A Mean Field Theory for a Layered Network Model of the Neocortex

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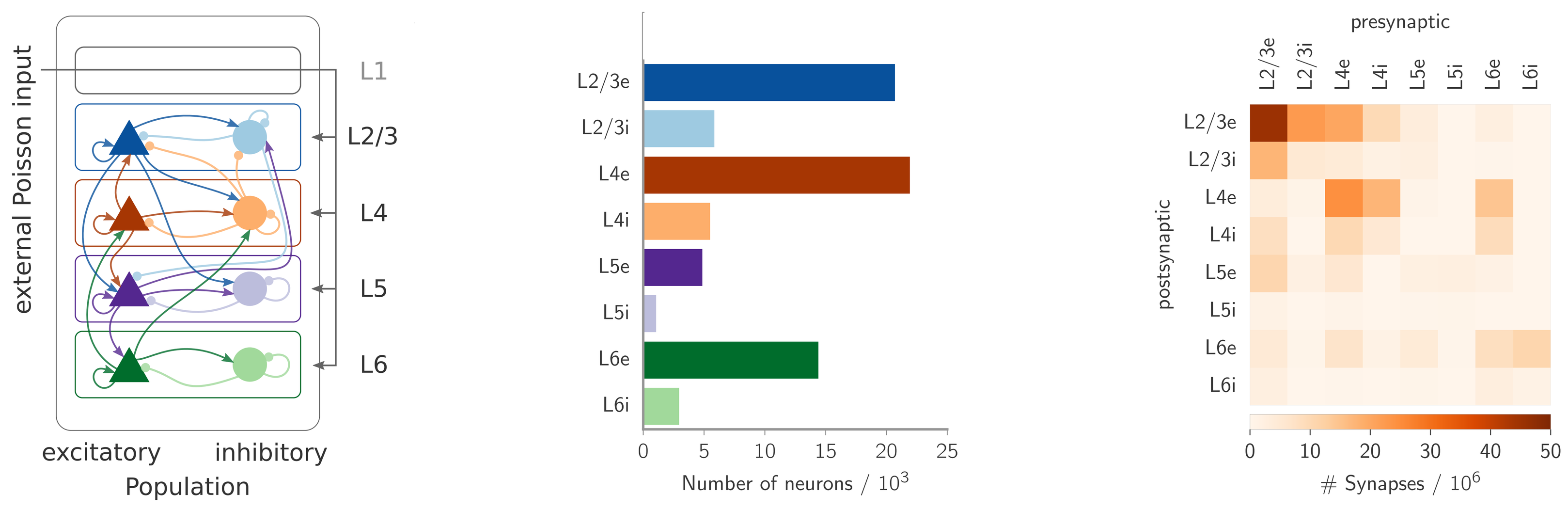
MOTIVATION

Current research on the relations between structure, activity and function of the neocortex relies heavily on numerical simulations of spiking network models. Recent models include one of the hallmarks of neocortical anatomy: its arrangement in several neuronal layers. Although numerical simulations can reproduce experimental measurements of activity, it remains unclear which network mechanisms govern the observed network activity, and how sensitive the model is to its various parameters. The presented mean field model represents an efficient way to tackle these aspects: It predicts the network activity assuming uncorrelated input to each neuron, and it can be employed as an effective tool for scanning large portions of the parameter space.

SPIKING NETWORK MODEL

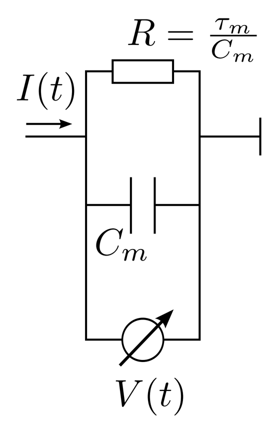
GLOBAL NETWORK STRUCTURE

8 populations are arranged in 4 layers, each containing an excitatory and inhibitory population. Neuron and synapse numbers are estimated from anatomical stainings, see [2] for details. Synapses are drawn randomly until a fixed number is reached. Both synapse weights and delays are drawn from appropriate Gaussian distributions. All synapses are static. Each neuron receives independent Poissonian spikes as input. Both spike times and membrane potentials are measured.



LEAKY INTEGRATE-AND-FIRE NEURON

Membrane potentials V_i are modeled as an RC circuit:



$$\tau_{\mathrm{m}} \frac{\mathrm{d}V_i(t)}{\mathrm{d}t} = -(V_i(t) - E_L) + \frac{\tau_{\mathrm{m}}}{C_{\mathrm{m}}} I_i(t)\,. \tag{1}$$

If $V_i(t)$ reaches the threshold θ:

$\Rightarrow$ Spike is emitted

$\Rightarrow$ $V_i(t) = E_L$ for refractory period τ_{rp}

CURRENT-BASED SYNAPSE MODEL

Each spike of neuron j elicits an exponentially decaying current in the postsynaptic neuron i. The amplitude is set by the synaptic weight w_{ij}. The total incoming current is a linear sum over all synapses:

$$I_i(t) = \sum_j w_{ij} \sum_k \exp\left(\frac{t - t_j^k - d_{ij}}{\tau_{\mathrm{syn}}}\right) \Theta(t - t_j^k - d_{ij})\,, \tag{2}$$

where t_j^k is the spike time of the k-th spike of neuron j and $\Theta(t)$ is the Heaviside function.

