) plays a key role in the basal ganglia. Abnormal neuronal activity in the STN plays a crucial role in the pathophysiology of Parkinson’s disease (PD) [4]. the STN receives topographically organized input from the cerebral cortex, and it provides the major glutamatergic excitation to the substantia nigra pars reticulata (SNr) [1] and internal part of the globus pallidus (GPi) (entopeduncular nucleus in rodents) that provide the basal ganglia (BG) output to the thalamus and brainstem. Dopamine (DA) modulates the efficacy (promotes LTP or LTD) of glutamatergic and GABAergic inputs to STN neurons directly, through pre- and postsynaptic receptors, and indirectly, through modulation of activity in all BG nuclei [2]. The STN is in a strategic position to exert a prominent control over the basal ganglia-related motor functions since it integrates the somatic motor information from various cortical/subcortical brain areas (including the motor cortex, thalamus and pedunculopontine nucleus) [3]. Figure 1 illustrates the activation of the cortico - basal ganglia thalamocortical circuit by DA neurons.

The understanding of the physiological role of DA within the neural circuit involving the BG and STN is important for the development of possible therapies for PD. Investigation on rat, nonhuman primate models and human PD patients have shown that the death of DA cells in the SNc modifies the firing pattern of STN neurons and can induce an increase of their firing rate that will eventually produce characteristic changes in motor behaviour. Chronic DA depletion that underlies the pathology of PD can be obtained experimentally by lesions of DA cells in the substantia nigra pars compacta (SNc) by means of 6-OHDA or MPTP. These lesions provoke changes in the activity of all nuclei connected with the BG, but contradictory reports exist about changes in the firing pattern of the homolateral STN. In this study, we investigate the changes in rodent STN neuronal activity using multielectrode recordings in the STN after 6-OHDA lesion in the SNc and compare these results with recordings performed in human PD patients [5].

Unilateral 6-OHDA lesioning was carried out in the SNc. Under anesthesia with ketamine/ xylazine the subject received one injection of 6μl of solution at the stereotaxic coordinates. Extracellular multiple single unit recordings with glass-coated platinum-plated tungsten electrodes and with micropipettes were performed in the STN 2 weeks after 6-OHDA lesion of the SNc. We could sort out multiple spike trains from the same channel and we recorded 109 pairs of neighbour cells [6]. Data from 15 rats (6 treated and 9 controls) anaesthetized with Equithesine showed no major differences in firing pattern and firing rate of single units between the two groups. However, the 6-OHDA treated group showed a significant increase (from 25% to 49%)

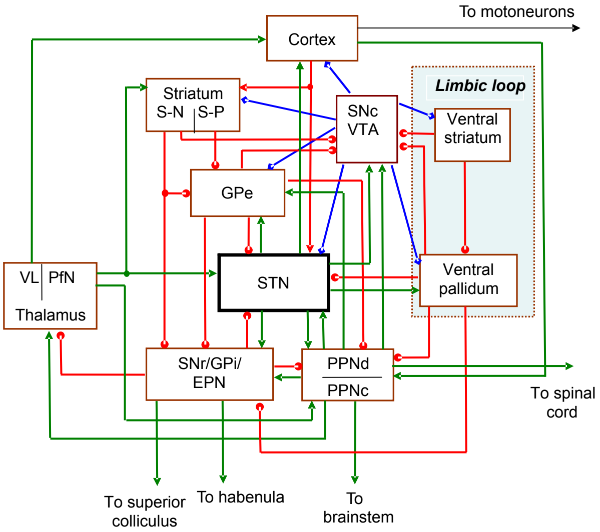

Figure 1: GPe and GPi, external and internal segment of the globus pallidus; D1 and D2, dopaminergic receptors; S-N and S-P, striatonigral and striatopallidal cells; SNr and SNc, substantia nigra pars reticulata and compacta; STN, subthalamic nucleus; PfN, parafascicular thalamic nucleus, PPNd and PPNc, pars dissipate and compacta of pedunculopontine nucleus; VL, ventral lateral nucleus; VTA, ventral tegmental area. Red arrows indicate inhibitory connections (GABAergic); green arrow, excitatory (Glu) connections; blue arrows indicate modulatory influence of DA.

in the number of synchronized cell pairs without an increased tendency to fire in burst.

In normal conditions DA, which modulates GABA release and excitatory inputs to projecting cells of STN, can influence in opposite ways the dischargers of different STN cells [2]. The absence of DA tends to decrease the differences of firing pattern among STN cells and therefore their synchronization can be stronger. Strong synchronization of STN neurons is likely to affect in a more efficient way the activation of their targets in the SNr, and eventually in the thalamus and neocortex, thus affecting motor activity. The synchronization could facilitate the funneling propagation and modify parallel propagation of signals from the neocortex through the BG [1].

Keywords: Basal Ganglia, Synchronization, Dopamine.

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Multilevel Constraints on a Cortical Attractor Model

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ABSTRACT

Computational neural network models have successfully reproduced several aspects of experimental data, such as activity levels, spike rates and spike discharge patterns, global oscillatory phenomena and functional criteria. What is largely missing however are attempts to unify and reproduce all these findings in a single model. We have previously developed a biophysically detailed attractor network model of cortical layer 2/3 constrained by cortical geometry, connectivity, firing rates and activity levels [1]. The network recalled stored memories and the activity level was roughly 1%, which corresponds to both recordings and metabolic constraints, and the connectivity and synaptic conductances were set to match experimental data [2]. The original model constituted some 1300 Hodgkin-Huxley type neurons but was later scaled up to the proportions of a rat brain with 22 million neurons [3]. Interestingly, the up-scaled model maintained its memory function and had fast (~ 50 ms) and coherent transitions between the attractor states despite the distances and associated axonal delays.

Recently we have also constrained the model with in vivo spike train statistics from delayed match to sample tasks [4]. We showed that the network operated in a regime of balanced excitation and inhibition with highly irregular low rate firing both during fixation and delay. Further, the elevation in firing rates during delay activity was much smaller than typically seen in attractor models reproducing this paradigm and in line with experimental data. This latter finding was due to the fact that the model operated in a regime of oscillatory activity both during fixation and delay. The frequency of these oscillations increased from alpha/beta during fixation to gamma-type oscillations during delay also in accordance with experimental findings. In order for attractor models to successfully reproduce the fixation/delay they must operate in a bistable regime [5]. It was found that oscillatory activity greatly enhanced the robustness of this regime towards changes in excitation level and produced highly irregular spike output without fine-tuning parameters.

In a fourth line of work [6], we have looked closer into global oscillations and found that we can reproduce many of the phenomena as measured by LFP and EEG, such as elevated power of gamma and theta oscillations during active processing, and alpha/beta during an idling state. Further, theta power correlated with working memory load as reported in literature.

The functional and mechanistic origin of these rhythms could then be studied, together with coherence and phase-locking patterns of both synthetic spike-LFP and LFP-LFP activity.

In conclusion, all this work shows that while a considerable amount of information has been derived from minimal models, which appear to be at an advantage when only a single phenomenon is to be reproduced, models of higher complexity can also contribute valuable knowledge. First of all, it is important to demonstrate that several functions and experimental observations can be reproduced in a single model and that they are not mutually exclusive. This is a crucial step in the verification of biological plausibility. Secondly, new knowledge might emerge from such unification as different levels are found to interact, for instance in the case of bistability robustness and irregular firing. Lastly, while complex models certainly have an increasing number of parameters, they can be constrained by even larger amounts of experimental data in the attempt to model observed phenomena. In doing so they can form a bridge between experimental data from microscopic to macroscopic and behavioral levels.

Keywords: Irregular firing, Oscillations, Modular attractor memory networks.

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On Gaussian Random Neuronal Field Model: Moment Neuronal Network Approach

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ABSTRACT

A novel model is proposed to describe the rich dynamics of spiking activities of leaky integrate-and-fire (LIF) neuronal networks via the moment neuronal network approach. Different from the existing neuronal field model (for example, Wilson-Cowan-Amari model) which only takes the first-order moment (mean firing rate) into considerations, we develop a Gaussian random field to qualitatively describe the spatiotemporal distribution of the first- and second-order moments: mean firing rate, variance or coefficient of variation (CV) equivalently, and the coefficient of correlation (CC), of spiking trains. By this neuronal field model, we find out that the firing rate response with respect to the input may be not sigmoidal or even monotonic if the inhibition is stronger than excitation, which leads fruitful dynamical behaviors, in comparison with the sigmoidal response. In addition, within this framework, we can analyse the synchronisation propagation in the LIF neuronal network. We use our Gaussian random field model to investigate how the three key factors: the ratio between inhibition and excitation, the size of synchronous cluster, and the background firing rate, decide the stability of a synfire chain.

Emergence of Bayesian Computation and Neural Codes for Hidden Causes through STDP in Generic Cortical Microcircuits

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ABSTRACT

There exists substantial evidence that Bayesian inference is carried out in the brain. But a model that explains how these computations could emerge in generic cortical microcircuits on the basis of experimentally supported learning algorithms has been missing. We show here, that Bayesian inference emerges in common motifs of generic cortical microcircuits (pyramidal neurons with local lateral inhibition) through STDP. In fact, we show that STDP approximates in such generic network motifs a very powerful method for the creation of implicit generative models: Expectation Maximization (EM). The particular version of the STDP rule that optimally supports EM, where the size of weight potentiation decreases rapidly as a function of the initial weight, but weight depression does not correlate with the initial weight size, agrees with experimental data. We also show that adaptation of intrinsic excitability of neurons could support Bayesian computation by creating priors for hidden causes of high-dimensional spike inputs.

Computer simulations of such networks of spiking neurons demonstrate the autonomous emergence of detectors for repeating spatio-temporal spike patterns through STDP, even in the presence of large noise and time-warps, emergence of orientation selective cells, as well learning to discriminate handwritten digits from the standard Machine Learning benchmark dataset MNIST without any supervision. The emergence of Bayesian computation through STDP works particularly well when the number of input spike trains approaches biologically realistic numbers (i.e., a few thousand). Altogether this framework drastically improves existing methods for demonstrating impressive computing and learning capabilities of networks of spiking neurons with STDP.

We propose, that networks of such emergent modules for Bayesian computation in different cortical areas provide a new basis for modelling computations and learning in large network of neurons in the brain. In fact, recurrent networks of such modules provide a new perspective for modelling the emergence and interlinking of assemblies that encode longterm memory.

A first description of the underlying principles, in a very simplified setting, has appeared in [1].

Keywords: Neural computation, probabilistic inference, neural coding, synaptic plasticity.

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Primary Visual Cortex Encodes Complementary Information About Naturalistic Movies at Different Temporal Scales

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ABSTRACT

Natural stimuli have a rich temporal structure, yet it is still unclear whether the encoding of such stimuli employs more than one response time scale. We investigated this issue by analyzing the activity of neurons recorded in primary visual cortex of anesthetized macaques during presentation of naturalistic color movies following procedures detailed in [1] and we quantified the amount of information carried by neural codes operating at different temporal scales. We divided the recording time into stimulus windows of 16-80 ms, and we computed the information carried by the neural response about which stimulus window was being shown. First we measured the information carried by the total number of spikes in the stimulus window (spike count). Then we measured the information carried by the temporal pattern of spikes, computed by subdividing each stimulus window into time bins of size Δt and considering the binary spike train given by the absence/presence of spikes inside each bin. The information conveyed by temporal spike patterns with a Δt of 8 or 16 ms was up to 20% more than that conveyed by the

spike count. This information gain did not increase further when considering resolutions finer than 8 ms, indicating that this is the precision of the spike patterns code. Coherently with the results of [2], we found that spike patterns carried information complementary to that carried by the phase of firing by quantifying if the joint knowledge of the spike pattern and the LFP phase of firing carried more information than either code considered alone. The information gained by the simultaneous knowledge of the phase of low frequency LFPs and of the spike patterns was 50% higher than the information carried by spike patterns alone and 15% higher than the information carried by the phase of firing alone. This suggests that the information carried by slow LFP fluctuations complements that carried by spike patterns.

In summary, we found evidence for complementary response time scales for the encoding of naturalistic stimuli in visual cortex. Informative codes range from spike timing precision at 10ms resolution to the much coarser phase of firing with respect to low frequency fluctuations. These findings indicate that sensory cortices may enhance their information capacity by multiplexing complementary information at different time scales.

