A network model of the neocortex accounting for its laminar structure

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September 21, 2015

Supervisor: Prof. Jens Timmer

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Central goals of the thesis

Implement a spiking network model of the neocortex

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Develop a mean field theory for the neocortical model

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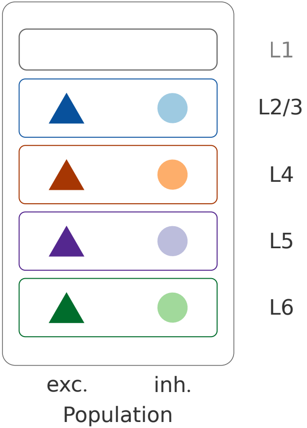
Layered structure

8 Populations of size N_a

Synapse numbers C_{ab}

External input of frequency ν_{ext}



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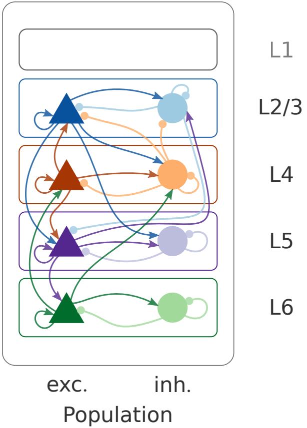

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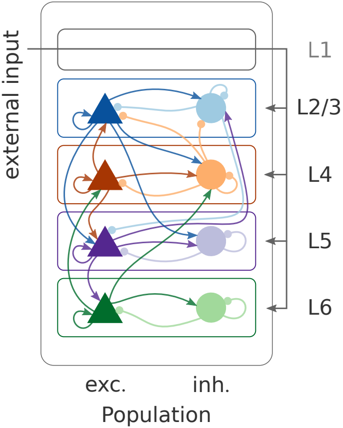
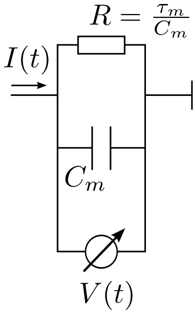


Membrane dynamics

$$\tau_\mathrm{m} \frac{\mathrm{d}V_i(t)}{\mathrm{d}t} = -V_i(t) + \frac{\tau_\mathrm{m}}{C_\mathrm{m}} I_i(t)$$

$V_i(t)$	Membrane potential
τ_m	Membrane time constant
C_m	Membrane capacity
$I_i(t)$	Input current



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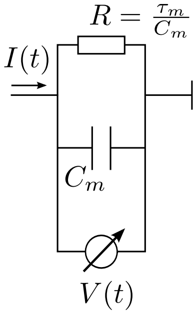


If $V_i(t)$ reaches the threshold θ:

- Spike is emitted
- $V_i(t) = V_r$ for refractory period τ_{rp}

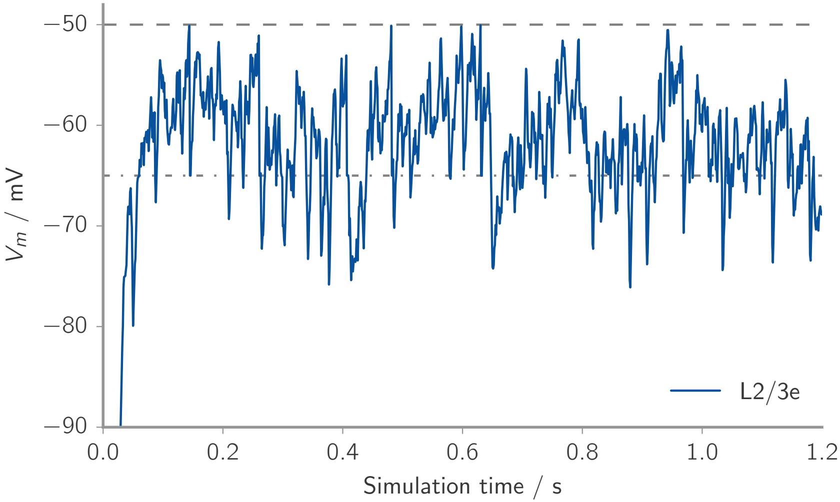
Synapse dynamics

Single spike

$$I_{\text{syn}}(t) = w \exp\left(\frac{-t}{\tau_{\text{syn}}}\right)$$

w	Synaptic strength
τ_{syn}	Synaptic time constant

Example



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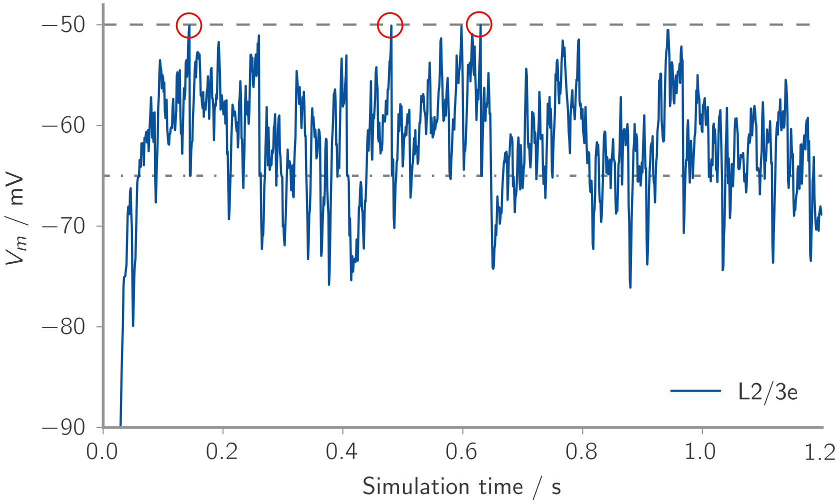

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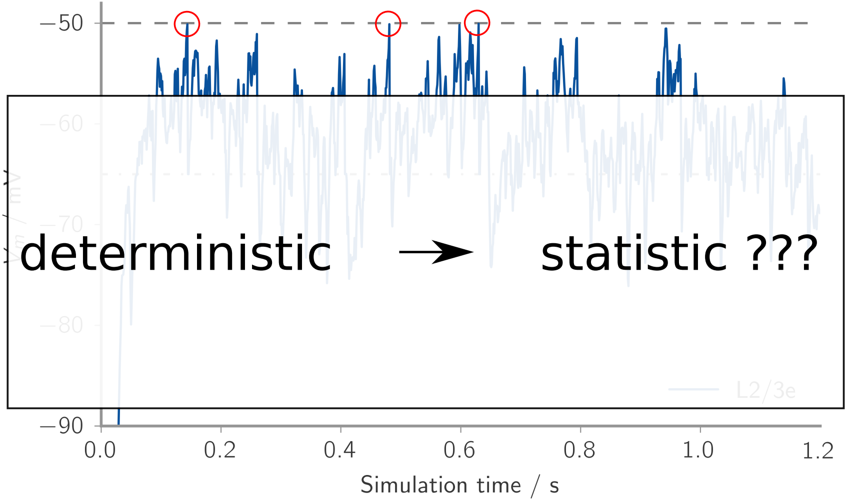
−50
−60
−70
−80
−90
V_m / mV
deterministic → statistic ???
L2/3e
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Simulation time / s

Statistical description

Sparse network: $\epsilon = C/N \to 0$

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Input current:

$$\frac{\tau_\mathrm{m}}{C_\mathrm{m}} I_i(t) = \mu(t) + \sigma(t)\sqrt{\tau_\mathrm{m}}\eta_i(t)$$

$\mu(t)$	Average input
$\sigma(t)$	Amplitude of fluctuation
$\eta_i(t)$	Gaussian white noise

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Uncorrelated input: $\langle \eta_i(t)\, \eta_j(t') \rangle = \delta_{ij}\, \delta(t - t')$

stochastic input $\xleftrightarrow{?}$ membrane potential distributions

Fokker–Planck equation

$$\tau_{\mathrm{m}} \frac{\partial P(V,t)}{\partial t} = \frac{\sigma^2(t)}{2} \frac{\partial^2 P(V,t)}{\partial V^2} + \frac{\partial}{\partial V}[(V - \mu(t))P(V,t)]$$

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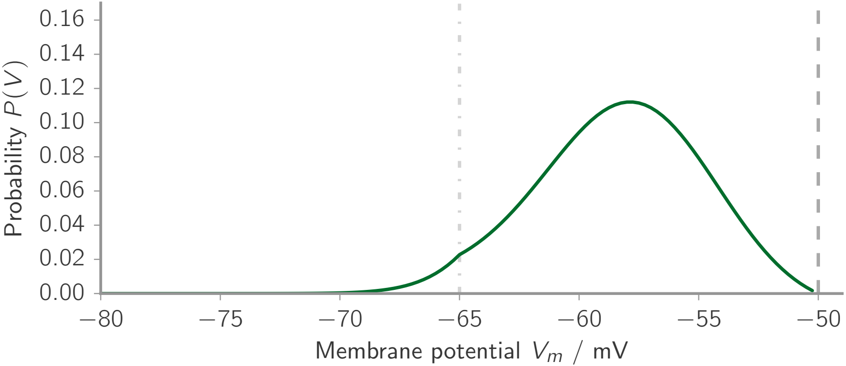