MEAN FIELD THEORY

STATISTICAL INPUT

The mean field model based on Brunel's work [1] predicts firing rates for spiking network models of leaky integrate-and-fire neurons (Equation (1)). For a sparsely connected network with uncorrelated input to the neurons, the input current $I_i(t)$ to neuron i in population a can be described by the stochastic differential equation

$$\frac{\tau_{\mathrm{m}}}{C_{\mathrm{m}}} I_i(t) = \mu_a(t) + \sigma_a(t)\sqrt{\tau_{\mathrm{m}}}\eta_i(t) \tag{3}$$

with mean μ and variance density σ^2 of the Gaussian white noise η_i :

$$\mu_a = \tau_{\mathrm{m}} \sum_{b \in \mathrm{pop.}} C_{ab} J_{ab} \nu_b + \tau_{\mathrm{m}} C_a^{\mathrm{ext}} J \nu_{\mathrm{ext}}\,; \tag{4}$$

$$\sigma_a{}^2 = \tau_{\mathrm{m}} \sum_{b \in \mathrm{pop.}} C_{ab} J_{ab}{}^2 \nu_b + \tau_{\mathrm{m}} C_a^{\mathrm{ext}} J^2 \nu_{\mathrm{ext}}\,. \tag{5}$$

DESCRIPTION BY MEMBRANE POTENTIALS

Transformation via

1. $\Rightarrow$ Fokker-Planck equation for membrane potential distributions;
2. $\Rightarrow$ stationary solution to Fokker-Planck equation;
3. $\Rightarrow$ normalization condition for probability distributions

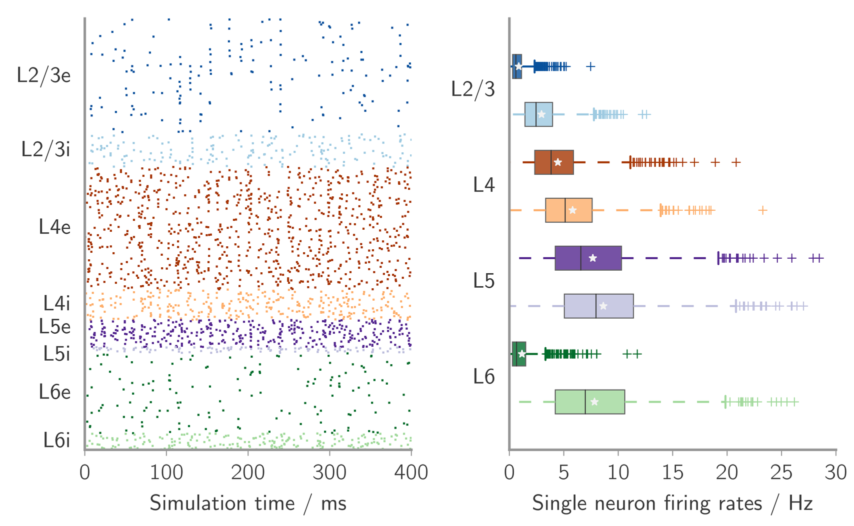
leads to self-consistency equations for the firing rates ν_a of each population,

$$\frac{1}{\nu_a} = \tau_{rp} + \tau_{\mathrm{m}}\sqrt{\pi} \int_{\frac{V_r - \mu_a}{\sigma_a}}^{\frac{\theta - \mu_a}{\sigma_a}} e^{u^2}\,(1 + \mathrm{erf}(u))\,\mathrm{d}u\,, \tag{6}$$

which are coupled via the integration boundaries. Solutions are found numerically.

