

# Bernstein Conference on Computational Neuroscience 27 09 - 01 10

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## Structural motifs and correlation dynamics in networks of spiking neurons

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The dynamics of random recurrent networks has been analyzed in detail, but the influence of non-random connectivity patt on activity dynamics is not well understood. Here we study the effect of certain structural motifs on pairwise correlations in networks of excitatory and inhibitory neurons in a balanced asynchronous-irregular state. For analytical tractability, spike to conceived as linearly interacting stochastic point processes. In this case, firing rates and correlation functions are fully deter the matrix of linear response kernels. Simple analytic expressions have been derived in [2]. We find that the matrix of integ cross-covariance functions can be written as a power series of the underlying network's connectivity matrix. In terms of netw structure, higher matrix powers of this series expansion can be interpreted as contributions of motifs of increasing complexi Generally, such higher order motifs can strongly affect correlations. Their impact can be estimated from the spectral radius connectivity matrix. Using numerical simulations, we demonstrate that not only differences in average in-degree and comm but also in higher order motif distributions can lead to dramatic effects regarding pairwise correlations. To illustrate the infl network structure in more detail, we study connectivity matrices with certain symmetry properties. Specifically we focus on dependent connectivity profiles. The distance dependence of correlations can then be determined from the connectivity prc the influence of higher order contributions can be understood analytically.

#### References

[1] Song S., Per S., Reigl M., Nelson S., Chklovskii D. (2005). Highly nonrandom features of synaptic connectivity in local cortical circuits. PLoS Bio [2] Hawkes, A. G. (1971). Point spectra of some mutually exciting point processes. Journal of the Royal Statistical Society (London) B, 33, 438443

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EVENT ABSTRACT

#### NeurOnline: A software framework to perform online analysis and control of electrophysiological recordings

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The interaction with neuronal networks in electrophysiological experiments is a difficult and often crucial task, requiring pr up-to-date information about the dynamic state of the network. Electrode arrays, in principle, allow a very detailed observa system state because multiple sites can be recorded simultaneously. However, the online and on-site analysis of such high-dimensional data obtained with a high sampling rate requires a well-designed data analysis system.

The NeurOnline project aims at developing an open-source software framework to be used by experimentalists to perform analyses of electrophysiological recordings made with various experimental setups. It consists of an integrated set of Pythor that control C++ code. The Python language opens the possibility to design, implement and apply the analysis on-site, becau makes the extension of existing modules and the creation of new ones comparatively easy. The C++ language ensures high performance. The latter is crucial for online analysis, especially when multiple channels are recorded with high sampling ra

The collaboration of this software development project with two laboratories at the University of Freiburg has already led tc promising applications and first results. (1) In the Biomicrotechnology lab (IMTEK) Patrick Dini studies the dynamics of ne assemblies cultured on high-density multi-electrode arrays. NeurOnline is currently used to record and filter the data, to de sort spikes, and to schedule the successive selection of electrode subsets. The small distance between electrodes ( $14\mu$ m), in combination with new online analysis algorithms, allow us to follow action potential propagation across the electrode array unprecedented detail. (2) In the Neurobiology and Biophysics lab (Faculty of Biology), Jens Kremkow uses visual stimuli to neurons in the thalamus and the visual cortex of anesthetized rats. He employs adaptive stimulus sampling, which involves the visual stimulus depending on the recorded activity of neurons. The use of NeurOnline to record data, to detect and sort and to control the display of visual stimuli leads to a fast and reliable online receptive field characterization of cells in the L<sup>1</sup> V1.

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#### Non-equilibrium encoding of time-dependent input signals by net with effective refractoriness

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Spike trains emitted by cortical neurons can be effectively described by stochastic point processes. The Poisson process with refractoriness is a particularly simple point process, which admits the mathematical analysis of its dynamic properties. As w through the generalization to randomly distributed refractory times (Fig. A), this process can represent a large class of well-renewal processes, including certain types of gamma- and log-normal processes. These are frequently used models for static neuronal spike trains. To study the non-equilibrium dynamics of ensembles of such processes we employ a description in te occupation numbers of two states: Active and refractory. These occupation numbers follow a distributed delay differential e Based on this dynamics, the time-dependent spike rate of an ensemble of processes encoding an arbitrary input trajectory c studied. In particular, we consider the case of a step change of the input rate, which induces a stochastic transient of the out rate (Fig. B). Moreover, for the periodic response to periodic input profiles, we obtain the mapping of the discrete spectra or and output, by which all harmonics are coupled linearly, with coefficients depending on the refractoriness. For the special c cosine input and a fixed refractory time, we find resonances, phase jumps and frequency doubling in the time-dependent er spike rate. Since a large class of renewal processes can be represented as Poisson processes with random refractory time, ou approach represents a widely applicable framework to define and analyze non-stationary point process models of neural ac

Figure 1: Ensemble of Poisson processes with random refractoriness, with different widths of the refractory time distributio Probability density of refractory time (dotted lines) and normalized hazard function for constant input rate (solid lines). B: ' of the ensemble rate upon step change of the input rate at t=0. Theoretical result (solid lines) and simulation of an ensemblprocesses averaged over 225 trials (crosses). Error bars denote the standard deviation over trials.

