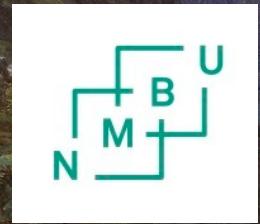


Modelling electric brain signals

Gaute T. Einevoll

*Norwegian University of Life Sciences (NMBU), Ås;
University of Oslo, Norway*



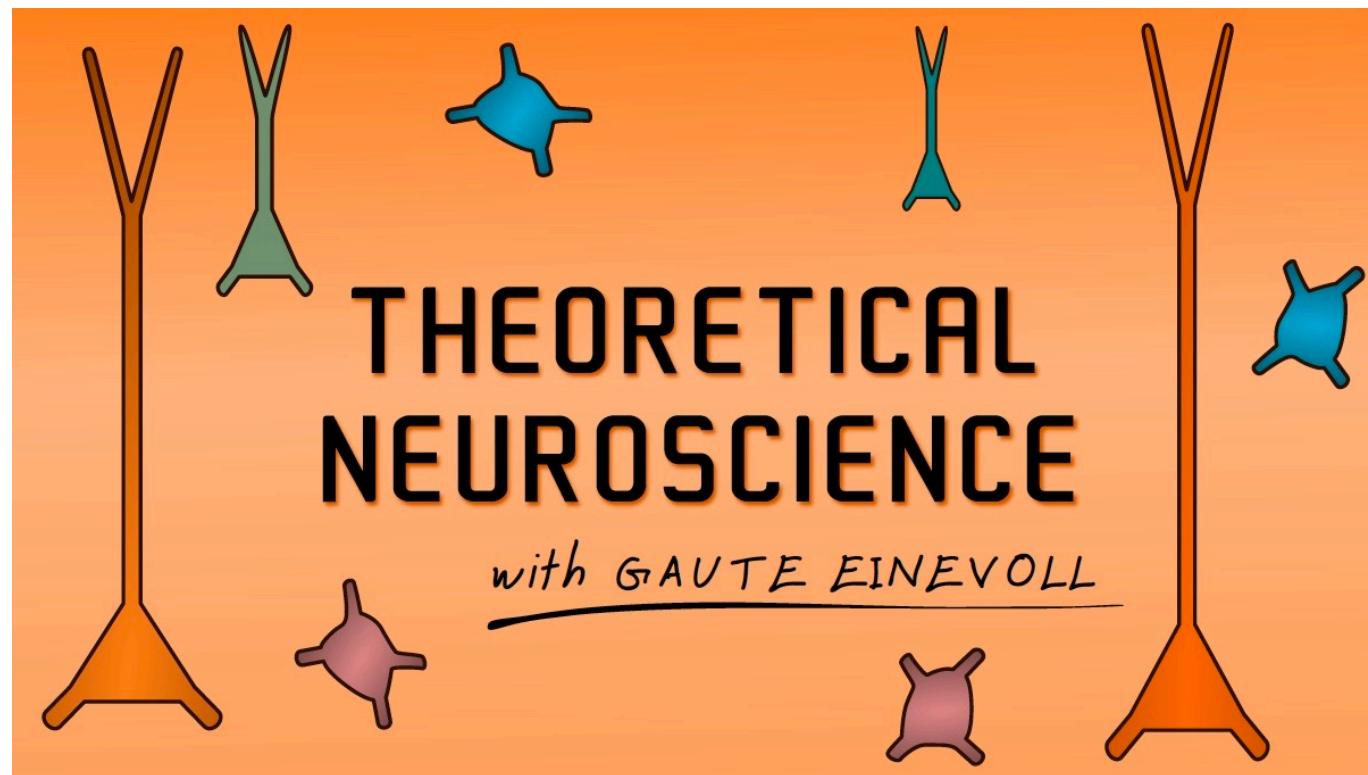
Podcast on interface between neuroscience and AI