Keywords: Information processing, Sensory coding, Temporal codes

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Modulation of Gamma Oscillations in Simulations of Cortical Networks is Sensitive to Network Topology

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ABSTRACT

Electroencephalography (EEG)—and other more localized measurements, e.g. of local field potentials (LFP)—readily highlight 'rhythmic' oscillatory brain signals [1, 2]. Mathematical approaches have contributed to explaining *how* oscillations arise e.g. via emergent synchronization of many periodically spiking individual neurons [1, 3]. In comparison, the fundamental question of the function of oscillations remains largely unresolved, despite many theories. We are aiming to assess the hypothesis that communication between physically different brain regions (e.g. the thalamus and neocortex) is facilitated by *modulation* of neuronal oscillations, where we mean *modulation* in the sense relevant to communications engineering.

There has been much recent qualitative discussion of supporting experimental evidence for mechanisms analogous to amplitude modulation in the brain [4, 5]. Recent experiments where LFPs in the cortex were recorded and analysed (and associated simulations) [4], have suggested that two different neuronal communication channels convey independent information about visual stimuli from the thalamus to the visual cortex. In particular, the 'amplitude' of neural spike rate input to a cortical network was observed to 'modulate' the power of that network's gamma frequency oscillations. This effect was quantified using information theory [4], using an Erdős-Rényi random network model. However, for oscillations to act as modulated carrier waves, mechanisms for both modulation and demodulation, as well as selective filtering are required. This is beyond the capabilities of information theory. Instead, hypothesis confirmation requires biologically feasible neuronal mechanisms for these concepts to be demonstrated.

As a first step towards assessing such hypotheses, we have reproduced the core results of [4] via simulation of the same model. This model consists of a network of 5000 recurrently connected integrate-and-fire model neurons. The network has 4000 excitatory neurons (to model pyramidal cortical neurons that produce excitatory AMPA currents) and 1000 inhibitory neurons (to model cortical interneurons that produce inhibitory GABA currents). Connected neurons receive current input with 1-ms propagation delays, with exponential rise and fall times. The LFP of this network is modelled in a simple way as proportional to the sum of the excitatory currents in the network. Each neuron in the network receives a correlated input, which models inputs received from the thalamus. One of the key results of [4] was to show that if these input signals are modelled as a Poisson spike train with a certain time varying rate, $\nu(t) = \nu_o + \xi(t)$, where ν_o is a constant, and $\xi(t)$ is a noise process, then the power spectrum of the LFP increases with increasing ν_o in the gamma frequency range.

Many recent experimental studies have found that the topology of local networks in the cortex

has a 'small-world' structure [6]. Small-world networks are random networks that are characterized by connections between nodes such that there is a high level of local clustering, but an overall relatively short mean-shortest path between nodes [7]. We therefore modified the model of [4] to assess whether emergent gamma oscillations were sensitive to the level of local clustering. We replaced the Erdős-Rényi network model with the small world network model of [7], where a small world network is generated by rewiring links in a regular network. This model, known as the Watts-Strogatz model, has previously been used in many studies of networks of model neurons, e.g. [8], and is produced by randomly rewiring links within a regular lattice, with a probability p.

We have found that generating a network using the Watts-Strogatz process leads to significant changes in the power spectrum of the LFP. Indeed, unless the network has only a very small amount of local clustering (i.e. rewiring probability p is close to unity), neurons in the network spike at rates close to saturation. For large p, modulations in the power spectrum with changing ν_o are qualitatively similar to those of [4]. To compare different values of p for the same ν_o, we computed the resultant power spectrum for three values of p (SW) for $\nu_o = 2.4$, and that of the Erdős-Rényi (ER) network for comparison. We found that a small amount of local clustering significantly increases the LFP power for all frequencies, while the peak LFP power shifts to lower frequencies as p decreases.

Finally, we found that the model of [7] with $p = 1$ provides different results to the Erdős-Rényi network. This is somewhat surprising, since one may assume both networks should result in a random network with every node having identical connection probabilities. We are currently investigating this difference, as well as how other network topologies affect the power spectrum.

Mark D. McDonnell is the recipient of an Australian Research Council Australian Research Fellowship (project number DP1093425).

Keywords: gamma oscillations, integrate-and-fire neurons, small world cortical networks.

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A Neurocomputational Model of Deviance Detection in Stimulus-Specific Adaptation

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ABSTRACT

Regular sequences of tones have long been used to assess the response properties of neurons sensitive to sound. One such property, evident in neurons at multiple sites along the auditory pathway, is *stimulus-specific adaptation* (SSA), whereby tones that appear in the sequence often (standards) evoke fewer spikes on average than those that appear rarely (deviants) [4, 1, 7]. SSA thus provides a rudimentary mechanism for tracking the statistics of a sequence and highlighting the tones that stand out against a monotone background. Here we describe a model neural circuit able to reproduce a variety of qualitative experimental observations from SSA studies and, most importantly, able to perform genuine deviance (as opposed to rarity) detection where other models have hitherto failed.

The suggestion that SSA might arise from adaptation on the inputs to a neuron (e.g., due to synaptic depression or the facilitation of inhibition) was advanced in one of the earliest papers to describe the phenomenon [4]. In line with this proposal, the first model we present incorporates neurons that receive depressing synapses [6] converging from a tonotopically-ordered array of input neurons. The repeated presentation of a tone depletes the synaptic resources associated with a localised region of the input array, leading to a reduced response in the post-synaptic target. Conversely, the presentation of a new tone activates distinct synaptic resources, which in turn leads to a large 'deviant' response. The properties of this model have been more thoroughly investigated in [2].

Despite its simplicity, this model can account for several characteristics of the SSA response. First, decreasing the frequency separation between the standard and deviant tones reduces the magnitude of the SSA, because it increases the overlap in the synaptic resources consumed by the transmission of the signal. Secondly, increasing the rarity of the deviant increases the magnitude of the SSA, because the synaptic resources associated with the deviant are given longer to recover. Thirdly, if the standard and the deviant tones are swapped in the middle of a sequence, SSA neurons eventually respond to the new deviant, as the distribution of synaptic resources adjusts to reflect the new stimulus statistics. This accords with findings from *switching-blocks experiments* [4].

A notable deficiency of this model is its failure to predict larger responses for deviants embedded in a sequence containing one standard than for deviants embedded in many standards—as others who have developed similar models have noted [3, 5]. This subtlety is captured in the distinction we draw between *rarity* and *deviance*. A tone which appears with 10% probability on average amid a uniform background of standard tones is a proper deviant by virtue of its violation of a pattern; a tone which appears with 10% probability amid a background of nine other distinct and equiprobable tones is not deemed a deviant—although it appears with the same rarity. Surprisingly, one physiological study reported that more than half of the SSA neurons tested were sensitive to deviance; i.e., the response to deviant tones embedded in a single standard exceeded or matched that elicited in response to the same deviant presented amongst many standards [3].

The authors of the aforementioned study [3] concluded that it is "necessary to assume that in the presence of oddball sequences, the adaptation channels become narrower than in other conditions." Here we contend that such an assumption is unnecessary and difficult to realise in practice: it requires a separate circuit to recognise oddball sequences and then to modulate the input bandwidths. The second model we present circumvents this demand by employing multiple layers of depressing synapses, such that another type of SSA neuron is formed in the later layers, which receives input both directly from the tonotopic array and from other SSA neurons via depressing synapses. (The connections between SSA neurons may be recurrent or strictly feed-forward.) These latter neurons exhibit the desired response property, i.e., they respond most vigourously to deviants presented in a single-standard configuration.

At this juncture we are unaware of any pattern in the data from physiological SSA experiments that is incompatible with our second model. The model requires only a few free parameters to be tuned (e.g., input bandwidth and synaptic time constants) in order to match data obtained from real neurons in response to oddball sequences. This gives rise to the prospect that, once the model has been fitted to data from a real neuron measured in response to oddball sequences (in which each element is statistically independent of every other), it can be used to make explicit predictions regarding the response of the same neuron to more complex sequences such as Markov chains.

Keywords: Stimulus-specific adaptation, synaptic depression, oddball sequences.

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Effects of Type 1 and Type 2 Synapses
on Oscillations in Models of Recurrent Cortical Networks

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ABSTRACT

Rodents use whiskers to sample the space around them. Tactile information from whiskers is relayed to and processed in a region of the somatosensory cortex called the barrel cortex. Typical of cortical regions, the barrel cortex has a six-layered structure with layer IV receiving input [1]. Understanding information processing capabilities of this layer IV circuit is crucial to the understanding of tactile sensory processing in cortex.

Synaptic depression is the decrease in efficacy of synaptic response with repeated stimulation. Based on short-term depression properties, synapses between layer IV excitatory neurons are either type 1 or type 2 [2]. Type 1 synapses show diminished response to a stimulus pulse only when neurotransmitter was released in response to the previous pulse (release-dependent depression). The rate at which the response is restored (recovery rate) is constant and independent of stimulation frequency. Type 2 synapses, on the other hand, depress even when no neurotransmitter was released in response to the previous pulse (release-independent depression). That is, they also depress in the event of a release failure. Recovery rate is dependent on stimulation frequency. Synapses stimulated at higher frequencies recover faster than those stimulated at lower frequencies.

Individually, type 1 synapses encode changes to stimulation frequency in their response. In contrast, type 2 synapses encode the stimulation frequency. The implications of type 1 and type 2 dynamics for information transmission through a single neuron are largely unexplored. Also unknown are the computational capabilities provided by these synapses to a network of neurons. There is therefore much scope for insights to be gained by exploring these problems using experimentally relevant computational models of type 1 and type 2 synapses.

As a starting point, we have investigated the impact of extending existing simulation results based on networks of neuron models [3], to include synapses of both types. The existing model consists of a network of 5000 recurrently connected integrate-and-fire model neurons. The network has 4000 excitatory neurons (to model pyramidal cortical neurons that produce excitatory AMPA currents) and 1000 inhibitory neurons (to model cortical interneurons that produce inhibitory GABA currents).

The local field potential (LFP) of this network is modelled in a simple way as proportional

to the sum of the excitatory currents in the network. Each neuron in the network receives a correlated input, which models inputs received from the thalamus. One of the key results of [3] was to show that if these input signals are modelled as a Poisson spike train with a certain time varying rate, $\nu(t) = \nu_o + \xi(t)$, where ν_o is a constant, and $\xi(t)$ is a noise process, then the power spectrum of the LFP increases with increasing ν_o in the gamma frequency range.

Based on this model for the LFP, we are undertaking a comparative study of how the power spectrum depends on the proportion of type 1 and type 2 synapses, with the aim of assessing the potential impact for information transmission in the network. In particular, the work of [3] suggests that two different neuronal communication channels convey independent information from the thalamus to cortex, and we aim to compare this result to the case where the two types of synapses are present.

Our preliminary results suggest that for the same inputs, introducing plastic synapses decreases the mean population spike rate of pyramidal neurons by about 25% while that of interneurons decreases by about 50%. Further, the network simulated with type 2 synapses exhibits a 10% decrease in the mean population spike rate of interneurons when compared to the network simulated with type 1 synapses. The mean spike rate of pyramidal neurons remains stable.

Mark D. McDonnell is the recipient of an Australian Research Council Australian Research Fellowship (project number DP1093425).

Keywords: short term plasticity, synaptic communication.

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An Information Theoretic Approach to Inferring the Optimal Number of Electrodes for Future Cochlear Implants

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ABSTRACT

Cochlear implants [1] can restore hearing when deafness has been caused by the loss of *inner hair cells* in the cochlea (inner ear). In a healthy ear, these cells transduce sounds into action potentials in fibres of the auditory nerve, which propagate to the brain where they are processed and perceived as sound. The purpose of a cochlear implant is to mimic the behavior of missing hair cells, via a microphone linked to an array of electrodes that are surgically implanted in the inner ear. Electrical current produced by the electrodes spreads through the inner ear, and evokes action potentials in the auditory nerve that the brain can learn to interpret as sounds.

An unresolved problem in the design of cochlear implants is that of how many electrodes achieves best hearing performance in patients. The limiting factor is that more electrodes mean that each would stimulate larger overlapping populations of fibres within the auditory nerve [1]. This problem is often referred to as 'current spread' [2].