Self-consistency equation

$$\frac{1}{\nu_a} = \tau_{rp} + \tau_{\mathrm{m}}\sqrt{\pi}\int_{\frac{V_{\mathrm{r}}-\mu_a}{\sigma_a}}^{\frac{\theta-\mu_a}{\sigma_a}} e^{u^2}\left(1+\mathrm{erf}(u)\right)\mathrm{d}u$$

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Statistical input:

$$\mu_a = \tau_{\mathrm{m}} \sum_{b\,\in\,\mathrm{pop.}} C_{ab}\,J_{ab}\,\nu_b + \tau_{\mathrm{m}}\big(C_{\mathrm{ext}}\big)_a\,J\,\nu_{\mathrm{ext}}\,;$$

$${\sigma_a}^2 = \tau_{\mathrm{m}} \sum_{b\,\in\,\mathrm{pop.}} C_{ab}\,{J_{ab}}^2\,\nu_b + \tau_{\mathrm{m}}\big(C_{\mathrm{ext}}\big)_a\,J^2\,\nu_{\mathrm{ext}}$$

Predictions

Firing rates ν_a

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Membrane potential distribution $P_a(V)$

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Firing rates ν_a

Membrane potential distribution $P_a(V)$

Irregularity
= Coefficient of variation of interspike intervals

$$\mathrm{CV}_{\mathrm{ISI}} = \frac{\sigma_{\mathrm{ISI}}}{\mu_{\mathrm{ISI}}}$$

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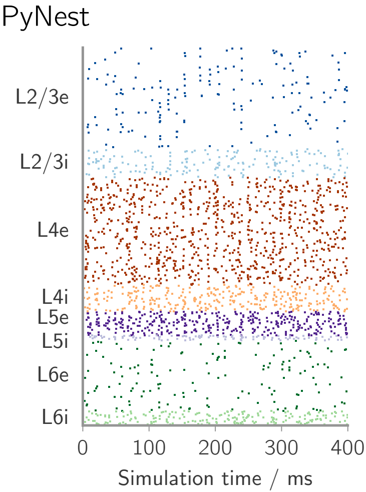
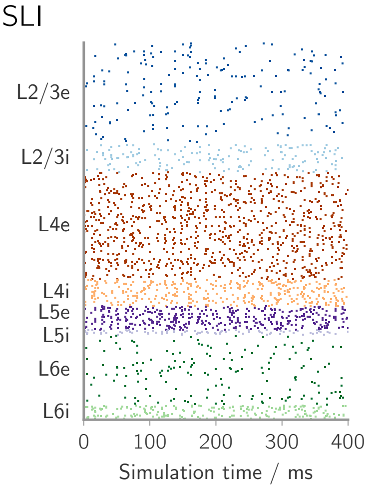
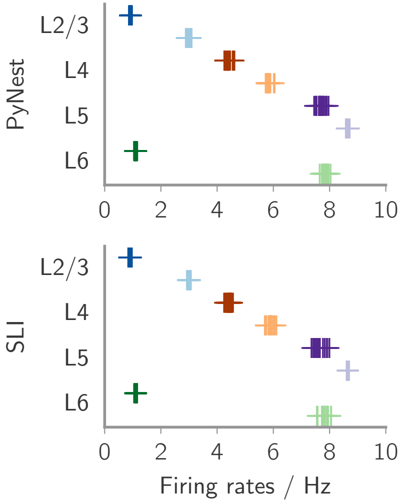
Implementation of spiking network model