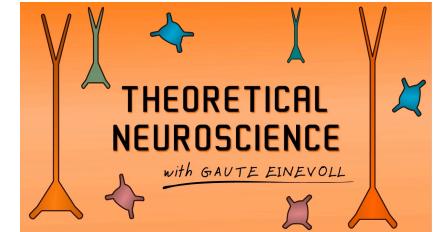


VETT OG
VITENSKAP
med GAUTE EINEVOLL

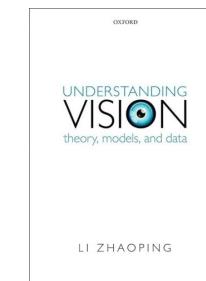
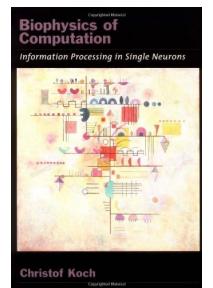
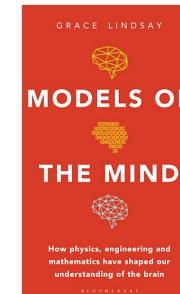
New podcast



First podcasts in series



- #1: Grace Lindsay: On models of the mind
- #2: Christof Koch: On biophysics of computation
- #3: Arvind Kumar: On the neural code
- #4: Sacha van Albada: On multi-area cortex models
- #5: Li Zhaoping: On how vision works
- #6: Henrik Lindén: On central pattern generators in the spinal cord
- #7:



theoreticalneuroscience.no



SVERRE MØRKEN 2002

COMMENTARY

PSYCHIATRIC DRUG DISCOVERY

Revolution Stalled

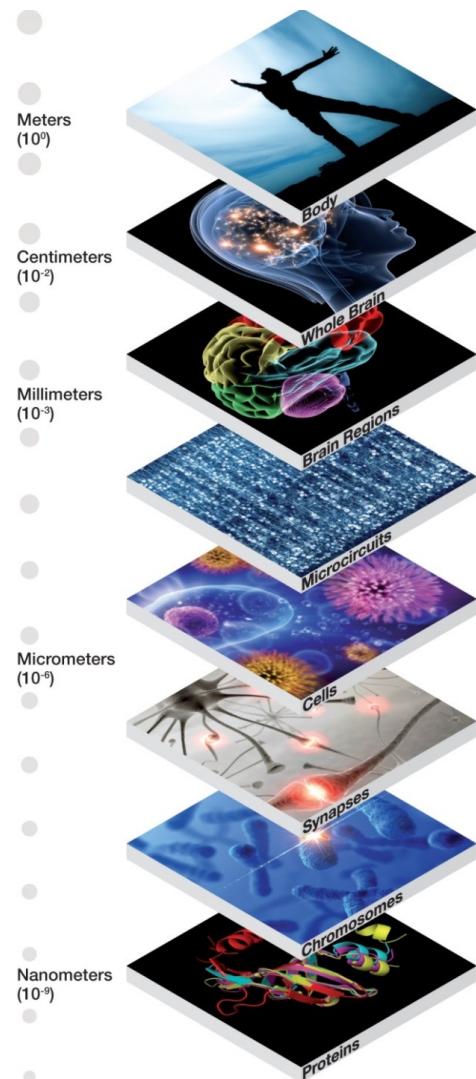
Steven E. Hyman

Drug discovery is at a near standstill for treating psychiatric disorders such as schizophrenia, bipolar disorder, depression, and common forms of autism. Despite high prevalence and unmet medical need, major pharmaceutical companies are deemphasizing or exiting psychiatry, thus removing significant capacity from efforts to discover new medicines. In this Commentary, I develop a view of what has gone wrong scientifically and ask what can be done to address this parlous situation.

