Conditions for and detectability of extremely fast oscillations in neuronal activity

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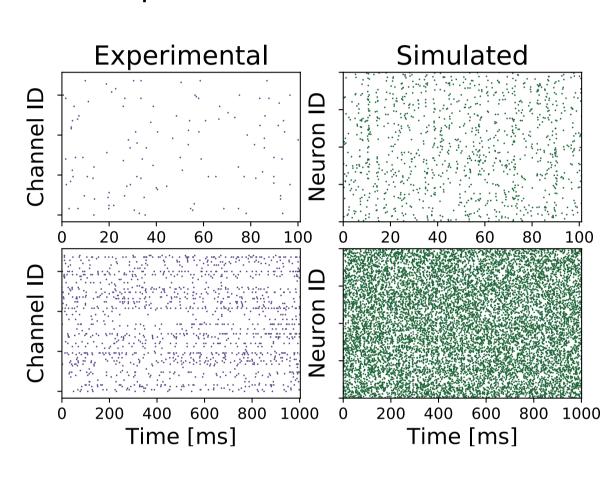
Introduction

Extremely fast oscillations in spike neuronal activity (> 200 Hz) are observed in some spiking network models, but seem to lack in experimental recordings. This raises the question whether these oscillations are an artefact of the network model or the simulation technique employed or whether they may be overlooked in experimental recordings due to lack of data.

To better understand these observations, we first use simulations of the cortical microcircuit model by Potjans and Diesmann [1] to eliminate possible simulation artefacts. We then downsample data from these simulations to explore the effect of reduced amounts of data.

Building on work by Bos et al [2], we then investigate how difference in delay distributions influences the presence of extremely fast oscillations and test for presence of these oscillations in a complex, data-driven model of the visual system [3].
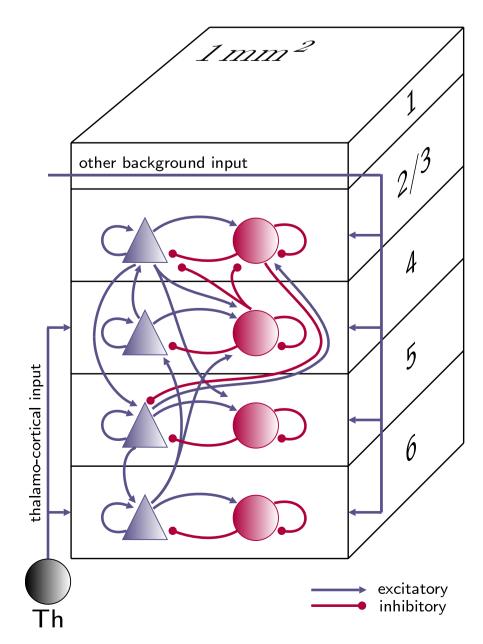
Results presented here are based on the master thesis of Runar Helin [4].

Exemplary experimental and simulated spike trains. Left: Spike activity recorded from 86 single units in motor cortex of a macaque monkey during a delayed reach-to-grasp task [5], for 100 ms (top) and 1000 ms (bottom) showing now discernible oscillations. Right: Spike activity from 2000 neurons in L4I of the cortical microcircuit model [1] showing stripes at roughly 6 ms intervals corresponding to extremely fast oscillations.