It is efficient to avoid using more electrodes if doing so does not give a performance improvement. Whether an improvement can be gained by inclusion of more electrodes depends crucially on physical properties such as distance of the electrode array from the auditory nerve, and current spread. Future technologies may allow the electrode array to be placed closer to the nerve, which would allow smaller currents. Consequently, current spread would be reduced and more electrodes may be used to transmit more detailed sound information to the auditory nerve.

We have recently developed an information theoretic approach to determining the optimal number of electrodes, and their positions along the basilar membrane, for a simple one dimensional cochlea model, and linearly attenuated current spread [3]. This approach is based on the model of Figure 1; the optimal number of electrodes is the value M that maximizes the mutual information between the random variables X_e and Z. The information theoretic approach uses the assumption that spike generation is stochastic [2, 4], and the fact that most information transmission channels are optimized when only a finite number of symbols are used to represent information [5].

Here we extend this approach, which is based on the model of [2], to make use of more biologically realistic models of the complex three-dimensional geometry of the cochlea [6], as well as an improved model of stochastic action potential production in fibres of the auditory nerve developed in [4]. We also compare the results obtained when the cochlear implant is assumed to use bipolar stimulation, with that of monopolar stimulation.

Mark D. McDonnell is the recipient of an Australian Research Council Australian Research Fellowship (project number DP1093425).

Keywords: cochlear implants, information theory, biomedical prosthetic.

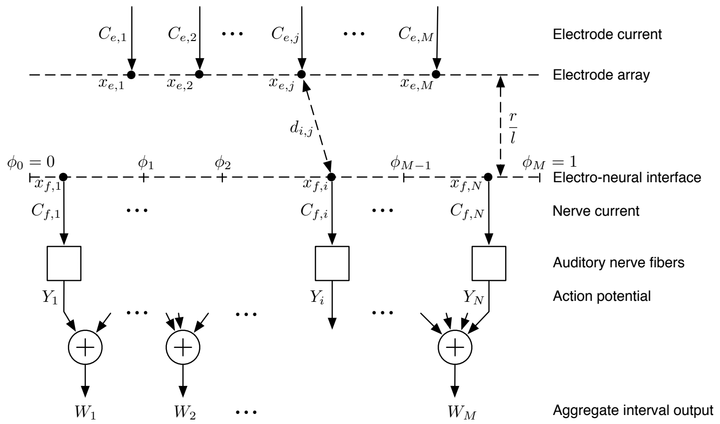

Figure 1: Geometry of our model and the variables associated with the conversion from electrode current to an output that is interpreted by the brain. The auditory input is modelled as the random variable, X_e, which maps to an electrode location with index j between 1 and M, and normalized electrode location $x_{\mathrm{e},j}$. This *single* electrode produces current $C_{\mathrm{e},j}$ Amps for every sample of X_e. After attenuation due to propagation of a normalized distance $d_{i,j}$, this current decreases to $C_{\mathrm{f},i}$ Amps at nerve fibre i, located at normalized location $x_{\mathrm{f},i}$, where $i = 1,..,N$. Whether a fibre produces an action potential or not is represented by the random variable Y_i. It is assumed that the brain has learnt to associate action potentials in fibre i with the electrode closest to that fibre; the set $\phi_0,..,\phi_M$ are the normalized locations of the boundaries of the intervals within which all fibres are associated with an electrode. The aggregate interval outputs, $W_1,..,W_M$ are random variables, the outcomes of which are the sum of the number of action potentials produced by fibres located within each interval. These determine the output Z, which is the index m for the W_m with the largest outcome, and which the brain must use to decide on which electrode location was stimulated. (*Figure adapted from [3])*

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The Multiple Time Scales of Spike After-Effects

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ABSTRACT

Most single neurons threshold models in the literature account for spike-frequency adaptation by means of a single exponential spike-triggered current. However, it is well known that, in real neurons adaptation occurs on multiple timescales [1], ranging from tens of milliseconds to seconds. Here, we use a Leaky Integrate-and-Fire model with escape noise [2] extended with two adaptive mechanisms: each time a spike is fired, both an adaptive current and a change in the threshold are triggered. Importantly, the functional shape of these two processes are not imposed a priori but are directly extracted from the data. We find that pyramidal neurons of the cortex have a moving threshold that last for 200 ms and a spike triggered adapting current that lasts for at least 20 seconds. Fast-Spiking and non-Fast-Spiking interneurons have less adapting current and no moving threshold. The shape of the spike after effect can determine alone the neuron class and it approaches a power-law in the case of the pyramidal neurons. Our model is able to predict up to 70% of the observed spikes with an accuracy of 2 ms and accurately predicts the firing-rate modulations on large timescales. These adaptation processes also influence the synaptic plasticity rules that maximize information transfer. The different types of spike after-effects may indicate that different cell types use a different coding strategy.

Keywords: Single-neuron models, spike-frequency adaptation, cell classes.

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Deterministic Bias in Spike-Train Similarity Measures Used for Fitting

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ABSTRACT

Multiple types of measures have been developed to measure the similarity between two spike trains. These were extensively used either to classify neuron responses according to stimuli or to validate mathematical models that predict spike times. Here we analyze the existing similarity measures in the light of trial-to-trial variability. Using only a small sets of spike trains it is often impossible to discriminate correctly between different generative processes [1]. We find that many existing similarity measures do not discriminate shifts in overall firing intensity or changes in the amount of jitter in the spike timing. We find that it is possible to modify some of the existing measures by taking into account the variance of the measure across spike trains from the same set. In so doing we remove a sample bias and we find that it is possible to discriminate generating processes for all the test cases studied. Finally, we demonstrate that such bias will always favour more deterministic models if similarity measures that do not remove the sample bias are used for validating mathematical models with respect to a small set of experimentally observed spike trains.

Keywords: Spike-Train Similarity Measures, Small-sample bias.

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Spike-Frequency-Adaptation Benefits Neural Population Coding

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ABSTRACT

The phenomenon of spike frequency adaptation (SFA) is observed in spiking neurons of various different systems [1] including pyramidal neurons in the neocortex. Here, we explore the effect of SFA on the signal-to-noise ratio of the population rate code. We use a novel theoretical approach to the ensemble activity of non-renewal point processes in order to derive general expression for the serial interval and second order count statistics of superimposed processes [2]. Applying this approach to a rate model that approximates a conductance-based I&F model [3] allows us to make predictions for ensembles of regular spiking neurons with SFA. Finally, we validate our model prediction of noise reduction in the population activity of SFA neurons in an ensemble of *in vivo* spike train recordings from rat cortical neurons.

Theoretical approach. We employ a master equation for general non-renewal processes to calculate the interval and count statistics of superimposed processes governed by a slow adaptation variable. To study SFA neurons we define an ensemble point process by the specific hazard function (rate model) given in [3], which incorporates an adaptation variable with an exponential decay time constant. This model was shown to approximate a more detailed neuron model including voltage dynamics and conductance-based synapses.

Negative serial interval correlations. Our rate model predicts negative serial correlation of the inter-spike intervals (ISIs) under stationary input conditions [3] in agreement with biophysical models of SFA neurons (e.g. [3,4]). Indeed, negative serial interval correlations have been repeatedly reported in the spontaneous activity of spiking neurons (for review see [5]). We show that this non-renewal property transfers to the superposition of k individual processes, i.e. the pooled population activity of an ensemble of SFA neurons exhibits negative serial correlations [2].

Regularization of the counting process. Next, we derived the variance of the spike count and the Fano factor (FF; variance divided by mean) for an observation interval of arbitrary length (Fig. 1, left). We show that the FF of the superimposed non-renewal process with negative serial correlations is smaller then the FF for the superimposed renewal process with identical marginal ISI distribution. Thus, the SFA mechanism at the single neuron level regularizes the counting process that describes the population activity of many SFA neurons [2]. We confirm this result in a small population of 5 cortical neurons which were recorded intracellular from the somatosensory cortex of the anesthetized rat. All neurons displayed regular spiking and exhibited short-lived negative serial interval correlations [6]. When we superimpose the spike trains of al 5 neurons we find the predicted result of a low FF when compared to the control where we randomly shuffled the order of the ISIs of each individual process before superposition in order to enforce renewalty (Fig. 1, right).

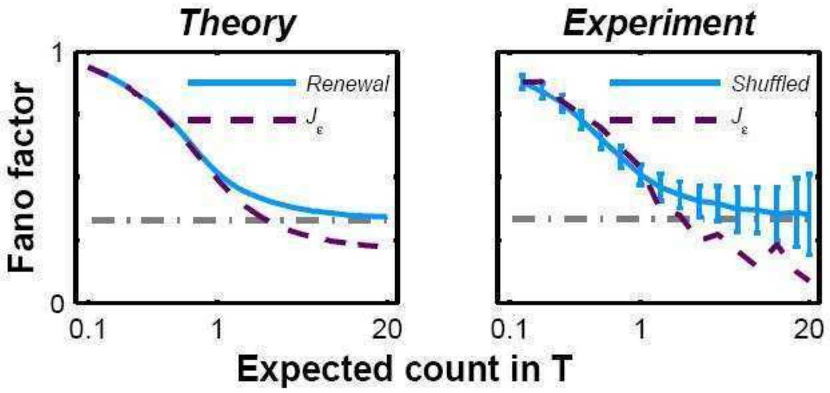

Figure 1: Adaptation reduces the Fano factor of the ensemble process. Left: Dashed line: Theoretical FF for arbitrary observation time normalized to unit mean interval. Solid line: FF for equivalent renewal ensemble process. Dash-dotted line: CV2. Right: Dashed: The estimated FF for the pooled spike trains of 5 cortical neurons. Solid: FF for the superposition of shuffled spike trains and standard deviation across 100 repeated shufflings.

Implications for neural coding and decoding. The reduction of the count variance in the population activity of SFA neurons effectively reduces the noise of a population rate code, a result that was previously established for at the single neuron level (e.g. [7,5,6]). If we take the perspective of a postsynaptic decoder, we may consider the neuronal population activity which provides the converging input to a receiver neuron. By using the Kulback-Leibler-Divergence (KLD) between two states of input characterized by a small change in the population rate, we show that the KLD is larger for an ensemble of adapting presynaptic neurons than for an ensemble of non-adapting neurons, resulting in a gain of information [2].

Our results provide a novel interpretation of the neural population code where an improved signal-to-noise ratio at the population level emerges from the neuron-intrinsic property of SFA. This is in contrast to prevailing models of population coding that assume Poisson statistics for the superimposed neural ensemble activity. At the level of the post-synaptic receiver, the regularization of the ensemble process improves the discrimination of different input rates.

Keywords: rate coding, non-renewal point process, Fano factor

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Spontaneous Oscillations, Information Transmission and Signal Detection in Ampullary Electroreceptors

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ABSTRACT

Peripheral ampullary electroreceptors of some freshwater fish exhibit spontaneous oscillations in their sensory epithelium. At the same time, primary electroreceptor afferents are characterized by the background tonic spiking, adapting to external thermal and electrical stimuli. The existence of two distinct coupled oscillators in the electroreceptor system results in a biperiodic firing of primary afferents [1], characterized by long-lasting serial correlations of interspike intervals [2]. Using modeling we explore the functional significance of biperiodic organization of electroreceptors in enhancement of information transmission and detection of external electrical signals. We show that the coherent oscillations may lead to significant enhancement of information transfer and to enhanced discriminability of weak signals [3, 4]. Theoretical predictions are supported by an analysis of experimental recording from the paddlefish electroreceptors.

Keywords: Electroreceptors, Oscillations, Serial correlations, Information rate.

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Information-Optimal Neural Coding in Poisson Neurons

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ABSTRACT

The firing rate of afferent neurons is limited. Also, the time available for decoding the message in the brain is limited. We obtain the optimal tuning function for a population of the Poisson neurons by maximizing the Shannon mutual information and investigate how optimal coding changes with the time available for decoding. We prove that the information-optimal tuning function is discrete [1].

In other words, we prove that the optimal tuning function has a multi-step form and the number of steps depends on the decoding time. The number of discrete steps undergoes a hierarchy of phase transitions from mono-population coding, for small decoding time, toward multi-population coding with two, three more subpopulations for larger decoding times. We postulate that the presence of subpopulations with specific neural characteristics, such as the threshold to stimulus, could be a signature of an optimal coding strategy and we use the mammalian auditory system as an example.