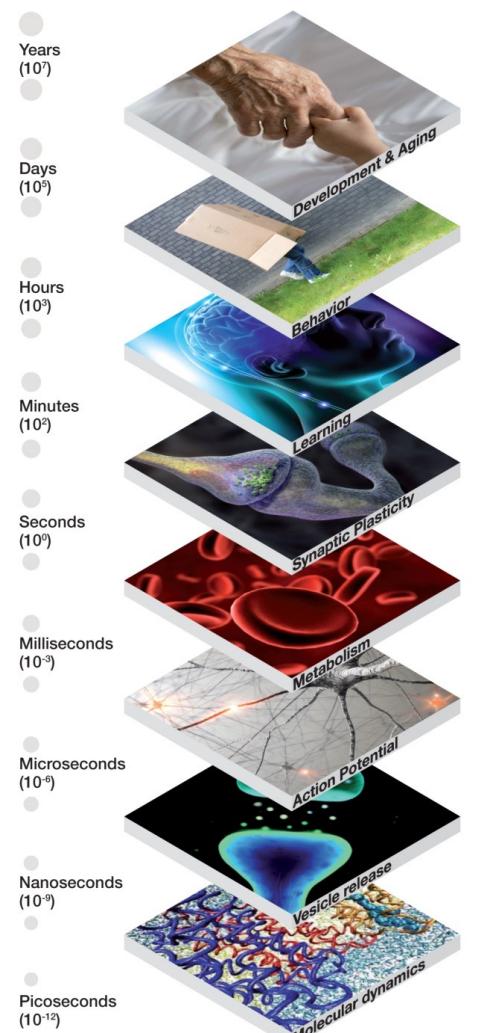
From an economic perspective, drugs for psychiatric disorders have historically been among the largest sources of revenue (Table 1) for the pharmaceutical industry. Given the high prevalence of psychiatric disorders (1), their massive effect

expertise and financial resources from therapeutics discovery. Here, I describe how we arrived at this crossroads and how we might get back on a productive path of discovery.