Statistical comparison



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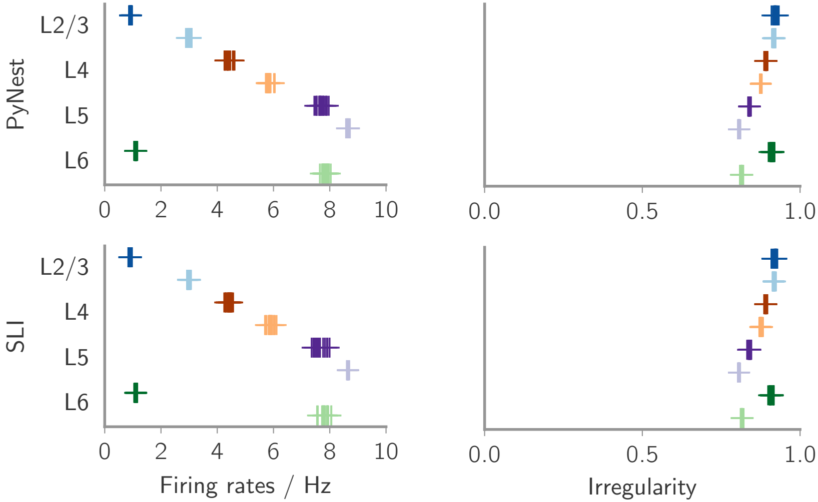
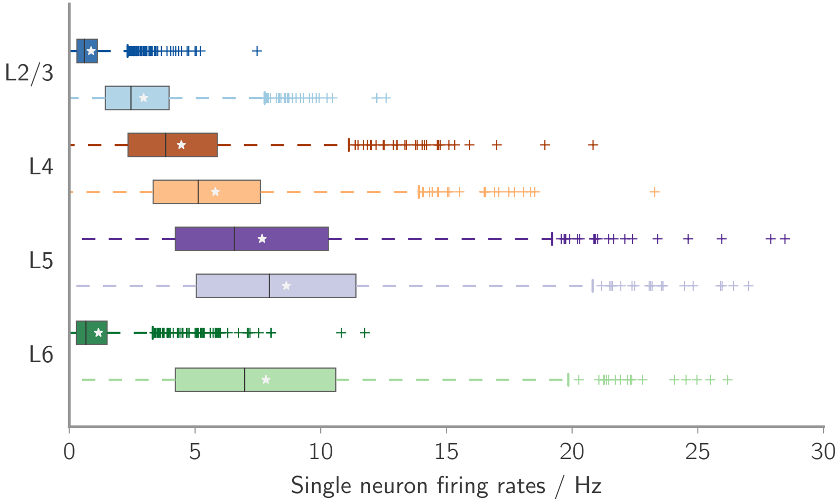
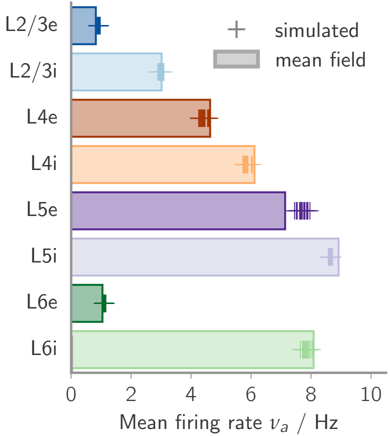


Single neuron activity



Mean field vs. simulation



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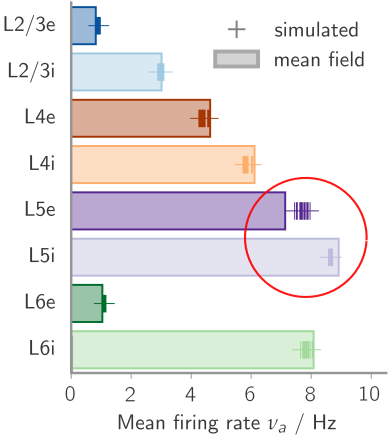

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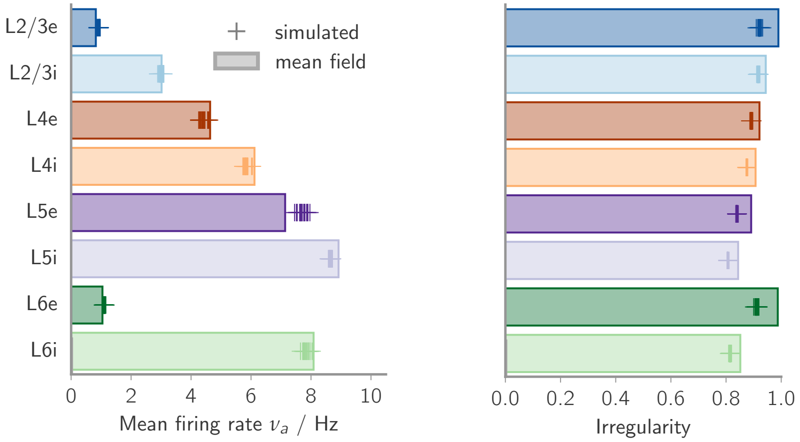