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### The impact of spiking irregularity on the estimation of higher-orde correlations

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Nonlinear response properties make neurons extremely sensitive to the higher-order structure of their input [1]. Whether o higher-order correlations are important for cortical information processing, however, can only be decided by the analysis of experimental data.

Common data analysis methods [2] to investigate the potential role of higher-order correlations assign one correlation para each subgroup of N neurons, yielding 2<sup>N</sup>-1 parameters to be estimated. The corresponding requirements with respect to the size renders the application of these methods to electrophysiological recordings of the spike activity of large populations im In contrast, the recently developed empirical de-Poissonization (EDP) [3] aims for population-averaged correlations, and re only one parameter per order of correlation (i.e., N parameters in total), resulting in a biologically feasible requirement rega sample size. Specifically, EDP infers higher-order correlations from the population spike count.

A central assumption of higher-order correlation measures is that the values in subsequent counting windows are independ single-neuron spike trains, this effectively implies Bernoulli or Poisson statistics. Recent studies investigating spiking irregu however, emphasize that Poissonian spiking is not common to neurons in all brain areas [4]. For instance, neurons in motor tend to fire much more regular than those in visual areas. Hence, in order to avoid misinterpretation of results, the impact c irregularity on higher-order correlation measures has to be investigated. This, in turn, requires a method to generate surrog with prescribed irregularity that at the same time allows to control the higher-order correlation structure of the population. In this contribution, we extend the "thinning method" [5] to generate populations of correlated non-Poissonian spike trains. Specifically, we consider log-normal interspike-interval distributions for which the higher-order structure can be controlled biologically realistic regimes. The robustness of EDP is then investigated by systematically simulating and analyzing such log populations. We find that the results are the more biased the larger the counting window is. The maximal order of correlation to be underestimated for regular spiking, while it may be overestimated for very irregular spiking.

#### References

[1] Abeles, *Corticonics - Neural Circuits of the Cerebral Cortex* (Cambridge University Press, 1991); Bohte et al, Neural Comput **12**, 153 (2000); Kul Neural Comput **15**, 67 (2003)

[2] Martignon et al, Biol Cybern 73, 69 (1995); Martignon et al, Neural Comput 12, 2621 (2000); Amari et al, Neural Comput 15, 127 (2003)

[3] Ehm et al, Electronic Journal of Statistics 1, 473 (2007)

[4] Shinomoto et al, PLoS Comput Biol 5, e1000433 (2009); Maimon & Assad, Neuron 62, 426 (2009)

[5] Lewis & Shedler, Naval Research Logistics Quarterly **26**, 403 (1979); Devroye, Non-uniform Variate Generation (Springer, New York, 1986); Be Gerstein, Neural Comput **12**, 2597 (2000)

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EVENT ABSTRACT

#### An Online Brain-Machine Interface Using Decoding Of Movement Direction From The Human Electrocorticogram

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Brain-machine interfaces (BMIs) can be characterized by the approach used to translate brain signals into effector moveme we use a "direct motor" BMI approach where movements of an artificial effector (e.g. movement of an arm prosthesis to the controlled by motor cortical signals that control the equivalent movements of the corresponding body part (e.g. arm movem right). This approach has been successfully applied in monkeys and humans by accurately extracting parameters of moveme the spiking activity of multiple single-units. Here we show that the same approach can be realized using brain activity meas directly at the surface of the human cortex (electrocorticogram, ECoG). Three subjects suffering from intractable pharmacoepilepsy voluntarily participated in the study after having given their informed consent (study approved by the Freiburg Un Hospital's Ethics Committee). As a part of pre-surgical diagnosis all subjects had 8x8 ECoG grid implants (4 mm electrode c 10 mm inter-electrode distance, Ad-Tech Medical Instruments, USA) over the hand and arm motor cortex. Subjects interact an experimental paradigm shown on a computer screen. Each trial consisted of a pause phase (1-2 sec) followed by a prepar informative cue (1-2 sec) which informed the subject to prepare for executing or imagining a hand/arm movement to the let right using the hand contralateral to the implantation site. After a delay of 2-3 sec, a go cue was presented and subjects had perform the movement execution or imagination within the next two seconds. Subsequently, a cursor on the screen was mov according to the movement direction decoded from the subjects' ECoG signals. Closed loop BMI control of movement direct realized using low-pass filtered (symmetric Savitzky-Golay filter, 2nd order, between 0.25 and 1 sec window length) ECoG s during movement execution or movement imagination. For movement execution significant BMI control was achieved for a subjects in all 7 sessions with correct directional decoding in 69%-86% of the trials (79% on average across all sessions). Mo imagination was carried out with only one subject where 3 out of 4 sessions showed significant BMI control with correct dec 66%-72% of the trials (69% on average). In summary, our results demonstrate the principle feasibility of an online direct mc using ECoG signals. Thus, for a direct motor BMI, ECoG might be used in conjunction or as an alternative to the intra-cortic signals, with possible advantages due to reduced invasiveness.