Spatial scales

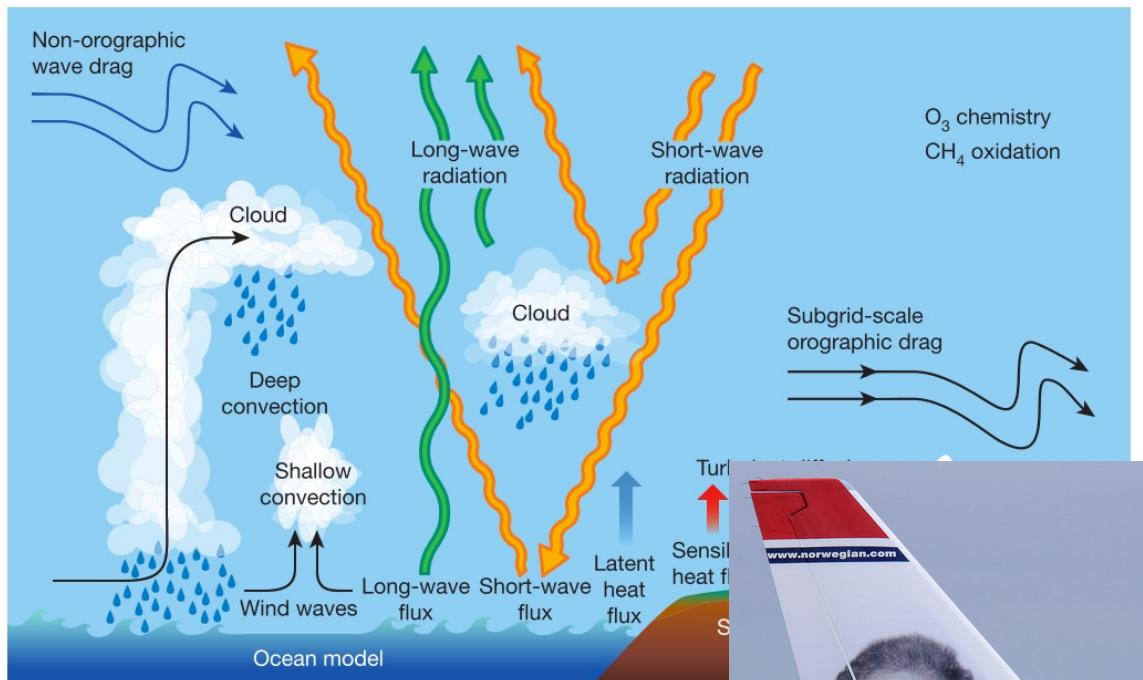


Time scales



Human Brain Project

Weather prediction



Vilhelm Bjerknes (~1900):
“*Weather prediction is a mathematical problem*”



- 1954: First weather forecast from mathematical models
- Now all weather forecasts are computed from such models
- Steadily improved quality:
Predicts one day better into the future per decade!

REVIEW

doi:10.1038/nature14956

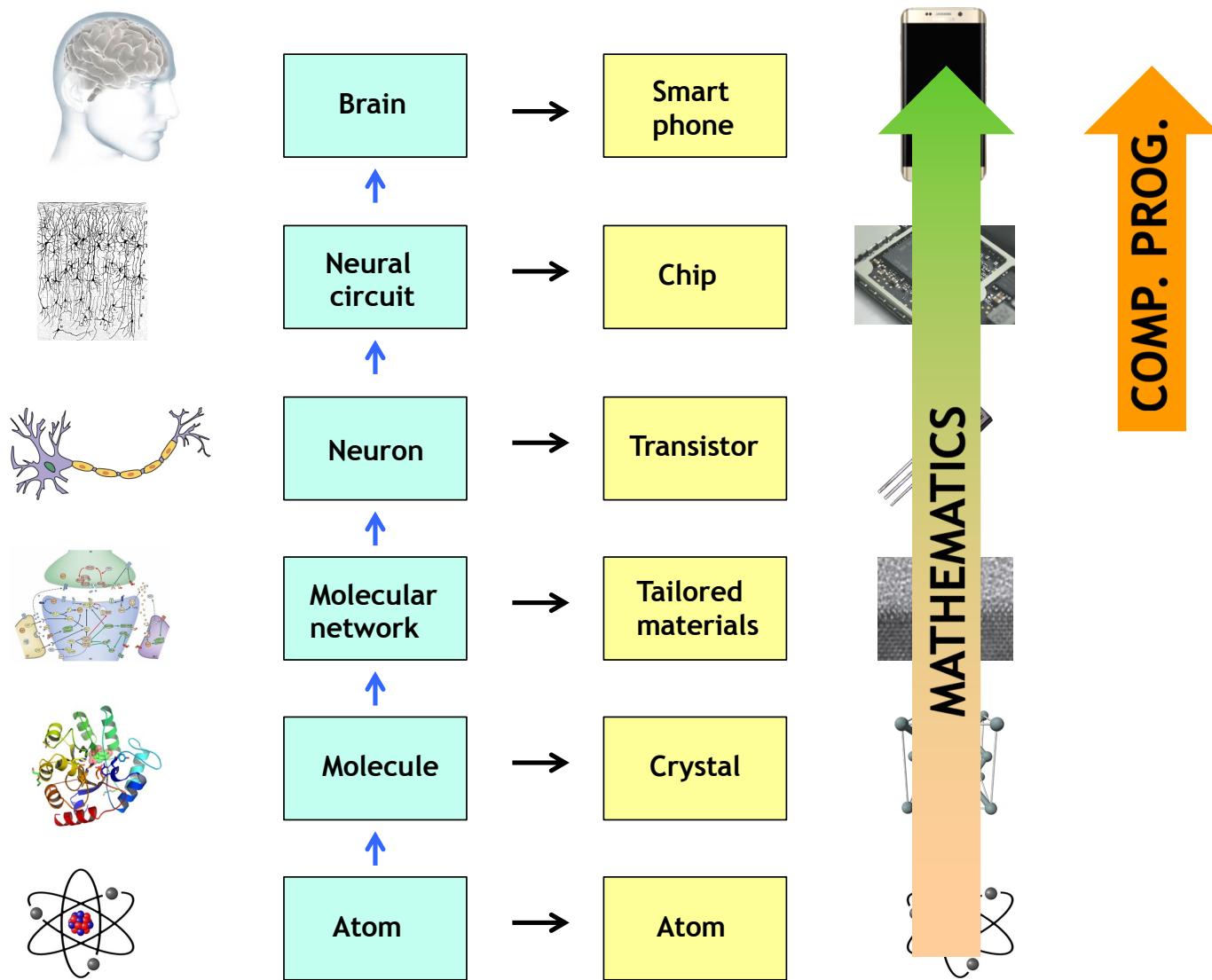
The quiet revolution of numerical weather prediction