Keywords: Optimal neural coding, Poisson neuron, Phase transitions.

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Estimation of Functional Connections in the Premotor Center of an Insect Brain

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ABSTRACT

An approach is reported to estimate the functional connection from the possible anatomical connections and physiological response of each neuron. Here we focus on the brain of *Bombyx mori*, a male silkmoth, which exhibits a programmed behavior for the pheromone orientation on a pheromone detection[1]. The neuroethological experiments revealed that the motor command is generated in the premotor center, composed of the lateral accessory lobe (LAL) and the ventral protocerebrum (VPC). The morphology and the physiological response to the pheromone stimulus are obtained for each main type of LAL-VPC neuron through the intensive electrophysiological and immunohistochemical experiments[2]. However, how the motor command is generated in LAL-VPC, or the information pathway in the network, is still unknown. That is, each piece of puzzle is fairly well investigated, though they are not yet fit in to reveal the whole picture. The goal of our study is to investigate the functional connection in LAL-VPC to elucidate the mechanism of the motor command generation for the programmed behavior.

The present approach is to consider an artificial three-layered neural network (Fig.1) based on the experimental findings of LAL-VPC neuron[3] (Fig.2). Each input/output unit corresponds to one type of neuron. Each connection corresponds to input/output terminal of a neuron. And each hidden unit corresponds to a neuropile region, where LAL-VPC neurons connect each other. To describe the discrete time dynamics of LAL-VPC, input unit expresses a neuron state at time t, while corresponding output unit expresses its state at t+1. Input/output signals are given by the physiology data of each neuron[2]. Then, back-propagation (BP) algorithm is used to obtain the connection weight, which corresponds to the functional connection strength to generate the LAL-VPC dynamics.

The network has 86 units for input/output layers, 10 hidden units, and 189 connections based on the experimental data. Among 2,000 BP trials, about 10% attained the error below a certain threshold, converging to the close connection vectors. 61 connections are zero, that is, one third of the anatomically observed connections are not used. Several main connections correspond to each physiological type. Two neurons fail to reproduce the observed physiology, for which missing connections are predicted. An extended framework using more extensive data followed by a simulation is now undergoing, to reveal the dynamics in LAL-VPC by integrating the multi-level neuron data.

Keywords: Functional connection, Insect brain, Premotor center.

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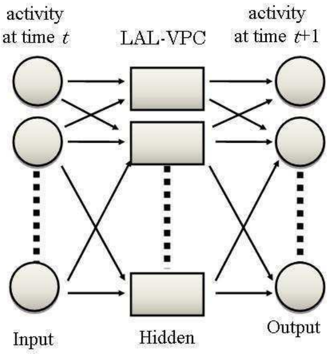

Figure 1: Three-layered neural network

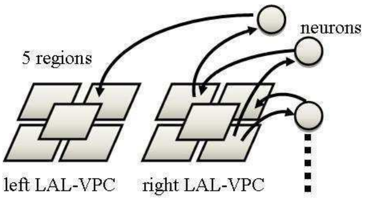

Figure 2: 5 neuropile regions in LAL-VPC

Neural Coding in Graphs of BAMs

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ABSTRACT

In the last years we have developed large neural network models for the realization of complex cognitive tasks in a neural network architecture that resembles the network of the cerebral cortex (e.g. [1]). We have used networks of several $(10-40)$ cortical modules that may correspond to cortical hypercolumns, but contain only two populations of neurons (one excitatory, one inhibitory) with several hundred up to about two thousand neurons per module (a real cortical hypercolumn has in the order of 10^5 neurons [2, 3]). The excitatory populations in these so-called 'cortical networks' are organized as a graph of Bidirectional Associative Memories (BAMs, [4]), where edges of the graph correspond to BAMs connecting two neural populations or modules and nodes of the graph correspond to excitatory populations with associative feedback connections (and inhibitory interneurons).

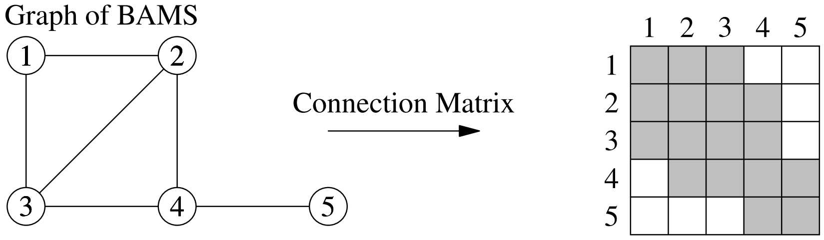

Figure 1: The right part shows the block matrix structure of the cortical connections corresponding to the graph on the left. Each block corresponds to one module, the diagonal represents local intracortical connections, the off-diagonal cortico-cortical long range connections ([2]).

The neural code in each of these modules consists essentially of the firing pattern of the excitatory population, where mainly it is the subset of active neurons that codes the contents to be represented, but also temporal aspects play a role, like the temporal order in which subgroups of the population are activated and the degree of synchronicity within activated subgroups.

These features can be used to distinguish different properties of the patterns that are presented which we need to distinguish and control when performing complex tasks like language understanding with these cortical networks. The most important pattern properties or situations are:

- exactly fitting/matching input pattern
- incomplete information or partially matching pattern
- superposition of several patterns

- conflicting information
- new information (to be learned)
- unimportant random patterns.

In the talk we want to discuss how to distinguish these situations based on the internal activation pattern of the module.

Keywords: bi-directional associative memory; cortical module; large scale simulations; cell assemblies; neural patterns

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Multiple Spike Trains Observed in a Short-Time Window

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ABSTRACT

Information obtained in experiments in which the spikes are recorded, usually from a single neuron or from quite limited number of them, is fundamentally different from that which a neuron receives from the network of interconnected neurons. In the experiments, a spike train is recorded for a relatively long period of time and the properties of the firing are deduced. If the type of the investigated firing is transient, like in the stimulated activity, then the extensive length of the record is replaced by repetitions assuming that these are identical and independent copies of the same phenomenon. In natural conditions, neuron receives a large number of spike trains, up to several thousands, and the information has to be deduced in short-time intervals. This creates a discrepancy between what can be read from the experiments and how real neurons perform.

To estimate the firing frequency in the parallel neuronal data is rather simple task even if the time window available for the observation is very short. In our recent paper [1] we showed how to estimate the coefficient of variation of interspike intervals under the scenario with the short-time window. The aim of the present contribution is to introduce and compare several nonparametric methods for estimation of the cumulative distribution function of the interspike intervals under the same restriction posed on the observation.

Keywords: interspike interval, statistical inference, parallel processing

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Individual Firing Frequencies Estimated From Superimposed Spike Trains

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ABSTRACT

When analyzing the pooled record of several independent spike trains with silent (refractory) period, one can identify specific groups of the spikes appearing in time intervals shorter than the silent period (these are usually called doublets, triplets, . . . , see Figure 1). We show how the firing frequencies (intensities) of individual spike trains are related to the relative frequencies of occurence of these groups of spikes in the superimposed spike train. The derived analytical expression allows the estimation of the intensities of individual records from the knowledge of the pooled record. In [3], this problem was solved for two independent spike trains and the result is generalized for any number of independent records here. The task is analogous to the problem of coincidence detection, [1, 2].

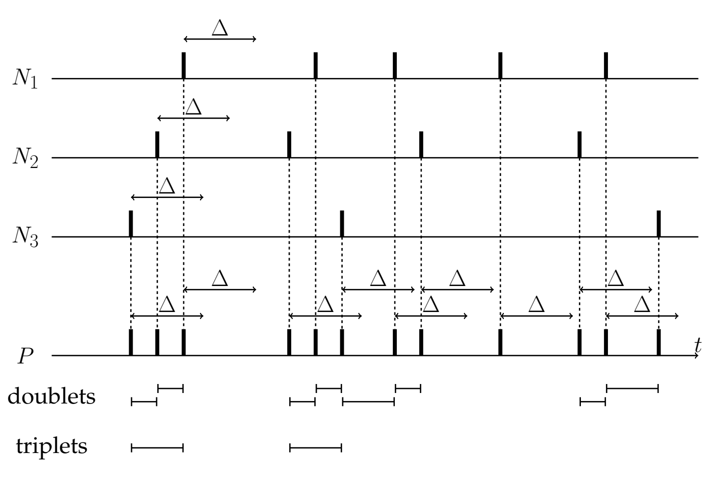

Figure 1: A schematic example of three spike trains N_1, N_2, N_3 with the same silent period Δ. The pooled record is denoted by P. During the depicted time interval 12 spikes, 8 doublets and 2 triplets are observed. The doublets and the triplets in P are highlighted at the bottom.

Keywords: firing frequences estimation, spike train, superposition.

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Using Classical Ablations and Modern Molecular Biology to Study Neural Codes

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ABSTRACT

To connect neuronal activity to function, there must be means to carry out interventions. Even though an old and seemingly heavy-handed technique, selective ablations remain the shoulders on which we interpret the role of neuronal activity in behavior. The importance of this technique is illustrated by finding across several examples in which neuronal activity has not predicted the outcome of selective ablations of the tissue under investigations. Molecular biology offers many means to carry out much more subtle and targeted interventions. We have made substantial progress in developing these tools for use in awake monkey experiments, with targeting selective brain regions, neuronal types and projection patterns. These tools should open up a whole new world for interpreting the connection between neuronal activity and behavior.

The Encoding of Information by Neurons in the Temporal Visual Cortical Areas, the Hippocampus, and the Orbitofrontal Cortex

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ABSTRACT

In the inferior temporal visual cortex (IT) most of the information about the stimulus presented is available in the number of spikes emitted by single neurons in a fixed time period, the firing rate. Most of the rate information is available in short periods, e.g. 20-40 ms of neuronal firing, with the timing of spikes within a response carrying little information [1].

Across a population of neurons, the firing rate information provided by each neuron tends to be independent; that is, the information increases approximately linearly with the number of neurons [1]. An implication of the independence is that the response profiles to a set of stimuli of different neurons are uncorrelated, and weak ergodicity applies [2].

The information in the firing rate across a population of neurons can be read moderately efficiently by a decoding procedure as simple as a dot product. This is the simplest type of processing that might be performed by a neuron, as it involves taking a dot product of the incoming firing rates with the receiving synaptic weights to obtain the activation of the neuron. This type of information encoding ensures that the simple emergent properties of associative neuronal networks such as generalization, completion, and graceful degradation can be realized naturally and simply [1].

There is little additional information to the great deal available in the firing rates from any stimulus-dependent cross-correlations or synchronization that may be present, even during top-down attentional search (¡ 5% of the total) [3]. Stimulus-dependent synchronization might in any case only be useful for grouping different neuronal populations, and would not easily provide a solution to the binding problem in vision. Instead, the binding problem in vision may be solved by the presence of neurons that respond to combinations of features in a given spatial position with respect to each other [1].

The neuronal firing rate probability distribution is exponential or gamma, with relatively distributed representations in perceptual systems such as IT and the taste and olfactory cortical systems ($a = 0.7$), with more sparse representations in memory systems such as the hippocampus ($a = 0.3$) in line with the need to increase memory capacity [1]. (The sparseness $a = (3_{i=1,S} r_i/S)^2 / 3_{i=1,S}(ri^2/S)$ where r_i is the firing rate of the neuron to stimulus i in the set of S stimuli.)

Decoding of the information available from multiple voxels with fMRI indicates great redundancy consistent with the signal reflecting the average of tens of thousands of neurons [4]. More information is encoded by single neurons, which is the level at which the information is exchanged between the computing elements of the brain, the neurons, and the level at which information must be encoded.

The noise in the brain caused by the approximately Poisson nature of neuronal firing for a given mean rate is greater with graded as compared with uniform firing rate distributions in integrate-

and-fire attractor network models of decision-making and memory recall [5]. The implication is that the beneficial effects of noise in the brain [6] extend up to realistically large cortical neuronal networks. Interestingly, the networks show a decrease in the Fano factor of 1 during spontaneous activity to a value of 0.5 after the network has entered a stimulus-driven decision states, and the Fano factor smaller as the difference $\Delta\lambda$ in the two inputs to the decision-making process increases [5].