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EVENT ABSTRACT

#### Number, reliability and precision of long-distance projections onto neocortical layer 5 pyramidalneurons

Philipp Schnepel<sup>1, 2</sup>, Martin Nawrot<sup>3</sup>, Ad AErtsen<sup>1, 2</sup> and Clemens Boucsein<sup>1, 2\*</sup>

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Current concepts of cortical information processing and most cortical network models largely rest on the assumption that the well-studied properties of local synaptic connections are sufficient to understand the generic properties of cortical networks view seems to be justified by the fact that vertical connectivity within local volumes is strong, and connection probability bet pairs of neurons in the lateral direction drops dramatically with increasing distance. However, recent neuroanatomical stud (Hellwig 2000; Binzegger et al., 2004; Stepanyants et al., 2009) have consistently suggested that an estimated fraction of 50 synapses on pyramidal neocortical neurons stem from cells outside the local volume (>300 $\mu$ m lateral distance). Hence, taki account long-distance horizontal connections might dramatically change the current view on cortical information processing Physiological characterization of long-distance lateral projections has been hampered by methodological constraints. Due to drop of connection probability with lateral distance, the success rate for paired recordings in slice preparations is extremely distances > 200  $\mu$ m.

Here, to overcome these problems, we employed photo stimulation in acute cortical slices to characterize parameters of syn physiology of long-distance horizontal connections in a range of  $200 \sim 1500 \,\mu\text{m}$  of lateral distance. We found that, even in t slice preparation with its limited amount of preserved projections, the probability of finding connected cells is still consider distances up to 2 mm. The average amplitude of EPSCs slightly dropped with distance, while strong connections were still p over long distances. Short and long range connections showed (1) an equally high synaptic reliability of 100% in most tested (2) the same level of amplitude variability, and (3) an equally high temporal precision of <1ms.

Thus, our data provide additional information for the parametrization of long-range connections in neural network models information processing. Taken together, our measurements suggest that long-distance horizontal connections constitute a refraction of synaptic links within the cortical network. While the average strength of these connections slightly drops with ine distance, they contribute with high reliability and high temporal precision to the single cell input in layer 5.

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#### References

1)Stepanyants A, Martinez LM, Ferecskó AS, Kisvárday ZF (2009) The fractions of short- and long-range connections in the visual cortex. Proc Natl S A 106(9):3555-60

2)Hellwig B (2000) A quantitative analysis of the local connectivity between pyramidal neurons in layers 2/3 of the rat visual cortex. Biol Cybern.  $\xi$  3)Binzegger T, Douglas RJ, Martin KA (2004) A quantitative map of the circuit of cat primary visual cortex. J Neurosci. 24(39):8441-53

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### Stereotypic spatiotemporal activity patterns during slow-wave action the neocortex

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Periodically alternating epochs of vigorous activity and complete silence are a characteristic feature of neocortical networks certain sleep cycles and deep states of anesthesia. The mechanisms leading to these low frequency (~1Hz) oscillations and tl functional role have not yet been fully understood. Evidence from both, experimental and theoretical studies show that slow oscillations can be generated autonomously by neocortical tissue, but become more regular through a thalamo-cortical feed Hints for a functional role of slow-wave activity come from EEG recordings in humans during sleep, showing that such activ propagates in stereotypic waves over the entire brain. This was interpreted as a possible mechanism for memory consolidati Here, we used an animal model to investigate such wave propagation on a much smaller scale, within the rat somatosensory Recordings from multiple extracellular micro-electrodes in combination with one intracellular recording in the anesthetized in vivo were utilized to monitor the spread of activity. We found that activity propagation in most animals clearly showed a direction, suggesting that it often originated from a single location in the cortex. In addition, the breakdown of the active sta followed a similar pattern with slightly weaker direction preference, but a clear correlation to the direction of activity spread supporting the notion of a wave-like phenomenon, similar to that observed after strong sensory stimulation in primary sens Taken together, our findings support the idea that activity waves during slow-wave sleep do not occur spontaneously at randocations within the network, as was suggested previously, but follow preferred synaptic pathways on a small spatial scale.

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