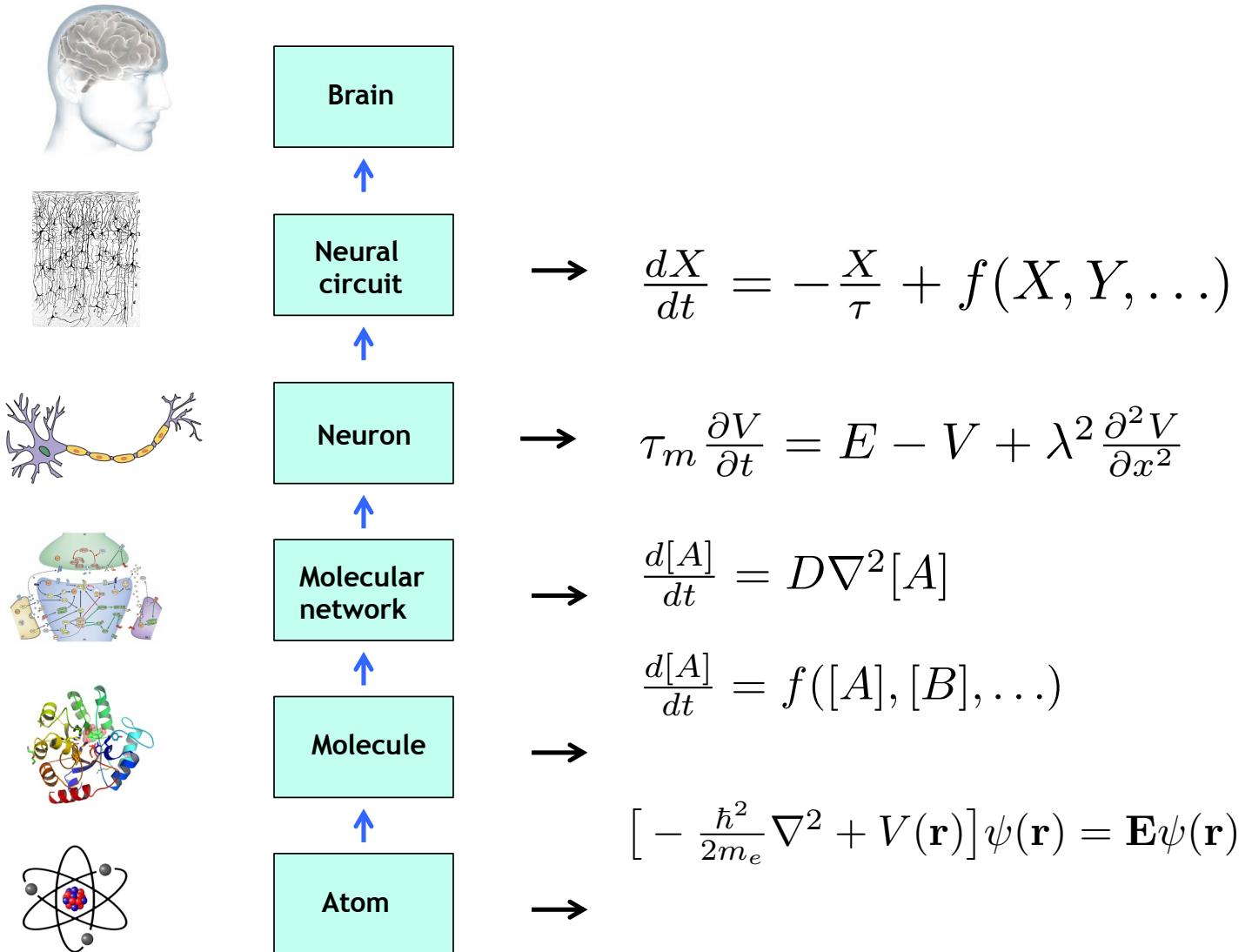
Peter Bauer¹, Alan Thorpe¹ & Gilbert Brunet²