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Stimulus Coding by Populations of First- and Second-Order Olfactory Neurons

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ABSTRACT

The mechanisms by which odor stimuli are received and transduced in the first-order olfactory neurons (ORNs) and how they are processed in the second-order neurons (mitral/tufted cells) of the olfactory bulb (OB) have been intensively studied during the last two decades [1, 2, 8]. However, much less is known on the global properties of the signals that the whole population of ORN delivers to the OB and how they are transformed by the population of mitral cells of the OB. In the framework of our continuing research on intensity coding in the olfactory system [6, 7], we have examined population coding of odor intensity in the first two neuron layers of the olfactory system.

Spiking activities of neurons were recorded with extracellular electrodes from the olfactory epithelium and bulb of frog *Rana ridibunda*. Three neuron populations were studied: (1) ORNs of the ventral olfactory epithelium; (2) mitral/tufted cells normally connected to the ventral and dorsal olfactory epithelia; (3) mitral cells connected only to the ventral epithelium after sectioning the dorsal epithelium. Four different odorants at various concentrations were applied as square pulses lasting for 2 seconds.

We estimated the time-varying firing rate by convoluting the spike trains with a Gaussian function (kernel) centered on each spike. The only free parameter in the method is the width of the kernel. We applied this method to our three populations. Instead of analyzing separately the time-varying rates of each spike train we summated them over several records in order to describe the collective behavior of diverse neuron populations defined anatomically (first- and second-order neurons) or functionally by their responses to a certain concentration or a given odorant.

Two main questions were addressed in the present study: (1) How do the firing rates of the first- or second-order neuron populations evolve in time after a stimulus of fixed duration? (2) How does the number of spikes fired by a neuron population depend on the odorant dose?

We report two key findings. (1) The rate functions of the three populations present clear distinguishing features. First, the second-order neurons are intrinsically less active (in spikes/s) than the first-order neurons on the same odorant concentration range. Second, the falling phase which follows the initial peak is symmetrical to the rising phase in first-order neurons for all odorants but asymmetrical in second-order neurons, either because of a long lasting excitation or a pronounced inhibition. (2) The firing activity of a neuron population, whether first- or second-order, is independent of the odorant concentration. This means that the total number of action potentials fired by a neuron in response to any concentration of an odorant is constant. This is in apparent contradiction with the concentration-dependent responses. The significance of these results, especially the surprising second one, will be discussed in the framework of population coding [1, 5] and energy demands [3, 4].

Keywords: firing frequency, spiking activity, population coding.

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On the Dependencies Between Spiking Times of a Couple of Neurons

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ABSTRACT

In the classical coding schema a neuron codes information in its spiking times. Information is transmitted from a neuron to the others through dendritic connections, and spiking times of a neuron is influenced by the activity of the neurons belonging to its network. Hence in order to study the information transmission it becomes necessary to develop models devoted to describe the joint behavior of two or more neurons. In this frame the development of models able to reproduce dependencies between the spike trains of neurons coupled according different laws is an important goal. Unfortunately the available mathematical methods are insufficient for this main purpose. Hence it seems necessary to start from simplified instances, such as the study of the dependencies between the times until the first spike of two neurons. After developing the necessary mathematical support for this problem, one can hope to become able to pursue the mathematical study considering the coupling of spike trains. In this work we limit our study to the dependencies between the times until the first spike for two neurons coupled according different laws. Extension to a larger number of neurons is immediate but implies more complex notation, hence we avoid it. On the contrary the switch from the coupling of the time until the first spike, to the coupling of ISIs presents further mathematical difficulties that are not yet solved but will be illustrated here.

Interspike intervals of a single neuron are often regarded as coming from a stochastic leaky integrate and fire model and their study corresponds to the study of the first passage time of a stochastic process, generally the Ornstein-Uhlenbeck one, through a boundary. Here we model the membrane potential evolution of the two neurons through a jump diffusion process where the jumps time of one neuron determine a jump in the membrane potential of the connected neuron. Other studies already exist on this model but here we focus on the study of the dependencies between the spike times of the two neurons. We develop a numerical method to determine the joint distribution of these first passage time that allows the study of their copula in some exemplificative instances.

Keywords: Spiking times, Dependencies, Leaky Integrate and Fire model

Dependencies Between Spike Times of a Couple of Neurons Modeled via a Two-Dimensional LIF Model

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ABSTRACT

There exists a large literature on the Stein's model (cf. [4], [2]). However, the largest part of these studies performs a diffusion limit on Stein's equation to get a mathematically tractable stochastic process. Use of these continuous processes has allowed the discovery of various neuronal features that are hidden in the original Stein's model, for instance the stochastic resonance.

In this work, we consider a diffusion limit (cf. [1]) of two or more neuronal dynamics governed by Stein's model to describe dependencies between their spike times. For this reason, we separate the PSPs impinging on each neuron into two groups, one with the PSPs coming from a common network and the other one with those typical of the specific neuron. In the case of two neurons, the Stein's equations are:

$$dX_1(t) = -\int_0^t \frac{X_1(s)}{\theta} ds + \delta_1 a dN(t) + a dM_1^+(t) + i dM_1^-(t) \tag{1}$$

$$dX_2(t) = -\int_0^t \frac{X_2(s)}{\theta} ds + \delta_2 a dN(t) + a dM_2^+(t) + i dM_2^-(t), \tag{2}$$

where $\theta > 0, a > 0, i < 0, \delta_1 = \pm 1, \delta_2 = \pm 1$ and $N(t), M_j^+(t), M_j^-(t)$ are independent Poisson processes with parameters, respectively, $\alpha t, \lambda_j t, \omega_j t$ for $j = 1, 2$. Here M_j^+ and M_j^- count the PSPs impinging on neuron j while N counts those common to the two neurons. Note that the values of δ_1 and δ_2 determine positive and/or negative common jumps on neurons and thus different association properties can be modeled by this model.

We study the diffusion limit of equations (1) and (2), superimposing a common threshold S and we describe the interspike intervals as first passage times of the bidimensional diffusion processes through the boundary. The introduced dependency between the two Stein's processes is maintained in the diffusion limit. Hence, the Brownian increment of the resulting two dimensional diffusion has a covariance matrix Σ with elements different from zero on both diagonals. More precisely, we obtain:

$$\Sigma = \begin{pmatrix} \sigma_1^2 + \sigma_C^2 & \delta_1 \delta_2 \sigma_C^2 \\ \delta_1 \delta_2 \sigma_C^2 & \sigma_2^2 + \sigma_C^2 \end{pmatrix}$$

where σ_1^2 and σ_2^2 are coefficients depending on the specific inputs on neurons 1 and 2 respectively, and $\delta_1 \delta_2 \sigma_C^2$ is the covariance between the two neurons, depending only on the common input.

Note that all these constants are related to those of the Stein's equations.
The aim of this work is to relate the introduced dependencies on the processes with those obtained on the spike times of the two neurons, through their joint law. We refer to [3] for some preliminary results obtained with a different approach to couple the neurons.

Some examples are given to illustrate different joint behaviors, both in the case of positive and negative dependencies.

Keywords: First passage times, Diffusion limits, Stein's model.

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Sound Encoding in the Auditory Pathway: Auditory Brainstem and Beyond

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ABSTRACT

Background

Auditory brainstem calculates horizontal direction (azimuth) of sound from the ITD (interaural time delay). Two theories exist about how brainstem circuit calculates the azimuth from the ITD. Jeffress [3] proposed in 1948 that azimuth is computed by an array of delay lines. The anatomical existence of such array in mammals is still under debate [2, 4]. Our group in 2005 explored the possibility of the stochastic algorithm [6]. We demonstrated that in cochlear implantees is azimuth detected same way as in normal hearing subjects [1].

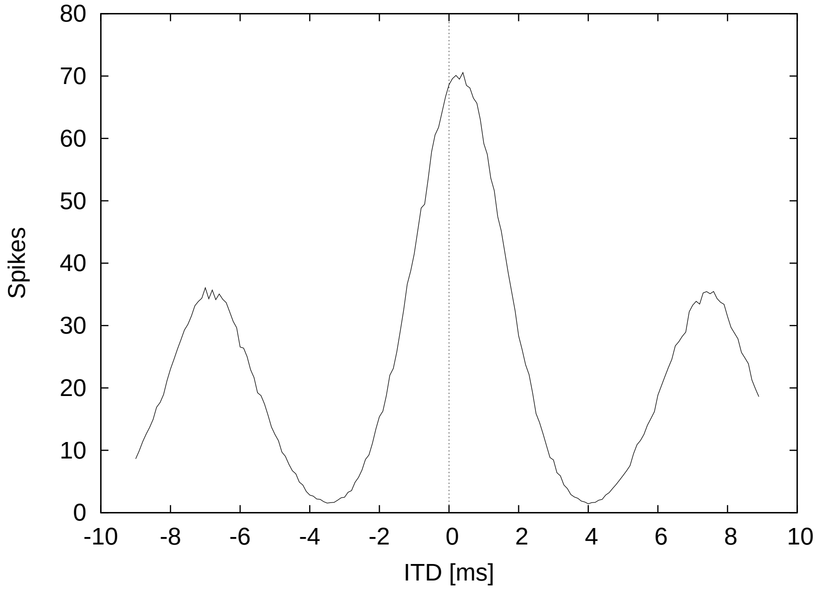

Figure 1: **Correlation model suits well to neurons as coincidence detectors.** Model using coincidence detection has properties of autocorrelation function. Side peaks are lower and the highest peak is offset in the full model of excitation together with inhibition. This is a numerical simulation of neural response to alternating stimulus. x-axis shows the ITD and on the y-axis are spikes.

Model and Results

We use the simplest yes-or-no neuronal model. The computation of output quantities is based on the stochastic processing. For simplicity of the model, we use the ergodic assumption that averaging over the population of neurons and averaging over several time periods yield same outputs. In the presentation we will explain where and how we violate this assumption. Our

approach makes possible to compare conditions with different stimulation protocols. For illustration we show in Figure 1 neural response to alternating stimuli. We model these stimuli in accordance with the experiments of Laback and Majdak [5]. In Figure 2 we use the stimulus corresponding to continuous pure tone stimulation.abstract

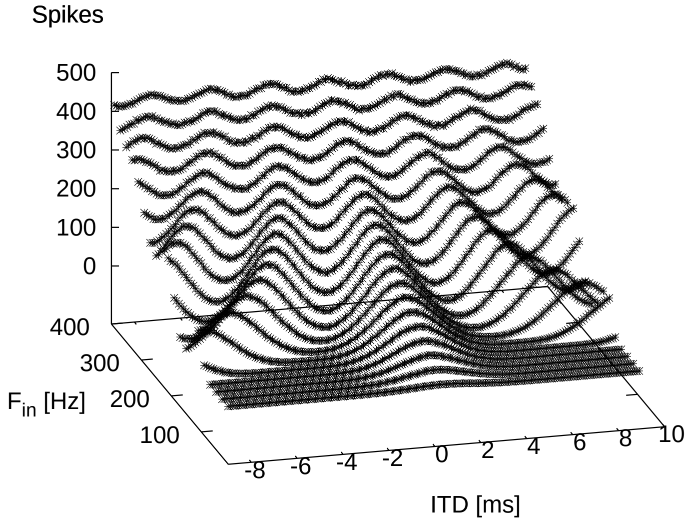

Figure 2: **Towards higher sound frequencies, the response range gets lower.** Axes description: the x-axis shows varying ITD, on the y-axis characteristic frequency is changed and the z-axis shows output spikes. The difference, why previous figure has one maximum and this figure shows series of periodic functions is in the envelope structure of the stimulus (alternating versus continuous).

Conclusion

Our results are useful in explaining some recent puzzling observations on the binaural cochlear implantees [5].

Keywords: Coincidence detection, directional hearing, interaural time delay, stochastic neuronal model, cochlear implants.

Acknowledgments: This work was supported by two projects MSM 0021620806 and MSM 6840770012 by the Ministry of Education of the Czech Republic.

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Waves in Potassium Driven Neuronal Media

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ABSTRACT

We consider a slowly varying extracellular concentration of potassium ions around excitable neurons. It opens a specific chemical pathway for neurons to interact. It can significantly influence the behavior of single neurons and that of large ensembles. The released chemical agent diffuses in the external medium and lowers thresholds of individual excitable units creating a kind of adaptive environment.