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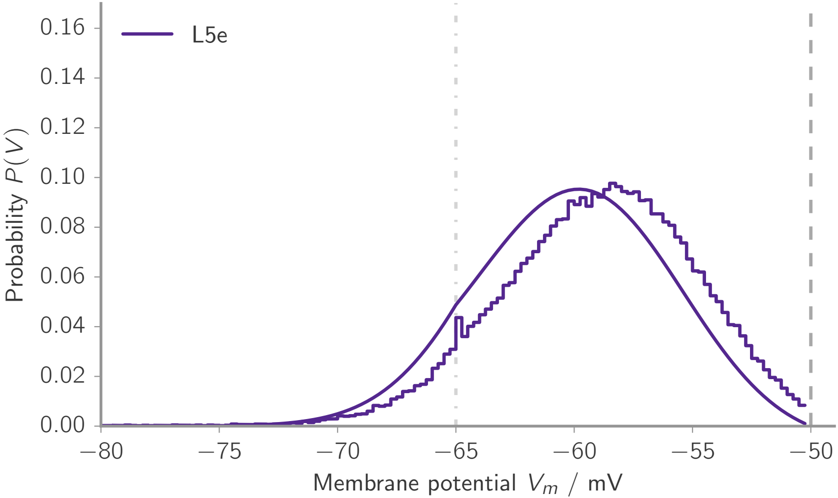
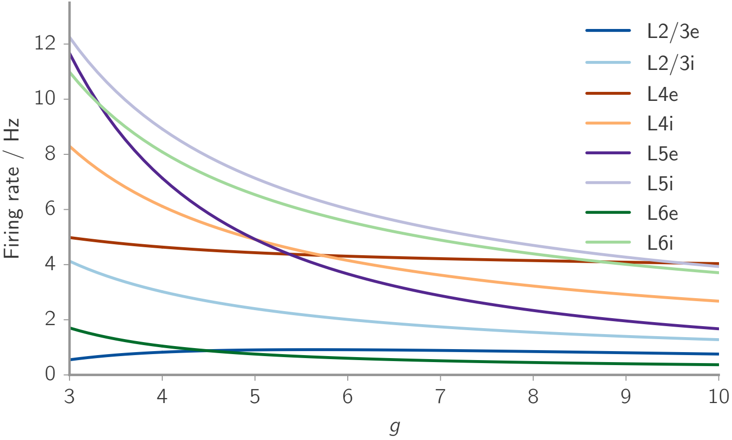


Applying mean field theory

Varying inhibitory synaptic strength g



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Implementation successful

- Results of Potjans and Diesmann reproduced

Mean field model yields good results

- Deviations due to neglecting correlations?

Mean field model also applicable as a tool

- Computationally much less expensive than simulation

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Outlook

Extension to more distinct neuron populations

Application to cortical computation, e. g. in the visual cortex

Temporal dynamics for rate based coding

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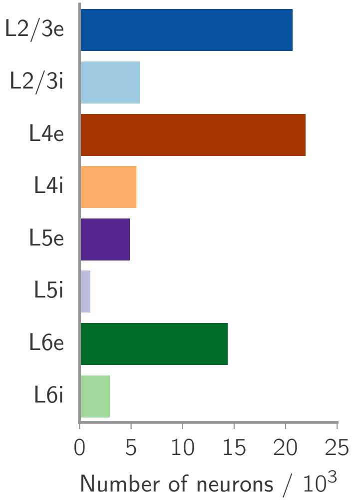
Acknowledgements

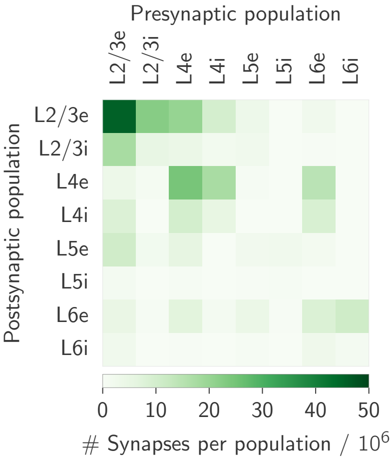
Thanks to

- Jens Timmer
- Stefan Rotter
- Benjamin Merkt

Appendix

Population sizes and synapse numbers





Single neuron firing rate in Brunel's model

Mean input:

$$
\begin{aligned}
& \mu(t) = \mu_I(t) + \mu_{\text{ext}} \\
\text{with} \qquad & \mu_I(t) = C_E\, J(1 - \gamma g)\nu(t-d)\tau_{\text{m}} \\
\text{and} \qquad & \mu_{\text{ext}} = C_E J \nu_{\text{ext}} \tau_{\text{m}}\,.
\end{aligned}
$$