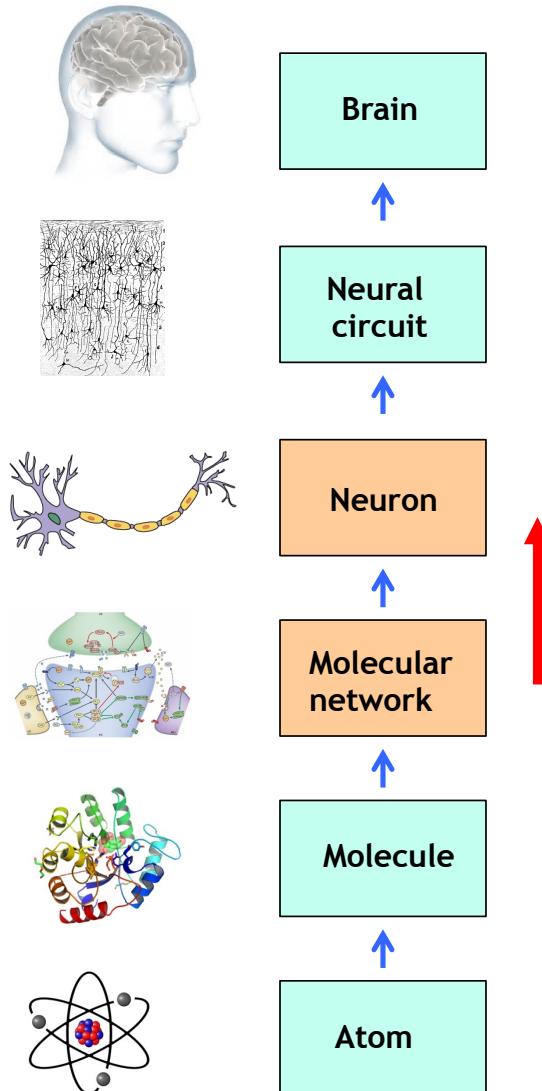
Bauer et al, Nature, 2016











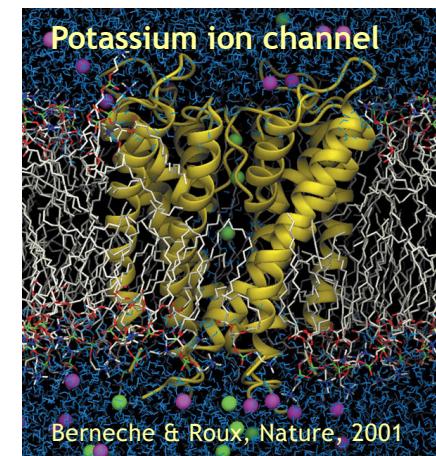
Hodgkin-Huxley equations

$$C_m \frac{dV(t)}{dt} + I_{Na}(t) + I_K(t) + I_{leak}(t) = 0$$

$$I_{Na}(t) = g_{Na}(V, t)(V(t) - E_{Na})$$

$$I_K(t) = g_K(V, t)(V(t) - E_K)$$

$$I_{leak} = g_{leak}(V - E_{leak})$$



LASCON2024

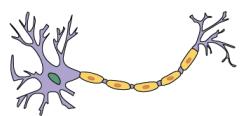
- Biophysical neuron models
- Simplified neuron models
- Synaptic plasticity