We address this problem by studying simplified excitable units given by a modified FitzHugh-Nagumo dynamics [1]. In our model the neurons interact only chemically via the released and diffusing potassium in the surrounding non-active medium and are permanently affected by noise which models the remaining activity at the low time scale.

First we study the dynamics of a single excitable unit embedded in the extracellular matter. That leads to a number of noise-induced effects, like self-modulation of firing rate in an individual neuron. After the consideration of two coupled neurons we consider the spatially extended situation. By holding parameters of the neuron fixed various patterns appear ranging from spirals and traveling waves to oscillons and inverted structures depending on the parameters of the medium. Also stochastic pacemakers at boundaries are found and discussed.

In the last part we reduce the dynamics to a stochastic two state description charecterized by waiting time density for rest and activated states of the neurons [2]. The effect of the environment characterized by the time depemdemt external potassium density leads to memory effect in the transition rates of the neurons. We discuss methods allowing a quialitative discussion of the reduced model.

Keywords: Excitable media, Noise induced temprary and spatial structures, Delay in Non Markovian Dynamics.

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Layer-Specific Modification of Spontaneous Cortical State Dynamics by Sensory Stimulation

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ABSTRACT

Until recently, spontaneous neocortical activity was thought to reflect only stochastic network fluctuations and internal noise sources. Emerging evidence, however, has suggested that the spontaneous dynamics of neural activity can be modulated and/or engaged by sensory stimulation. For instance, spontaneous population activity may contain traces of recent sensory experience [1,2], leading to the conjecture that spontaneous spatiotemporal neural dynamics may be shaped by sensory inputs. Using the mouse barrel cortex as a model, we asked whether naturalistic sensory stimulation can induce specific long-term changes in spontaneous cortical state dynamics. Adult mice were anaesthetized with a combination of light urethane and either Hypnorm/Hypnovel or Chlorprothixene, and a multi-electrode array (Neuronexus Technologies) was inserted into the whisker barrel cortex. Individual neurons were isolated from either superficial or deep cortical layers by spike-sorting based on a tetrode configuration of electrode sites, and monitored during periods of spontaneous and sensory-evoked activity. In some experiments, a linear array spanning the depth of the cortex was used to examine multi-unit activity in all layers. Whiskers were trimmed, and wide-field sensory stimulation was applied to the mystacial vibrissae with sandpaper. We observed that a stimulation pattern applied at 10 Hz with a cycle approximating the mouse whisking pattern resulted in a statistically significant increase in deep layer spontaneous single-unit activity, whereas superficial layer spontaneous activity was slightly decreased. These changes lasted for at least several minutes. The result was also apparent, although not as strong, in the multi-unit activity. We then used subspace projection approaches including principal component analysis and multi-dimensional scaling to analyse the effect of sensory stimulation on the spatiotemporal pattern of spontaneous activity. We found that sensory stimulation induces long-term changes in the trajectory followed by the subsequent spontaneous activity. Details of this change were dependent upon the cortical layer in which the neuronal ensemble laid. We conclude that sensory stimulation induces long-term plasticity in spontaneous cortical network state dynamics, and speculate that this might relate to mechanisms underlying distributed neocortical storage and/or reconsolidation of sensory "memories".

Keywords: spontaneous activity, cortical oscillations, sensory coding

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Neural Coding of Natural Vestibular Signals

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ABSTRACT

Despite a rather long history in vestibular physiology, the neural coding of vestibular signals at the cortical level is poorly understood. While many cortical areas show responses to vestibular stimulation, no "primary vestibular cortex" has been identified. Instead, the vestibular signals seem to be intermixed with signals from other modalities in multi-sensory areas responsive to, for example, vestibular and visual stimuli. Neural coding theories should explain such responses, not only in a qualitative manner, but also quantitatively.

Extending previous work about the statistics of natural vestibular stimuli [1], here we measure the stimulation of the human vestibular system in various natural conditions using motion capture technology, we describe these signals in terms of statistical properties, and we derive predictions for the neuronal representation of these signals by applying different theories. More specifically, we predict the layout of a hypothetical topographic vestibular map using Kohonen's self organizing map applied to the measured angular and linear accelerations of the head with 1) Euclidean and spherical distance measures between the map representations and the sensory signals, and 2) a distance measure derived from the Information Bottleneck Method [2], where the distance between map representations and the sensory signals is quantified in term of how informative the signals are about another latent variable of interest. In our case this is the tilt of the head relative to the gravity vector, which is behaviourally highly relevant, but due to the ambiguity of the otholitic responses between linear acceleration and tilt relative to gravity cannot be assessed directly.

We find marked differences between the two predicted representations in terms of how much of the limited representational resources are allocated to represent the measured linear and angular accelerations. For example, while in the first case the resulting map approximates the statistics of the sensed accelerations, the second map overemphasizes those accelerations, which are particularly informative about the head tilt. Finally, in a more speculative part, we briefly discuss our predictions in the context of differences in motion behaviour of elderly people. Here we are specifically interested in the impact of cognitive impairment on motion behavior and postural control, as they may be partly related to dysfunctions in vestibular processing and navigation. This research is based on a study with twenty subjects suffering from Alzheimer's disease (mild and medium severity), age 6580, whose long-term motion behaviour (duration up to 50 hours) is being recorded using accelerometric motion-capture technology [3].

Keywords: efficient coding, information bottleneck, self-organizing map, motion capture

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Effect of Feedback Projections Between Networks in Evolvable Hierarchically Organized Neural Circuits

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ABSTRACT

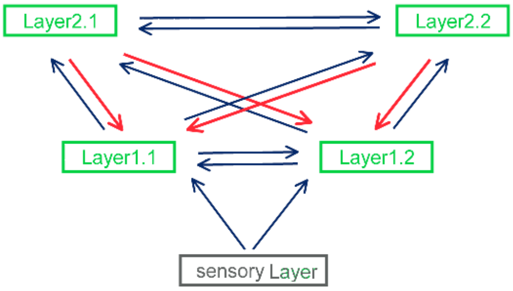

Figure 1: Thick red lines emphasize the feedback projections added to circuit FB.

In the present study we simulate the activity of a neural circuit undergoing developmental phases. The neural circuit is characterized by two layers of of feed-forward networks and we study the emergent properties of stimulus coding in presence of feedback projections between the layers of networks. In previous studies [1, 2] we have shown that the presence of feedback connections increase the complexity of spatio-temporal firing patterns. We use a simulation framework that allows us to combine several neural networks of biologically inspired spiking neurons into a neural circuit connected following a hierarchical organization, that can be static or changing over time, in addition to spike-timing dependent plasticity (STDP). In addition to spike trains we record neuromimetic signals, called Electrochipograms (EChG), similar to electro-corticograms (ECoG) and local field potentials (LFP) by the means of realistic virtual electrodes [3, 4]. Our simulation framework introduces also genetic features such that model parameters are coded in its genome and mimic brain evolution by the implementation of brain reproduction with certain probabilities of mutation in the selected genes belonging to the genome of the parent brain. We studied a layered hierarchical circuit, labeled FF circuit, with one sensory network stimulated by an external stimulus projecting to a two layered circuit with feedforward and horizontal connectivity between the neural networks that project to a “motor” network. The addition of feedback projections between the neural networks defined the FB circuit (Fig. 1). The whole circuit is formeed by 33,750 cells (six 2D toroidal networks of 75x75 cells), each neural network featuring apoptosis, STDP and synaptic pruning processes ([5, 6]). The external stimulus is a complex pattern which is applied for 500 ms followed by 1000 ms without stimulation. For both circuits, FF and FB, we have simulated 9 generations of “brains” with variations only in the genetic code responsible for the pattern of neuronal interconnectivity and programmed cell death. The aim is to determine invariant salient features that are likely to be unrelated to a particular genome but to the presence or absence of feedback projections. The rationale is that STDP embedded in the neural network models drives the build-up of auto-associative network links within each network. The spike train activity as well as EChGs (one EChG per network, then 6 channels EChG per circuit), characterized by virtual electrodes sampling an area of 900 cells (i.e. 16% of all cells), were recorded in our experiments. Among various time and frequency domain analyses that we perform with these signals we emphasize here the evoked potentials (EvP). At first, for each network with any genome, we compute the EvP as the difference between the EChGs evoked by the stimulus and the corresponding EChGs obtained with the same random seeds but

in presence only of background noise. Then, we compute the average of EvP over the 9 genomes, labeled EvP$_{Lx.y}$, e.g. EvP$_{L1.2}$ for the network 2 of Layer 1 (Fig. 1). Then, for each network, we compute the difference between EvP$_{Lx.y}$ for FB and FF circuits, labeled EvP$_{Lx.y}$*diff*. The last step consists in averaging the differences across networks located in the same layer such to get the potential EvP$_{Lx}$*diff* for layer x. Figure 2 shows a strong phasic onset response in both layers, thus suggesting the invariance of this response pattern depending only on the presence of feedback projections. Notice a significant late response appearing only in layer 2 after 400 ms from stimulus onset. We will present further results that illustrate several characteristics in neural coding that are determined by the presence of feedback connections.

Keywords: spiking neural network, gene regulatory network, computational biology.

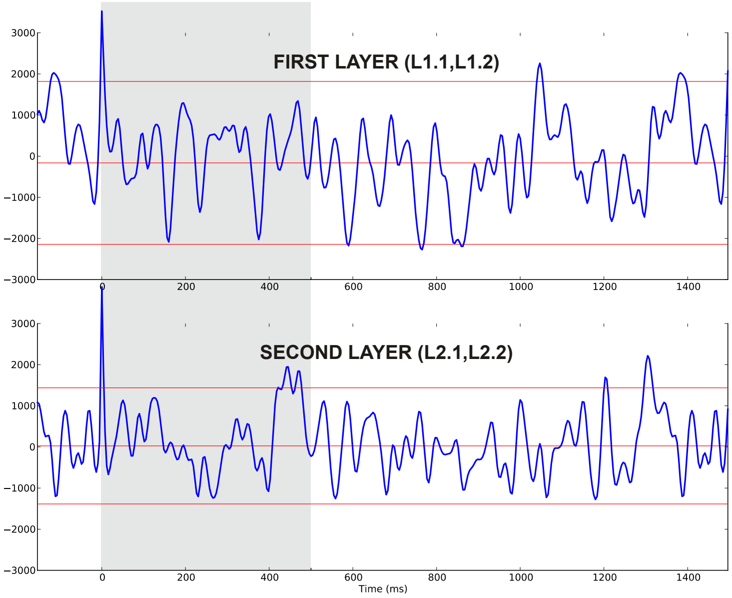

Figure 2: Averaged differential Evoked Potentials for the networks of layer 1 (upper panel) and the networks of layer 2 (lower panel) obtained by subtracting the EvP of circuit FF to the EvP of circuit FB. The grey area correspond to the stimulus delivery.

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Defining the Firing Rate for a Non-Poissonian Spike Train

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ABSTRACT

A rationale for estimating the neuronal firing rate in the neurophysiology lies in the presumption that neurons may express information in the frequency of spike occurrences. Since precise spike times are generally not reproduced by the same behavioral stimulus, neuronal spike firing has often been approximated by the inhomogeneous Poisson process in which spikes are derived independently from an instantaneous rate of firing. From real spike trains recorded in vivo, we further abstracted the deviation from ideal Poisson firing by measuring the local variation of inter-spike intervals, and revealed that a non-Poisson firing characteristic that may be called as regular or bursty is rather prevalent among cortical neurons and is stably correlated to the physiological functions of the cortical areas [5,6]. Two hypotheses have been proposed for potential advantage of using non-Poisson spike trains in transmitting information, namely, the sender may signal the firing irregularity by changing it in addition to the rate of firing [3], or alternatively, the receiver may estimate the firing rate accurately by making the most of non-Poisson inter-spike dependency in the received signals [1,2,4]. Here I take up the latter issue as a general problem of defining the firing rate for non-Poissonian spike trains.

Keywords: Firing patterns, Rate estimation.

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Quantifying Neural Encoding of Event Timing

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ABSTRACT

Single-neuron firing is often analyzed relative to an external event, such as successful task performance or the delivery of a stimulus. The perievent time histogram [1] (PETH) is generated by binning and counting the spikes across the repeated presentations of the stimulus. This allows examination how, on average, neural firing modulates before and after the alignment event.