Cortical microcircuit model

- Cortical microcircuit model covering approx 1 mm² cortical surface [1]
- Four cortical layers with one excitatory and one inhibitory population each
- Neuron numbers and connectivity based on neuroanatomical and -physiological data
- Some adjustments according to Bos et al [2]
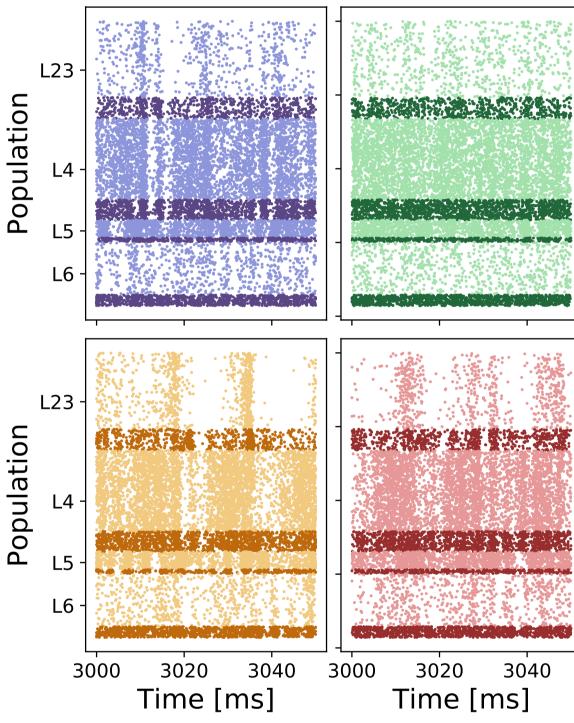- All simulations performed using NEST 2.14.0 [6].

Model summary

Model	
Populations	Nine; 8 cortical populations and 1 thalamic population
Topology	–
Connectivity	Random connections
Neuron model	Cortex: Leaky integrate-and-fire, fixed voltage threshold, fixed absolute refractory
Synapse model	Exponential-shaped postsynaptic currents
Plasticity	–
Input	Cortex: Independent fixed-rate Poisson spike trains
Measurements	Spike activity, membrane potentials

Populations	
Type	Elements
Cortical network	iaf neurons, 8 populations (2 per layer), type specific size N
Th	Poisson, 1 population, size Nth

Connectivity	
Type	Random connections with independently chosen pre- and postsynaptic neurons; see
Weights	Fixed, drawn from Gaussian distribution
Delays	Fixed, drawn from Gaussian distribution multiples of computation stepsize

Neuron and synapse model	
Name	iaf_psc_exp
Type	Leaky integrate-and-fire, exponential-shaped synaptic currents
Subthreshold	$\frac{dV}{dt} = \frac{I(t)}{C_m}$ if $(t > t^* + \tau_{rp})$
Dynamics	$V(t) = V_{reset}$ else $I_{syn}(t) = we^{-t/\tau_{syn}}$
Spiking	If $V(t-) < \theta \wedge V(t+) \geq \theta$ 1. set $t^* = t$, 2. emit spike with time stamp t^*

Input	
Background	Independent Poisson spikes to iaf neurons

Measurements	
	Spiking activity and membrane potentials from all neurons in every population.

Representation of the microcircuit model. The network size represents that of a cortical network under a patch with surface area 1 mm². Reprinted from [1] under the Creative Commons Attribution License CC 3.0.

Modifications after Bos et al [2]

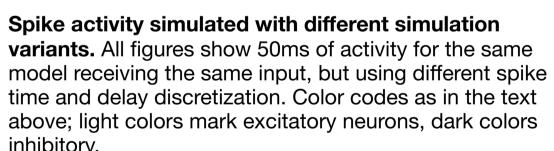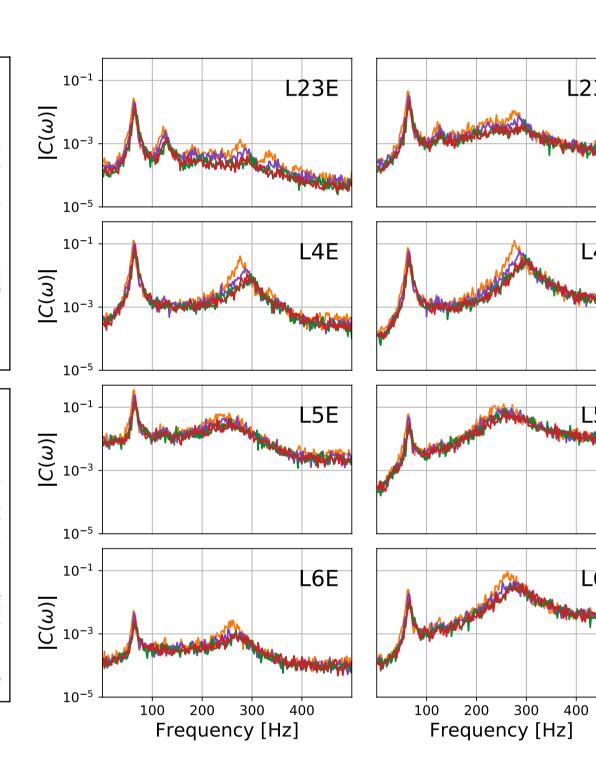|	Number of connections L4I→L4E	Std deviation excitatory delays	Std deviation of inhibitory delays	Number of ext. connections to L4E
Original	$K_{41,4E}$	0.75 ms	0.375 ms	2100
Modified	0.85 $K_{41,4E}$	1.50 ms	0.75 ms	1780