Amplitude of fluctuations:

$$
\begin{aligned}
& \sigma^2(t) = {\sigma_I}^2(t) + {\sigma_{\text{ext}}}^2 \\
\text{with} \qquad & {\sigma_I}^2(t) = C_E\, J^2(1 + \gamma g^2)\nu(t-d)\tau_{\text{m}} \\
\text{and} \qquad & {\sigma_{\text{ext}}}^2 = C_E J^2 \nu_{\text{ext}} \tau_{\text{m}}\,.
\end{aligned}
$$

Stationary solution

Constraints

$$
\begin{aligned}
P(\theta, t) &= 0 \\
\frac{\partial P(\theta, t)}{\partial V} &= -\frac{2\nu(t)\tau_{\mathrm{m}}}{\sigma^2(t)} \\
\frac{\partial P(V_{\mathrm{r}}^{+}, t)}{\partial V} - \frac{\partial P(V_{\mathrm{r}}^{-}, t)}{\partial V} &= -\frac{2\nu(t-\tau_{\mathrm{rp}})\tau_{\mathrm{m}}}{\sigma^2(t)} \\
\lim_{V\to-\infty} P(V, t) = 0\,; \qquad \lim_{V\to-\infty} &VP(V, t) = 0\,.
\end{aligned}
$$

Solution

$$
P_0(V) = 2\frac{\nu_0\tau_{\mathrm{m}}}{\sigma_0}\exp\left(-\frac{(V-\mu_0)^2}{{\sigma_0}^2}\right)\int_{\frac{V-\mu_0}{\sigma_0}}^{\frac{\theta-\mu_0}{\sigma_0}}\Theta\left(u-\frac{V_{\mathrm{r}}-\mu_0}{\sigma_0}\right)e^{u^2}\,\mathrm{d}u
$$

Self-consistency equation – derivation

Solution

$$P_0(V) = 2\frac{\nu_0 \tau_{\mathrm{m}}}{\sigma_0} \exp\left(-\frac{(V-\mu_0)^2}{{\sigma_0}^2}\right) \int_{\frac{V-\mu_0}{\sigma_0}}^{\frac{\theta-\mu_0}{\sigma_0}} \Theta\left(u - \frac{V_{\mathrm{r}}-\mu_0}{\sigma_0}\right) e^{u^2}\,\mathrm{d}u$$

$$\int_{-\infty}^{\theta} P_0(V)\,\mathrm{d}V + p_r = 1\,,$$

where $\qquad p_r = \nu_0 \tau_{\mathrm{rp}}.$

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

Predicted $P(V)$ and CV of ISI

Membrane potential distribution:

$$P_a(V) = 2\frac{\nu_a \tau_{\mathrm{m}}}{\sigma_a} \exp\left(-\frac{(V-\mu_a)^2}{{\sigma_a}^2}\right) \int_{\frac{V-\mu_a}{\sigma_a}}^{\frac{\theta-\mu_a}{\sigma_a}} \Theta\left(u - \frac{V_{\mathrm{r}}-\mu_a}{\sigma_a}\right) e^{u^2}\, \mathrm{d}u\,.$$

Irregularity:

$$\mathrm{CV}_{\mathrm{ISI}}^2 = 2\pi \left(\frac{\nu_a}{\tau_{\mathrm{m}}}\right)^2 \int_{\frac{V_{\mathrm{r}}-\mu_a}{\sigma_a}}^{\frac{\theta-\mu_a}{\sigma_a}} e^{x^2} \int_{-\infty}^{x} e^{u^2} \left(1+\mathrm{erf}(u)\right)^2 \mathrm{d}u\ \mathrm{d}x$$

Different synapse dynamics

Current based synapses (spiking network model):