However, the PETH contains no information about the single-trial reliability of the neural response, which is important from the perspective of a target neuron. Neurones can and do vary their responses from trial to trial and this variability can occur along several different dimensions such as the onset latency, duration and amplitude of the response. This variability will have an impact on what a downstream neuron can extract regarding *when* an event occurred.

We propose the concept of using the neural activity to predict the timing of the occurrence of an event, as opposed to using the event to predict the neural response [2]. We first estimate the likelihood of an observed spike train, under the assumption that it was generated by an inhomogeneous gamma process with rate profile similar to the PETH shifted by a small time. This is used to generate a probability distribution of the event occurrence, using Bayes' rule. By an information theoretic approach, this method yields a single value (in bits) that quantifies the reduction in uncertainty regarding the time of an external event following observation of the spike train.

We show that the approach is sensitive to the amplitude of a response, to the level of baseline firing, and to the consistency of a response between trials. Rather than attempting to account for any latency or amplitude changes from trial to trial, these are treated as genuine features of the cell's response because such variability degrades the cell's ability to represent the time of the alignment event and leads to smaller information values.

The technique can provide a useful means not only of determining which of several behavioral events a cell encodes best, but also of permitting objective comparison of different cell populations. In addition it is easy to apply to datasets of multiple simultaneously recorded neurones.

Keywords: Information Theory, Neural Coding, Timing.

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Sharpening Tuning Curves
With Spike-Time Dependent Plasticity

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ABSTRACT

Tuning curves are a common tool used to characterize the response properties of sensory neurons to relevant stimuli. They are obtained by plotting the mean firing rate of the neuron as a function of a stimulus parameter. One of the most famous examples of tuned neural responses is *orientation selectivity*, by which neurons in primary visual cortex (V1) of higher mammals (also called simple cells) exhibit tuned responses to oriented edges and gratings. The feed-forward input to simple cells is provided by the lateral geniculate nucleus (LGN), whose neurons do not show orientation preference. According to the original model of Hubel and Wiesel [7] orientation selectivity of simple cells arises mainly from the feed-forward anisotropic, specific connectivity patterns from LGN neurons to V1 simple cells. Following studies however suggested that also recurrent cortical connections play an important role in shaping orientation selectivity [9]. To model the effect of recurrent connectivity observed in the cortex, cooperative-competitive networks, or soft-WTA networks of neurons have been proposed [1]. Furthermore, it has been also recently shown that although the basic structure of the connectivity patterns underlying selectivity is innate, visual experience is essential for enhancing its specific features and for maintaining the responsiveness and selectivity of cortical neurons [5]. These evidences suggest that both fixed WTA architectures and plasticity or learning mechanisms are required for reproducing the robust feature selectivity properties of cortical neurons.

In this work we explore interaction between these two mechanisms and its effect on tuning curves, using both software simulations, and a neuromorphic VLSI system, comprising a network of silicon neurons with synaptic circuits that exhibit bio-physically realistic dynamics, and spike-driven plasticity [6, 8]. The theoretical basis for this work is based on [2], where Bennett shows that soft-WTA competition supports unsupervised learning, as it enhances the firing rate of the most active neurons hence increasing the probability of inducing learning on the afferent synapses.

In our experiments we implemented a network of Integrate-And-Fire (I&F) neurons with a Winner-Take-All (WTA) connectivity profile [4], using synapses that update their weights according to the spike-timing dependent learning algorithm described in [3]. The pre-specified initial conditions of the network we implemented, expressed in its feed-forward connectivity structure between the LGN and V1 neurons, give rise to coarse feature selectivity and broad tuning curves: uniform inputs induce a weakly localized activity at the output which reflect the nature of the particular connectivity profile used. The uniform input represents the activity of all the neurons in LGN which are tuned to the same feature of the stimulus. We show how the network's WTA mechanism amplifies and sharpens the neurons response profile and how this is equivalent to producing a teacher signal for the learning mechanism of the neurons receiving the strongest excitation.

As the network learns robustly to sharpen the pre-built broad selectivity profile, in both the bit-precise SW simulations and the noisy hardware implementation, the WTA architecture proposed plays an important role in shaping the coarse innate feature selectivity on the basis of experience.

Keywords: I&F neurons, Winner-Take-All circuits, competitive learning, unsupervised learning, spike-timing dependent plasticity, VLSI.

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Spontaneous and Evoked Responses of Olfactory Receptor Neurons Determine the Properties of Follower Neurons

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ABSTRACT

Olfactory coding begins in olfactory receptor neurons (ORNs). These neurons can be spontaneously active, but modify their spiking output when they encounter odorants. With electrophysiological recordings from ORNs and from three successive layers of follower cells, and with computational models, we explored how the olfactory system extracts signal from noise, and generates informative patterns of activity that represent different odorants.

In the insect olfactory system, ORNs and second order projection neurons (PNs) and local neurons (LNs) of the antennal lobe exhibit high baseline activity in the absence of deliberately delivered odor stimuli. However, third-order neurons (Kenyon Cells, KCs) exhibit very low baseline activity, and very sparse responses to odors, under the same conditions. (In vertebrates, similar observations have been made in first and second order olfactory neurons.) We used the locust olfactory system to explore where baseline activity originates and how it propagates through multiple layers of neurons. To locate the source of baseline activity, we reversibly silenced the ORNs by specifically cooling the antenna while tracking activity in each type of downstream cell. Cooling the antenna significantly lowered the spontaneous firing rate of ORNs and had three main effects downstream. First, odor responses were eliminated. Second, spontaneous spiking in PNs was nearly eliminated. Third, as the antenna cooled, the resting membrane potentials of PNs LNs, and KCs significantly decreased. These results demonstrate that the ORNs provide a constant barrage of spontaneous input that propagates to later stages of olfactory processing. This input contributes to the spike rates of PNs and helps determine the resting membrane potentials of higher-order neurons. With a simple Receiver-Operator Characteristic model we demonstrated discriminating signal from noise is best when firing thresholds in PNs are relatively low and thresholds in KCs are relatively high. This configuration permits the maximal convergence of information, and allows the transformation signals arising in highly sensitive but noisy ORNs into very sparse codes in KCs within two layers of neurons.

Pulses of odorants are represented as spatiotemporal patterns of spikes in neurons of the antennal lobe (AL; insects) and olfactory bulb (OB; vertebrates) [2]. These response patterns have been thought to arise primarily from interactions within the AL/OB [1], an idea supported, in part, by the assumption that olfactory receptor neurons (ORNs) respond to odorants with simple firing patterns. However, activating the AL directly with simple pulses of current evoked responses in AL neurons that were much less diverse, complex, and enduring than responses elicited by odorants. Similarly, models of the AL driven by simplistic inputs generated relatively simple output. How then are dynamic neural codes for odors generated? Consistent with recent results from several other species, our recordings from locust ORNs showed a great diversity of temporal structure. Furthermore, we found that, viewed as a population, many response features of ORNs were remarkably similar to those observed within the AL. Using a set of computational models constrained by our electrophysiological recordings, we found that the temporal heterogeneity of responses of ORNs critically underlies the generation of spatiotemporal odor codes in the AL. A test then performed in vivo confirmed that, given temporally homogeneous input, the AL cannot

create diverse spatiotemporal patterns on its own; however, given temporally heterogeneous input, the AL generated realistic firing patterns. Finally, given the temporally structured input provided by ORNs, we clarified several separate, additional contributions of the AL to olfactory information processing. Thus, our results demonstrate the origin and subsequent reformatting of spatiotemporal neural codes for odors [3].

Keywords: coding, sparse, spatiotemporal.

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Short-Term Potentiation in Pattern Recall Process of Sparsely Coded Neural Network

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ABSTRACT

The study of the synaptic plasticity and its models [2] showed that synaptic efficacy can change in a very short time window. This time scale could be small enough to possibly have an effect on pattern recall processes in neural network. We extended the model published in [1] with the short term potentiation of synapses. Our model is based on the two artificial neural nets which were among first [4, 3]. The purpose of this is to include the short term plasticity in pattern recall process as well. We have shown that this approach preserves the ability of the network to recognize the patterns stored to the network and that the network does not respond to other patterns at the same time. We show that this approach could dramatically increase the capacity of the network for the cost of a longer pattern recall process. We discuss that the network possesses two types of recall. The fast recall does not need the synaptic plasticity to recognize a pattern. The slower recall utilizes also the synaptic plasticity. This is something that we all experience in our daily lives. Specifically that some memories could be recalled promptly and other memories need much more time to unearth.

Keywords: associative memory, neural network, dynamic synapses

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Hebbian Plasticity Combined With Homeostasis Shows STDP-Like Behavior

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ABSTRACT

Memory formation as well as other functional properties of neural networks are dependent on the network connectivity. Connections between neurons are formed by synapses (synaptic weights) and are modified by different biological mechanisms. In this study, we considered the following three mechanisms: Hebbian, Homeostatic, and Spike-Timing-Dependent (STDP) plasticity. In Hebbian plasticity [5, 4] weight change depends on the activity rate of pre- and post-synaptic neuron and, thus, is a local learning rule, whereas in Homeostatic plasticity [8, 7] weight change depends only on the rate of the post-synaptic neuron. This mechanism adjusts all synapses of the incoming inputs of the neuron and, therefore, is a global plasticity process. STDP, like Hebbian plasticity, is a local process, however, differently from Hebbian plasticity (which can only produce long-term potentiation) it does not depend on the rates of pre- and post-synaptic neuron, but on the timing of the neuronal activity, and can either lead to long-term potentiation or long-term depression (LTP and LTD, [1, 3]). However, STDP can be reformulated in a rate description [2, 6].

In this study we are interested in the behavior of these three mechanisms with respect to the change of the dynamics when they interact with each other. To test this we analyzed single and two neuron systems analytically and numerically by looking at their fixed points in weight development. We found out that these fixed points change their position and stability state (from stable to unstable or vice versa) dependent on the parameter space related to these mechanisms. We show that an interaction of Homeostatic plasticity with both other mechanisms leads to a stable weight development. We also demonstrate that Hebbian together with Homeostatic plasticity shows qualitatively the same behavior as the rate description of STDP. This means that STDP, which has both LTP and LTD, can be a mixture of Hebbian and Homeostatic plasticity.

In general, we demonstrate that dynamically different plasticity mechanisms change their behavior dramatically when they interact with each other as they do in biology.

Keywords: Plasticity, Hebbian learning, Stability analysis

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Neural Latching Dynamics:
A Salutatory Code for Sustained Cognition

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ABSTRACT

A Potts associative memory, a simplified model of an extended cortical network, can retrieve up to $p_c \sim CS^2/[alnS]$ randomly assigned memory patterns, if C is the number of tensor connections per unit, S the number of Potts active states, and a the pattern sparseness [1]. That is, if memories are stored on the connections by a model Hebbian rule, analogous to the Hopfield model, attractor dynamics lead to the full cortical activity distribution from a partial, e.g. sensory cue. If patterns are correlated with each other and neural dynamics is endowed with plain fatigue, the network after retrieving the first pattern can hop to a second, to a third and so on what we have dubbed latching dynamics [2]. While with a few stored patterns latching dies out after a while, we find that it extends indefinitely in time above a critical value p_l, which in a mean-field regime is independent of C and scales up with S. I shall discuss the critical issue of the values of C and S for which $p_l < p_c$, allowing a cortical network to function as a memory when cued and then to sustain infinite spontaneous transitions. It may be that humans crossed p_l from below some hundred thousand years ago, through a kind of percolation phase transition.

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Evolution of Neural Networks under Unsupervised Learning

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ABSTRACT

We propose and analyze a mathematical model for an unsupervised learning. It has been observed that simulations of such processes result most often either in a network which is almost entirely connected, or, on the contrary, the connections are almost extinct. This poses a question whether a feed-forward network with almost constant finite in- and out- degrees can be a result of some natural evolution of a neural network, which initially admits all-to-all connections.

Making use of the recent results on bootstrap percolation in random graphs, first we argue that an unsupervised learning in a network with excitatory connections only can not produce the desired property of a feed-forward network. Then we show that the model which incorporates the inhibitory connections as well, admits a set of parameters which allow a stable critical regime which leads to a network with almost equal (small) in-and out- degrees.