Fast oscillations not simulation artefacts

Spiking network simulations usually use a fixed time-grid and restrict synaptic delays to multiples of the grid step. We tested several implementation variants to test for potential artefacts of time discretization.

Discrete spike times, discrete delays (default simulation)
Spike times bound to 0.1 ms time grid, delays rounded to nearest multiple of 0.1 ms.

Continuous spike times, discrete delays
Spike times not bound to time grid, delays rounded to nearest multiple of 0.1 ms.

Discrete spike times, continuous delays
Spike times implicitly bound to 0.1 ms time grid, continuous range of delays.

Continuous spike times, continuous delays
Spike times not bound to time grid and continuous range of delays.

Extremely fast oscillations (EFOs) are present for all four implementations and power spectra differ only minimally. EFOs are thus no discretization artefacts.

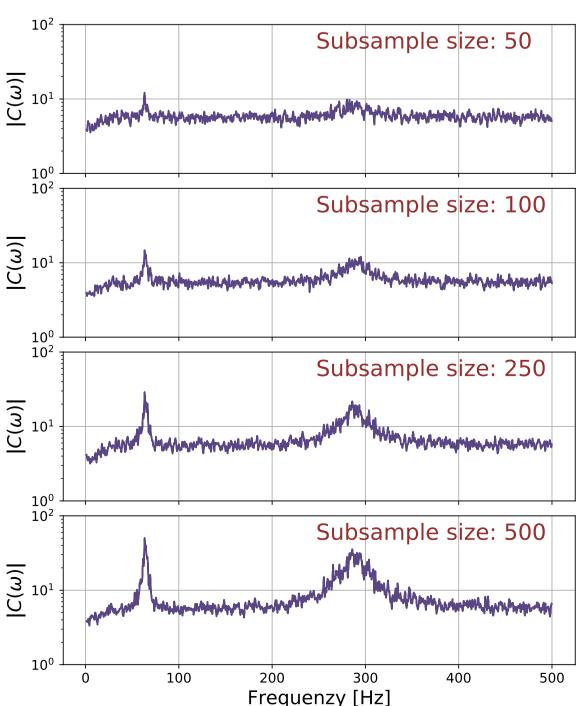For all further simulations, we employ the simulation mode for efficiency.

Spike activity simulated with different simulation variants. All figures show 50ms of activity for the same model receiving the same input, but using different spike time and delay discretization. Color codes as in the text above; light colors mark excitatory neurons, dark colors inhibitory.

Power spectral density of spike activity for different simulation variants. Figures show PSD for excitatory layers (left) and inhibitory layers (right) in different cortical layers for the same model and color code as for the spike trains to the left. Trains binned with 1ms resolution and PSD averaged across 18 windows of 500ms.

Detectability depends on neuron count

Model simulations provide in principle access to complete spike trains of all neurons in a model. In experimental recordings, spike trains can only be obtained from a subset of neurons in a population.