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

Voltage based synapses (mean field theory):

$$\frac{\tau_{\mathrm{m}}}{C_{\mathrm{m}}} I_i(t) = \tau_{\mathrm{m}} \sum_j J_{ij} \sum_k \delta(t - t_j^k - d_{ij})$$

Adapting for synapse model

Effective weight for mean input μ:

$$RI_e(t) = \frac{\tau_\mathrm{m}}{C_\mathrm{m}}\, w\, e^{\frac{t}{\tau_\mathrm{m}}} \qquad \text{exponential synapse}$$

$$RI_\delta(t) = \tau_\mathrm{m}\, J\, \delta(t) \qquad \text{delta synapse}$$

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$$RI_\delta(t) = \tau_\mathrm{m}\, J\, \delta(t) \qquad \text{delta synapse}$$

Matching the kernels (with $k_e(t) = e^{\frac{t}{\tau_\mathrm{m}}}$):

$$\int_0^\infty \delta(t)\,\mathrm{d}t = 1 = \int_0^\infty a_\mu k_e(t)\,\mathrm{d}t = a_\mu \tau_\mathrm{s}$$

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$$\int_0^\infty \delta(t)\,\mathrm{d}t = 1 = \int_0^\infty a_\mu k_e(t)\,\mathrm{d}t = a_\mu \tau_\mathrm{s}$$

Matching the synapses:

$$\int_0^\infty \tau_\mathrm{m}\, J\, a_\mu\, k_e(t)\,\mathrm{d}t = \int_0^\infty \frac{\tau_\mathrm{m}}{C_\mathrm{m}}\, w\, k_e(t)\,\mathrm{d}t$$

$$\Rightarrow \qquad J = \frac{w\,\tau_\mathrm{s}}{C_\mathrm{m}}$$

Adapting for synapse model

Effective weight for fluctuations $\sigma^2(t)$ Matching squared kernels:

$$\begin{aligned} 1 &= {a_\sigma}^2 \int_0^\infty (k_e(t))^2 \, \mathrm{d}t \\ &= {a_\sigma}^2 \, \frac{\tau_\mathrm{s}}{2} \\ \Rightarrow \qquad {a_\sigma}^2 &= 2/\tau_\mathrm{s} \end{aligned}$$

Adapting for synapse model

Effective weight for fluctuations $\sigma^2(t)$ Matching squared kernels:

$$
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1 &= {a_\sigma}^2 \int_0^\infty (k_e(t))^2 \, \mathrm{d}t \\
&= {a_\sigma}^2 \, \frac{\tau_\mathrm{s}}{2} \\
\Rightarrow \qquad {a_\sigma}^2 &= 2/\tau_\mathrm{s}
\end{aligned}
$$

Matching squared synapses:

$$
\begin{aligned}
\int_0^\infty (\tau_\mathrm{m} \, J \, a_\sigma \, k_e(t))^2 \, \mathrm{d}t &= \int_0^\infty \left(\frac{\tau_\mathrm{m}}{C_\mathrm{m}} \, w \, k_e(t) \right)^2 \mathrm{d}t \\
\Rightarrow \qquad {J_\mathrm{eff}}^2 &= \frac{w^2}{{C_\mathrm{m}}^2} \, \frac{\tau_\mathrm{s}}{2}
\end{aligned}
$$

Adapting for synapse model

Resulting equation for μ_a and σ_a:

$$\mu_a = \sum_{b \in \text{pop.}} (M_\text{local})_{ab}\, \nu_b + (M_\text{ext})_a\, \nu_\text{ext}\,;$$
$${\sigma_a}^2 = \sum_{b \in \text{pop.}} (S_\text{local})_{ab}\, \nu_b + (S_\text{ext})_a\, \nu_\text{ext}\,.$$

where

$$\begin{aligned}
(M_\text{local})_{ab} &:= \tau_\text{m}\, C_{ab}\, J_{ab}\,;\\
(M_\text{ext})_a &:= \tau_\text{m}\, (C_\text{ext})_a\, J\,;\\
(S_\text{local})_{ab} &:= \tau_\text{m}\, (1 + {\Delta_J}^2)\, C_{ab}\, ({J_\text{eff}}^2)_{ab}\,;\\
(S_\text{ext})_a &:= \tau_\text{m}\, (1 + {\Delta_J}^2)\, (C_\text{ext})_a\, {J_\text{eff}}^2
\end{aligned}$$

Comparing synchrony

Synchrony = Fano factor ($\frac{\sigma^2}{\mu}$) of PSTH

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