Auditory Coding in the Inner Hair Cell Ribbon Synapse

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ABSTRACT

The cochlear inner hair cell (IHC) ribbon synapse constitutes the primary coding synapse for auditory signals in the mammalian auditory system [1]. Various auditory models have been developed over the years that try to capture the stimulus response of the IHC ribbon synapse. Arguably, the most well known and widely used model is the Meddis model [2], together with a later modication known as the Sumner model [3]. Although these phenomenological models are successful in simulating a number of the synaptic responses observed experimentally, they fail to replicate all the response characteristics correctly [4].

Here, the IHC ribbon synapse models mentioned above will be reviewed, together with suggestions for modi?cations or improvements, that may be used to overcome some of these modeling problems.

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Inverse Suprathreshold Stochastic Resonance in a Network of Hodgkin-Huxley Model Neurons

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ABSTRACT

Stochastic resonance is a counter-intuitive effect that is said to occur when random noise has some kind of benefit to the processing of information or signals [1]. It only occurs in nonlinear systems, and is prevalent in nonlinear dynamical systems, such as in the spiking behaviour of neurons [2]. Recently a new form of 'noise-benefits' was described within the classical Hodgkin-Huxley model of neuronal spiking [3]. This was termed 'inverse stochastic resonance' [4], because unlike other forms of stochastic resonance, noise has the effect of decreasing a parameter of the output of the system, rather than increasing it [4, 5]. Moreover, there is a 'resonant-like' peak where that parameter is maximally decreased, rather than increased. In this case, the parameter is the mean spike rate, and therefore inverse stochastic resonance can be described as 'noise-induced inhibition.'

The work of [4, 5] considers a single Hodgkin-Huxley neuron stimulated by a constant signal (either an injected current, or a conductance based current). Here we expand on that work to show that a specific kind of stochastic resonance called *suprathreshold stochastic resonance* [6, 7, 8] can be demonstrated in a network of $N > 1$ parallel Hodgkin-Huxley model neurons, where each has an independent noise source. This requires several significant extensions to the model, including introduction of a randomly varying input current, and measuring performance as an average across the range of input currents. By extension of the term introduced in [4], the resulting effect may be termed *inverse suprathreshold stochastic resonance.*

We replaced the summing array of N threshold devices of [6] with an array of Hodgkin-Huxley model neurons as used by Gutkin [4]. Simulations of this were produced to provide population spike counts in a time interval of 1000ms. The input was the "current-driven mode" which essentially consists of $I(t) = \mu + \sigma w(t)$ where μ is a uniformly distributed random variable of magnitude 0 to 8, σ is chosen between 0 snd 4 and $w(t)$ is a standard Gaussian white noise. The correlation coefficient between the spike count averaged over 100 independent instances of neuron model with the recorded μ, plotted against the incremental σ produces the plot in Fig. 1.

Figure 1 shows that the network of Hodgkin-Huxley neuron model generally has an increasing spike rate as the noise introduced grows in magnitude. However a range of small noise levels that decreases the spike rate relative to both the absence of noise, and large noise levels is observed, like that termed inverse stochastic resonance by [4, 5].

Engineered dynamical systems or signal processing algorithms often rely on feedback as a means of control. We speculate that noise-induced inhibition that leads to *inverse suprathreshold stochastic resonance* may play an equivalent role as feedback in real biological neurons.

Observations of suprathreshold stochastic resonance has previously inspired new approaches to signal coding in cochlear implants [8]. The notion of inverse suprathreshold stochastic resonance may similarly be of benefit to other biomedical prosthetics or brain-machine interfaces (BMIs).

Sean S. C. Wong is funded by an Australian Postgraduate Award scholarship. Mark D. McDonnell is the recipient of an Australian Research Council Australian Research Fellowship (project number DP1093425).

Keywords: suprathreshold stochastic resonance, inverse stochastic resonance, Hodgkin-Huxley model.

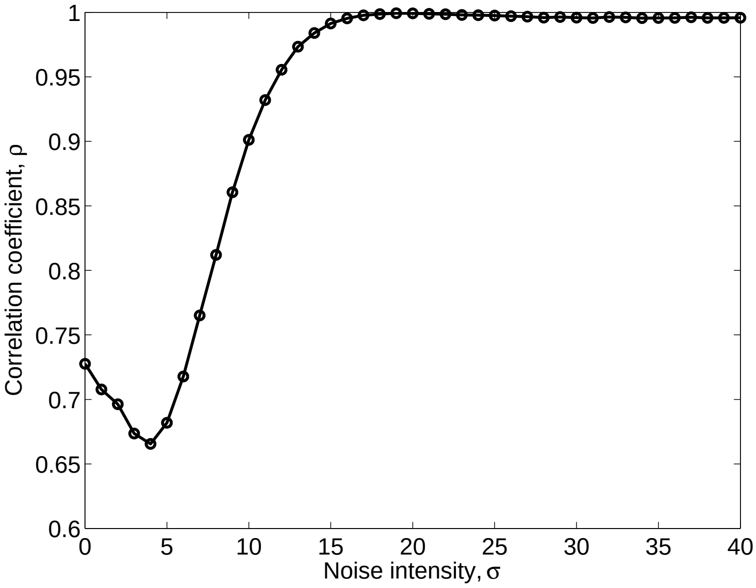

Figure 1: Plot of correlation coefficient vs noise level, σ, for a network consisting of 100 neurons, for a random input current, μ. The correlation coefficient is based on the spike count within 1000 ms.

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Firing Patterns Manifested by the Multi-Timescale Adaptive Threshold Model

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ABSTRACT

In order to numerically perform large-scale simulations of cortical neural networks and theoretically investigate their dynamics, we wish to establish an element neuron model that is not only computationally tractable and fast but also capable of accurately describing diverse spiking behaviors of biological neurons.

Recently, Izhikevich made assessment of 11 representative single neuron models on the basis of the diversity of their producible firing patterns and the implementation cost or the computational complexity [3, 4]. He demonstrated that there is a tendency for the computational cost and biological plausibility to become incompatible, namely, the simpler models are more computationally efficient but possess less capability in producing abundant firing patterns of biological neurons, and vice versa; the Hodgkin-Huxley (HH) model is evaluated as biologically highly plausible, reproducing a rich variety of firing patterns, but is expensive to implement; the leaky integrate-and-fire model is computationally efficient to implement and to perform simulations, but is poor in the firing patterns. In the assessment, the Izhikevich model deviated from this general incompatible tendency and was capable of not only producing rich variety of firing patterns but also being computationally fast.

In addition to the qualitative richness of firing patterns, it has recently been regarded important that neuron models can quantitatively reproduce and predict spike timing [2, 5]. The quantitative ability of single neuron models is evaluated by the performance of predicting the timing of individual spikes of biological neurons that are injected with fluctuating current. Previous results of the international competitions on the spike time prediction [2, 5, 6] eventually revealed that the simpler models rather achieved the higher predictive performance than biologically detailed models such as HH-type models. In the competitions, the multi-timescale adaptive threshold (MAT) model proposed by Kobayashi et al. [6], which belongs to the category of simple leaky integrator models such as the model proposed by Bugmann et al. [1], provided the highest performance in predicting the spike timing of biological neurons. However, it remains open whether the MAT model can reproduce a rich variety of firing patterns exhibited by cortical spiking neurons.

In this study, we examine the dynamical property of the MAT model for its capability of reproduing the standard table of 20 qualitatively distinct firing patterns, which we call the Izhikevich table. It turns out that the MAT model may reproduce some of the firing patterns, such as the bursting or the class 2 excitability, but is unable to produce specific patterns of more than half the number in the table. In order to overcome its poor performance of firing pattern reproducibility, we propose a minimal extension of the model, with which we succeed in reproducing all of the 20 patterns in the table.

Keywords: Simplified single neuron models, Firing patterns, Spike time prediction.

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Neural Coding in the Olfactory System of Insects

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ABSTRACT

Information coding in the olfactory system of insects has a long tradition in a handful of main animal models: Locust, honeybee, Drosophila, moths, and cockroach. In the last 3 years our group has concentrated on the specific problem of coding in the pheromone sub-system, in particular, the macro-glomerular complex (MGC) of moths. Contrary to earlier reports in locust [1], honeybee [2] and *Drosophila* [3], we were unable to observe oscillations in the local field potential in the MGC. We take this as an indication that the coding strategy in the MGC of moths may differ from the popular account of coding of odour information in locust [4, 5].

We have identified two important aspects of information coding in the MGC which I will discuss in this talk:

1. On the level of individual glomeruli in the MGC, the extreme sensitivity of the moth to conspecific pheromone blends implies a wide dynamical range for the recognition of the concentration of the chemical components. This wide dynamical range is implied by behaviour but has also been directly observed experimentally on the level of projection neurons in the MGC [6]. The common view that the dynamic range arises in the chemical transduction pathways within the ORNs is not enough as the dynamic range appears to be dependent on neuromodulation in the MGC [6].
2. On the level of the whole MGC network, the fact that sexual pheromones of moths are blends of two to three separate chemicals at fixed concentration ratios, implies that male moths need to recognise pheromone blend component ratios, in particular when sympatric, related species use pheromone blends that only differ in their component ratios [7]. This ratio recognition ability has to be concentration independent.

On the single glomerulus level we propose a model of nearly-critical rate dynamics. In a multi-scale model encompassing conductance based formulations, rate reductions and further mean field approximations we can consistently demonstrate that

1. the observed rate patterns in LN and PN responses can be explained by a generic network of inhibitory LNs
2. the LN network can form an implicit disinhibition pathway that could explain the late excitatory response of the PNs that is to a degree inconsistent with dominantly direct ORN input to PNs.
3. the dynamic range of PN responses becomes maximised in this model when we approach the critical point in the model dynamics where the baseline state becomes unstable.

On the network level we have formulated a model of neuronal competition for pheromone blend ratio recognition. The prototype model demonstrates component ratio recognition for two pheromone components in a 1:1 ratio. The core finding in this part of the work were that

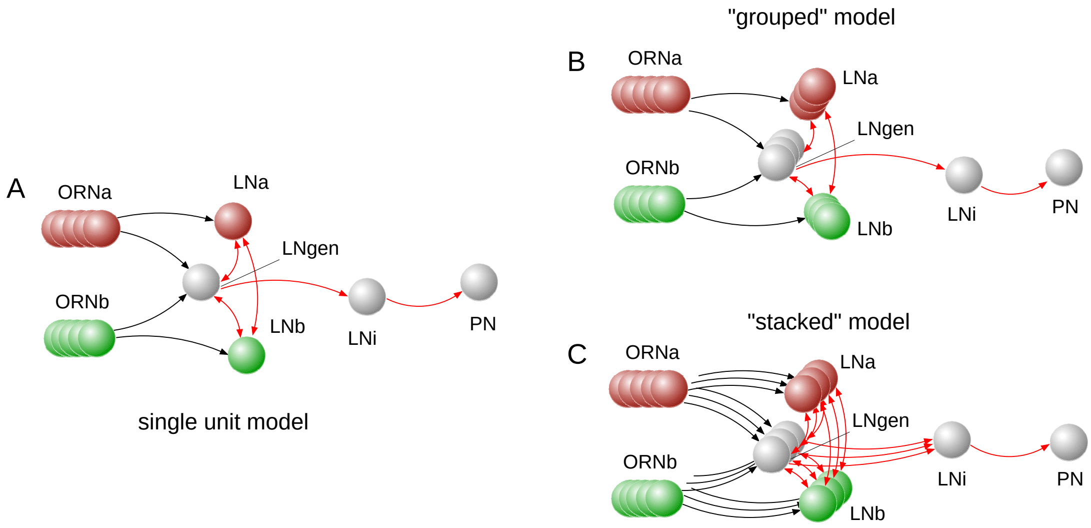

Figure 1: Minimal single LN model (A) and two more realistic (and more successful) populations models (B and C) for pheromone blend component concentration ratio recognition.

1. in a minimal model of three individual LNs which receive inputs from either of the receptor populations, or both, and compete through lateral inhibition (figure 1) the coding inadvertently reverts to a latency-to-first spike code.
2. the latency code is not beneficial for ratio recognition across a wide range of concentrations.
3. populations of neurons allow a more gradual competition (rate based coding) which improves ratio recognition, in particular its stability across concentrations.

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