We test the effect of sample size on the power spectral density by computing PSD from random subsets of spike trains, varying subset size.

Both gamma-oscillations and extremely fast oscillations are more prominent for large neuron counts.

The limited number of neurons recorded from in experiments may therefore explain why extremely fast oscillations are rarely detected, although the power spectrum for 100 neurons suggest that detecting these oscillations may be feasible with Utah arrays or similar tools.
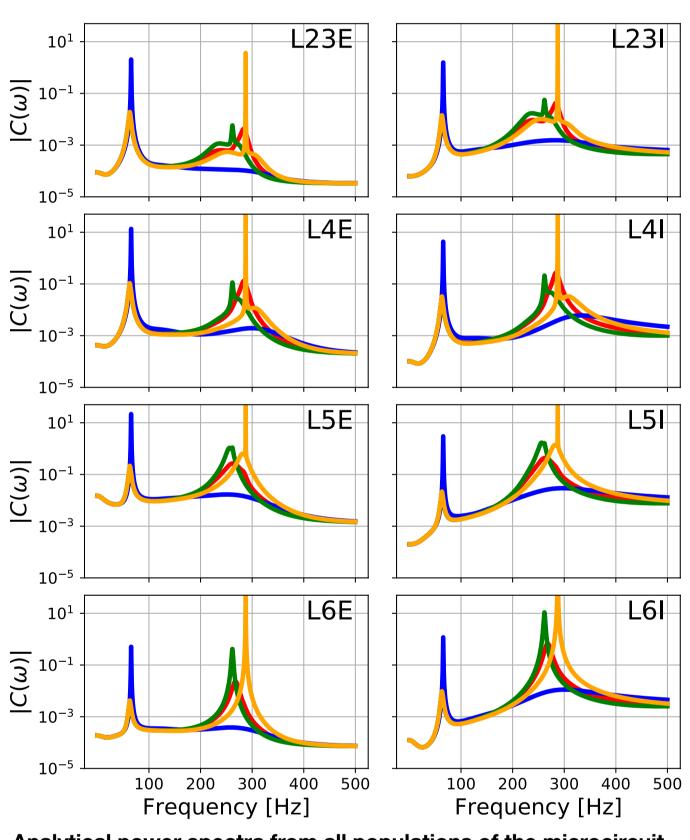

Power spectral density for different number of spike trains. PSD of spike trains of 50 (top), 100, 250 and 500 (bottom) L4I neurons, normalized to equal background power for all neuron counts. PSD is calculated over 9s of spike data, averaged over ten trials and smoothed with a Gaussian kernel of width 3 ms.

Delay distribution determines oscillations

We investigate the origin of extremely fast oscillations combining mean-field theory and linear response theory, extending results by Bos et al [2]. They expressed network dynamics in Fourier space as

$$\mathbf{R}(\omega) = \mathbf{M}_d(\omega)\big(\mathbf{R}(\omega) + \mathbf{X}(\omega)\big)$$

where $\mathbf{R}(\omega)$ is the vector of **population firing rates**, $\mathbf{X}(\omega)$ noise and $\mathbf{M}_d(\omega)$ the **effective connectivity matrix** incorporating delays with elements

$$M_{d,ij}(\omega) = M_{ij}(\omega) \int_{-\infty}^{\infty} e^{-i\omega y} p(y) dy .$$

Here, $M_{ij}(\omega)$ is the effective connectivity matrix and $p(y)$ the **delay distribution**. The **PSD** is given by

$$\mathbf{C}(\omega) = \langle \mathbf{Y}(\omega)\mathbf{Y}^T(-\omega)\rangle \quad \text{with activity} \quad \mathbf{Y}(\omega) = \mathbf{R}(\omega) + \mathbf{X}(\omega) .$$

We tested **truncated Gaussian** [1, 2], **exponential**, **uniform** and **lognormal** delay distributions, modifying only delays for connections between inhibitory populations.