Brain



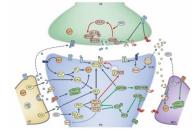
Neural circuit



Neuron



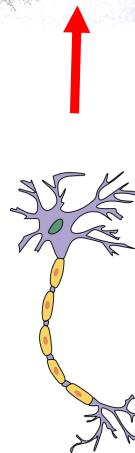
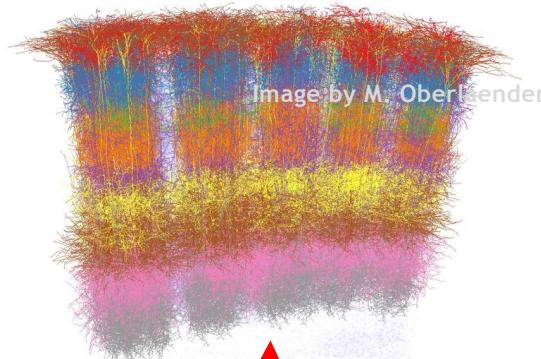
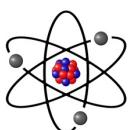
Molecular network



Molecule

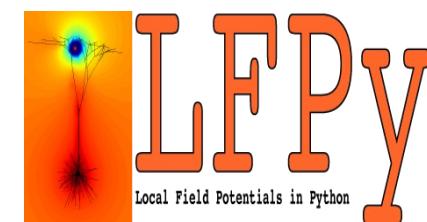


Atom



LASCON2024

- Small circuits
- Large circuits
- Tools:
 - NEST
 - NetPyne





“What I cannot create [*a model of*], I do not understand”