RESULTS

NETWORK ACTIVITY



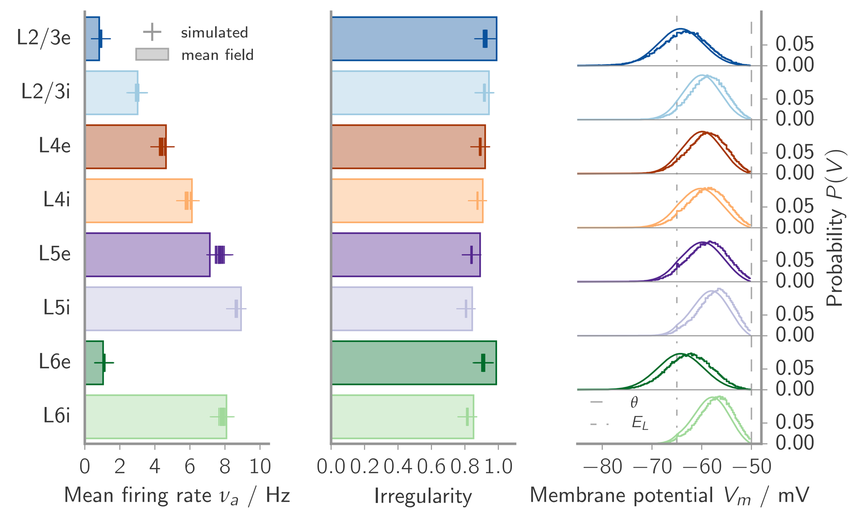
Raster plot:

- Spikes of 2.5 % of each population
- Asynchronous and irregular activity
- Little synchronization e. g. in L2/3e

Box plot of single neuron firing rates:

- Large fluctuations around the means (white stars)

PREDICTIONS VS. SIMULATION



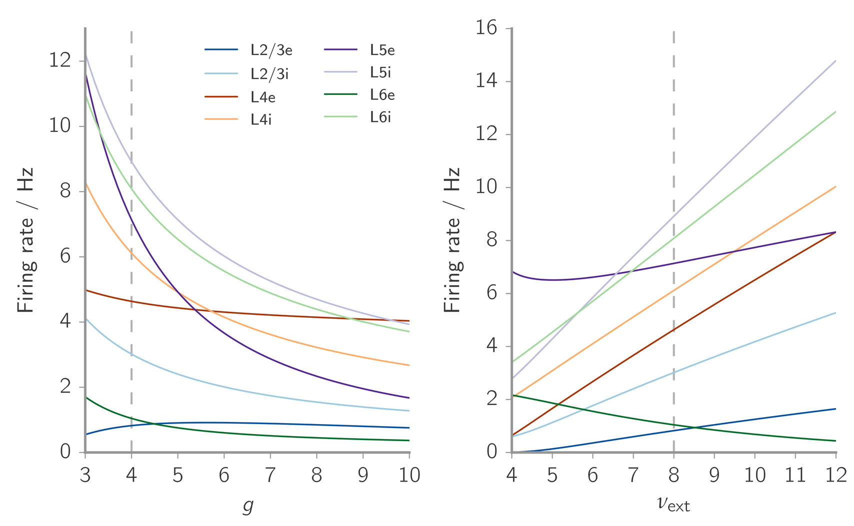
Firing rates and Irregularity:

- Compared to simulations of 20 different network realizations
- Irregularity = coefficient of variation of interspike intervals (ISI) = $\frac{\sigma_{\mathrm{ISI}}}{\mu_{\mathrm{ISI}}}$

Membrane potential distributions:

- Predictions (smooth curves) are solutions of Fokker-Planck eq.
- Steps at $E_L = -65\,\mathrm{mV}$: neurons coming out of refractory period

EXPLORING THE PARAMETER SPACE



Predicted firing rates for networks with different parameters:

- g: governs ratio of inhibition over excitation
- ν_{ext}: base rate of the external Poisson process
- Operating point in previous work: dashed lines
- Simulating the data would have taken days, predicting took seconds

CONCLUSION

- The mean field theory predicts firing rates and irregularity to a high accuracy (relative errors below 10 %).
- Deviations may be due to neglecting correlations, or due to the diffusion approximation assuming infinitesimally small PSCs.
- The theory can be applied as a convenient computational tool (greatly reduced numerical effort as compared to simulations, quasi-analytical description).

VARIABLES

SPIKING NETWORK MODEL

$V_i(t)$	Membrane potential
E_L	Resting potential
τ_{m}	Membrane time constant
C_{m}	Membrane capacity
$I_i(t)$	Input current
τ_{syn}	Synaptic time constant
w	Synaptic strength
d	Delay

MEAN FIELD THEORY

Recurrent (populations a and b):

C_{ab}	Number of synapses
J_{ab}	Synaptic weight
ν_a	Single neuron firing rate

External:

C_a^{ext}	Number of synapses
J	Synaptic weight *
ν_{ext}	Rate of Poisson process

* Synapses are modeled differently: Whereas the spiking network model uses current based exponential synapses (as in Equation (2)), the mean field theory is originally developed for synapses with delta-currents (each synapse elicits a fixed change in voltage instantaneously). To account for the difference, J is adapted.

REFERENCES

[1] N. Brunel. Dynamics of sparsely connected networks of excitatory and inhibitory spiking neurons. *Journal of Computational Neuroscience*, 2000
[2] T. Potjans and M. Diesmann. The cell-type specific cortical microcircuit: Relating structure and activity in a full-scale spiking network model. *Cerebral Cortex*, 2014