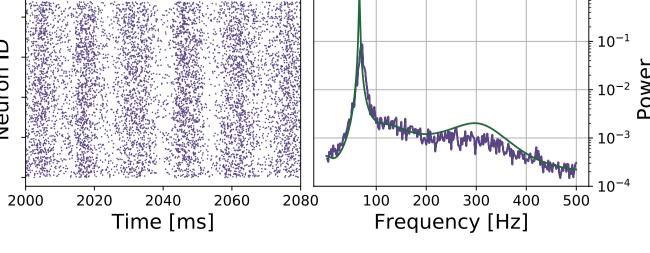### PSD for different delay distributions

Analytical power spectra from all populations of the microcircuit model using different delay distributions: Truncated Gaussian (red), exponential (blue), uniform (green) and lognormal (orange) for parameters given in the table. Parameter values were matched to result in equal mean delays.

No extremely fast oscillations for exponential delay distribution

The spectra above show no fast oscillations for exponentially distributed delays in agreement with earlier results [7]. This is corroborated by simulation results.

Network with exponentially distributed I→I delays. Spike response (left) and PSD (right) for population L4E of the microcircuit model. The thin line is the analytical PSD.
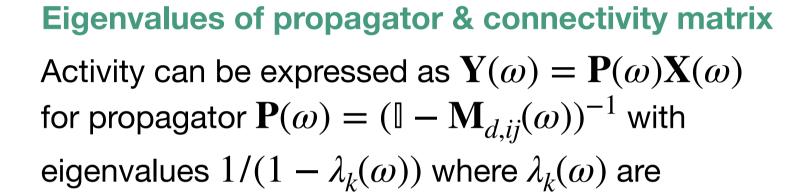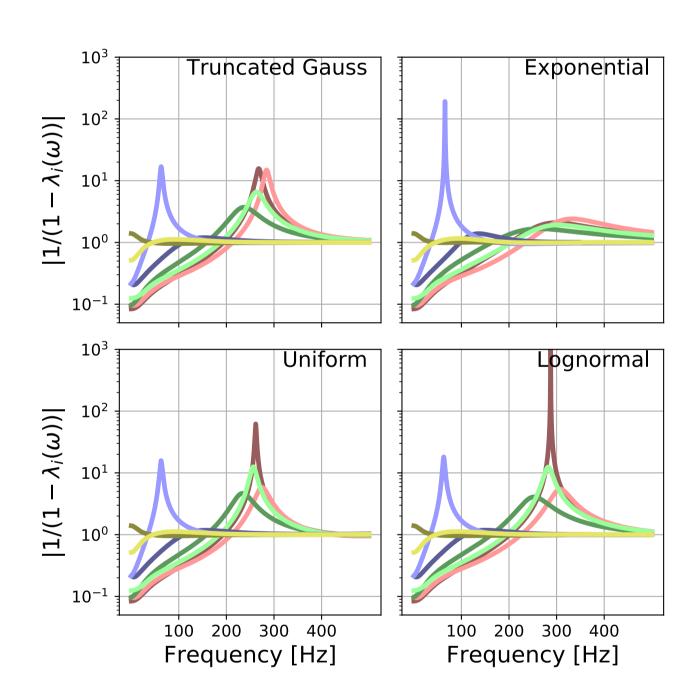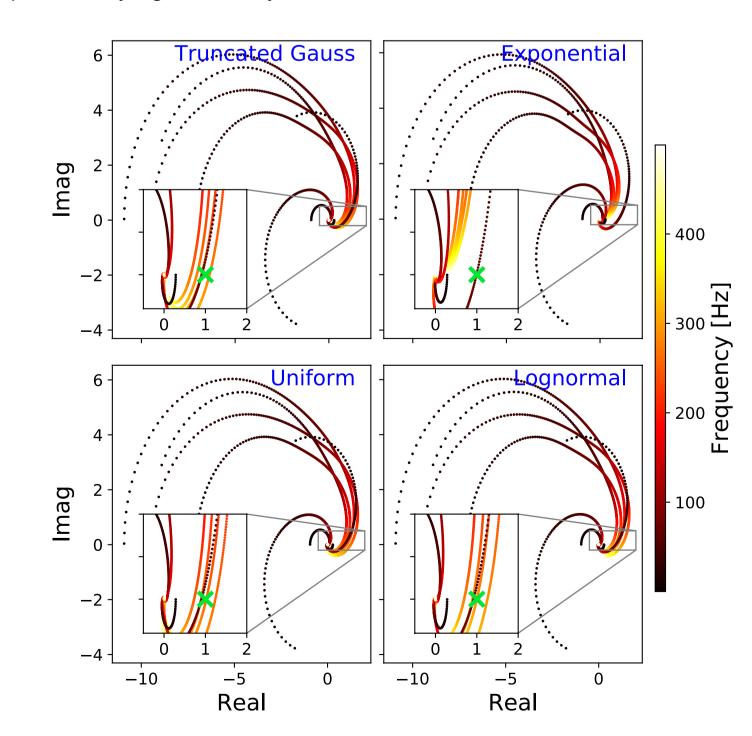
Eigenvalues of propagator & connectivity matrix

Activity can be expressed as $\mathbf{Y}(\omega) = \mathbf{P}(\omega)\mathbf{X}(\omega)$ for propagator $\mathbf{P}(\omega) = (\mathbb{I} - \mathbf{M}_{d,ij}(\omega))^{-1}$ with eigenvalues $1/(1 - \lambda_k(\omega))$ where $\lambda_k(\omega)$ are
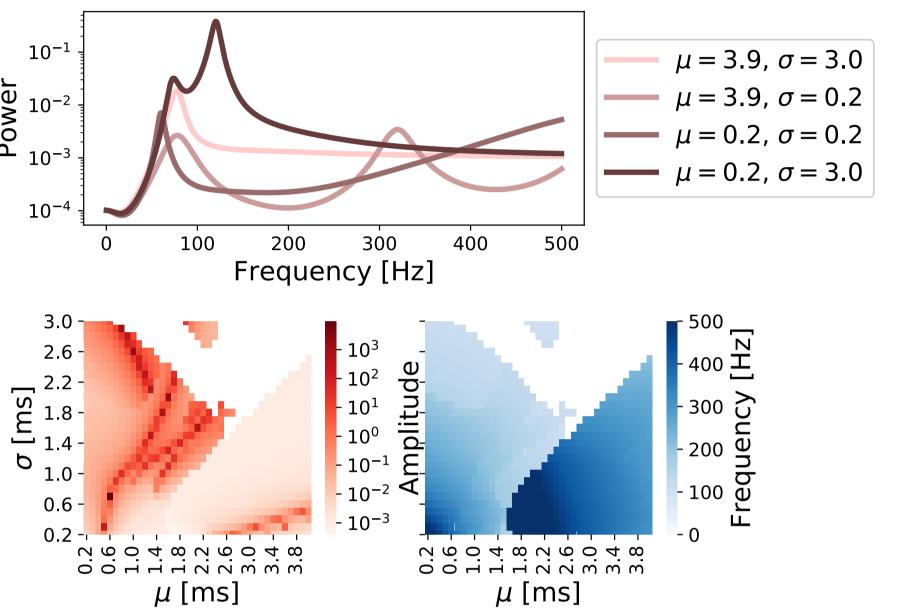

Propagator eigenvalues. Eigenvalues of $\mathbf{P}(\omega)$ as function of frequency for all delay distributions studied. Only the exponential distribution has no strong peak for any eigenvalue beyond 100 Hz.

Truncated Gaussian	Exponential	Uniform	Lognormal
$\mu = 0.75$ ms	$\lambda = 1.0356$ ms	$a = 0.0$ ms	$\mu = -0.1959$ ms
$\sigma = 0.75$ ms		$b = 1.9314$ ms	$\sigma = 0.5673$ ms

Trajectories of complex eigenvalues of the effective connectivity matrix for different delay distributions. Real and imaginary components are plotted as function of frequency, which is indicated by color. Trajectories passing near $1 + 0i$ correspond to resonances.

Oscillations depend on delay parameters

We extend our analysis from a single parameter set for each of four delay distributions to a systematic analysis of how existence and properties of a peak at very high frequencies depends on the details of the delay distribution. We focus on the truncated Gaussian distribution and again modify only connections between inhibitory populations.

Existence, location and amplitude of high-frequency peak depend on details of delay distribution. Top: PSD for population L4I for four different parameter combinations for truncated Gaussian delay distribution. One combination ($\mu = 3.9$ ms, $\sigma = 0.2$ ms) shows a clear high-frequency peak, while $\mu = 0.2$ ms, $\sigma = 3.0$ ms results in a "high-frequency" peak just above 100 Hz.

Bottom: Results of parameter scan for a range of parameter combinations for the truncated Gaussian delay distribution applied to all projections between inhibitory populations. The amplitude of the high-frequency peak is shown to the left (red), its location to the right (blue). White areas mark parameter combinations not producing a peak beyond 100 Hz.

No fast oscillations in the multi-area model

Delays vary much more widely across the full brain than within a local microcircuit. To explore the effects of very heterogeneous delays, we explore a data-driven multi-area model of the visual system by Schmidt et al [3], in which delays range up to some 60 ms for long interareal connections. The model consists of a total of 32 areas, each represented by a modified cortical microcircuit model. We simulate the full model, but show here only PSD for area V1. Oscillations are largely absent.
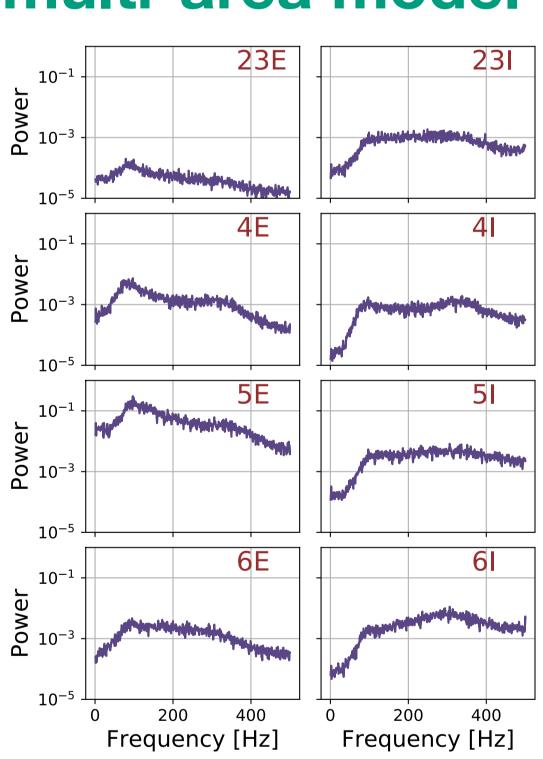

Power spectral densities of the 8 populations of area V1 of the multi-area model. The spectra are calculated from 20 seconds of simulation time, using a time histogram with bin size 1 ms and averaging PSD over 20 time windows of 1000 ms each.

Conclusions

We have studied extremely fast oscillations which are observed in simulations of neuronal network models, but appear to lack in experimental data. We showed that extremely fast oscillations

- are not a simulation artefact,
- may be difficult to detect experimentally due to the limited number of neurons recorded,
- depend on the form and the details of the delay distribution, and
- are not observed in a comprehensive visual pathway network model.

Further work will explore delay dependencies of network dynamics in greater detail.

References
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