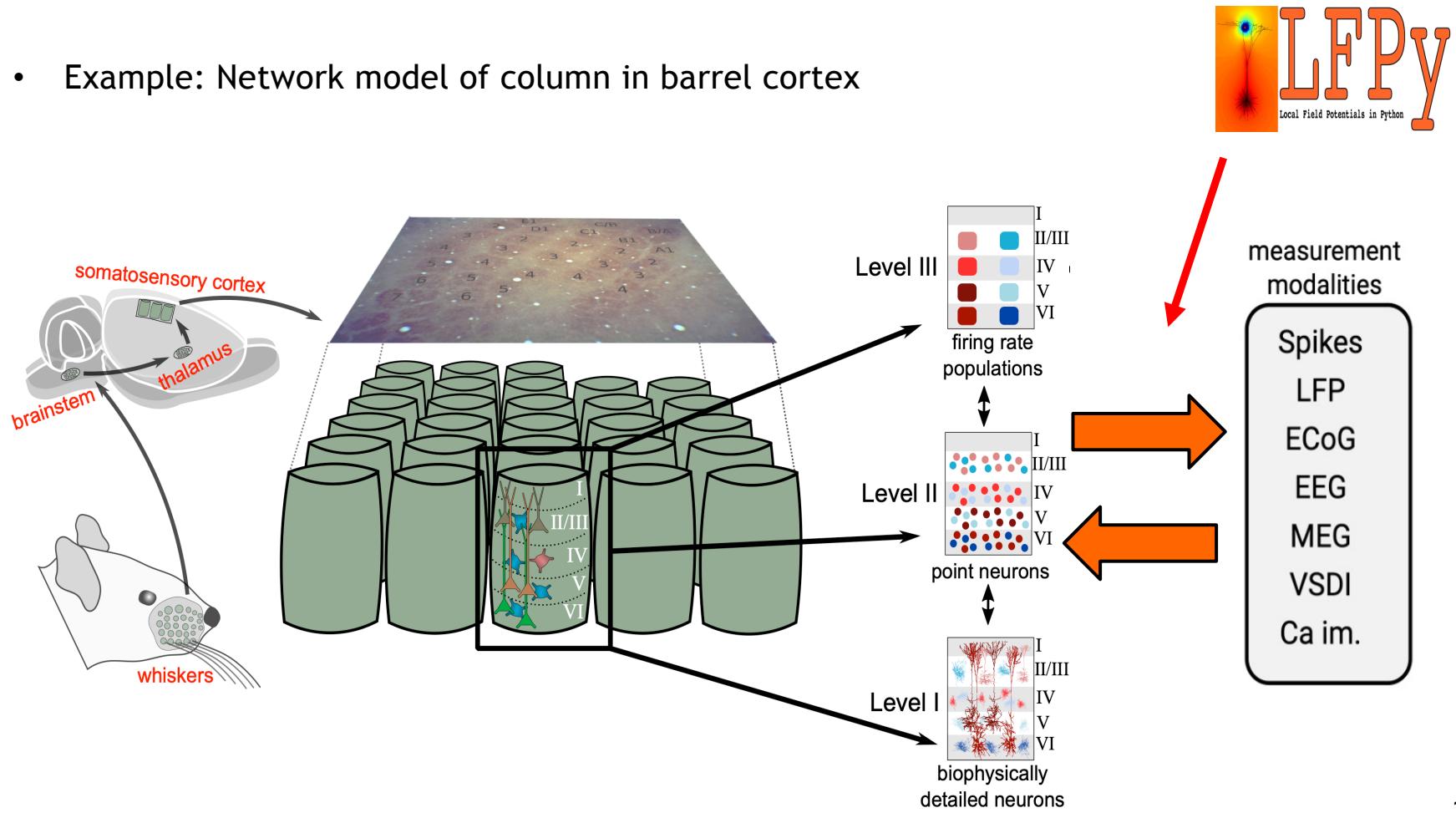
-Richard Feynman

Types of mathematical models in neuroscience

- Mechanistic models (“physics-type” models)
- Descriptive/statistical models (“data-analysis” models)
- Interpretive/normative models (“why”-models)

Multilevel + multimodal network modeling

- Example: Network model of column in barrel cortex



The Scientific Case for Brain Simulations

Gaute T. Einevoll,^{1,2,*} Alain Destexhe,^{3,4} Markus Diesmann,^{5,6,7} Sonja Grün,^{5,8} Viktor Jirsa,⁹ Marc de Kamps,¹⁰ Michele Migliore,¹¹ Torbjørn V. Ness,¹ Hans E. Plesser,^{1,5} and Felix Schürmann¹²

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²Department of Physics, University of Oslo, 0316 Oslo, Norway

³Paris-Saclay Institute of Neuroscience (NeuroPSI), Centre National de la Recherche Scientifique, 91198 Gif-sur-Yvette, France

⁴European Institute for Theoretical Neuroscience, 75012 Paris, France

⁵Institute of Neuroscience and Medicine (INM-6), Institute for Advanced Simulation (IAS-6), and JARA-Institut Brain Structure-Function Relationships (INM-10), Jülich Research Centre, 52425 Jülich, Germany

⁶Department of Psychiatry, Psychotherapy, and Psychosomatics, RWTH Aachen University, 52074 Aachen, Germany

⁷Department of Physics, RWTH Aachen University, 52074 Aachen, Germany

⁸Theoretical Systems Neurobiology, RWTH Aachen University, 52074 Aachen, Germany

⁹Institut de Neurosciences des Systèmes (INS), INSERM, Aix Marseille Université, 13005 Marseille, France

¹⁰Institute for Artificial and Biological Intelligence, School of Computing, Leeds LS2 9JT, UK

¹¹Institute of Biophysics, National Research Council, 90146 Palermo, Italy

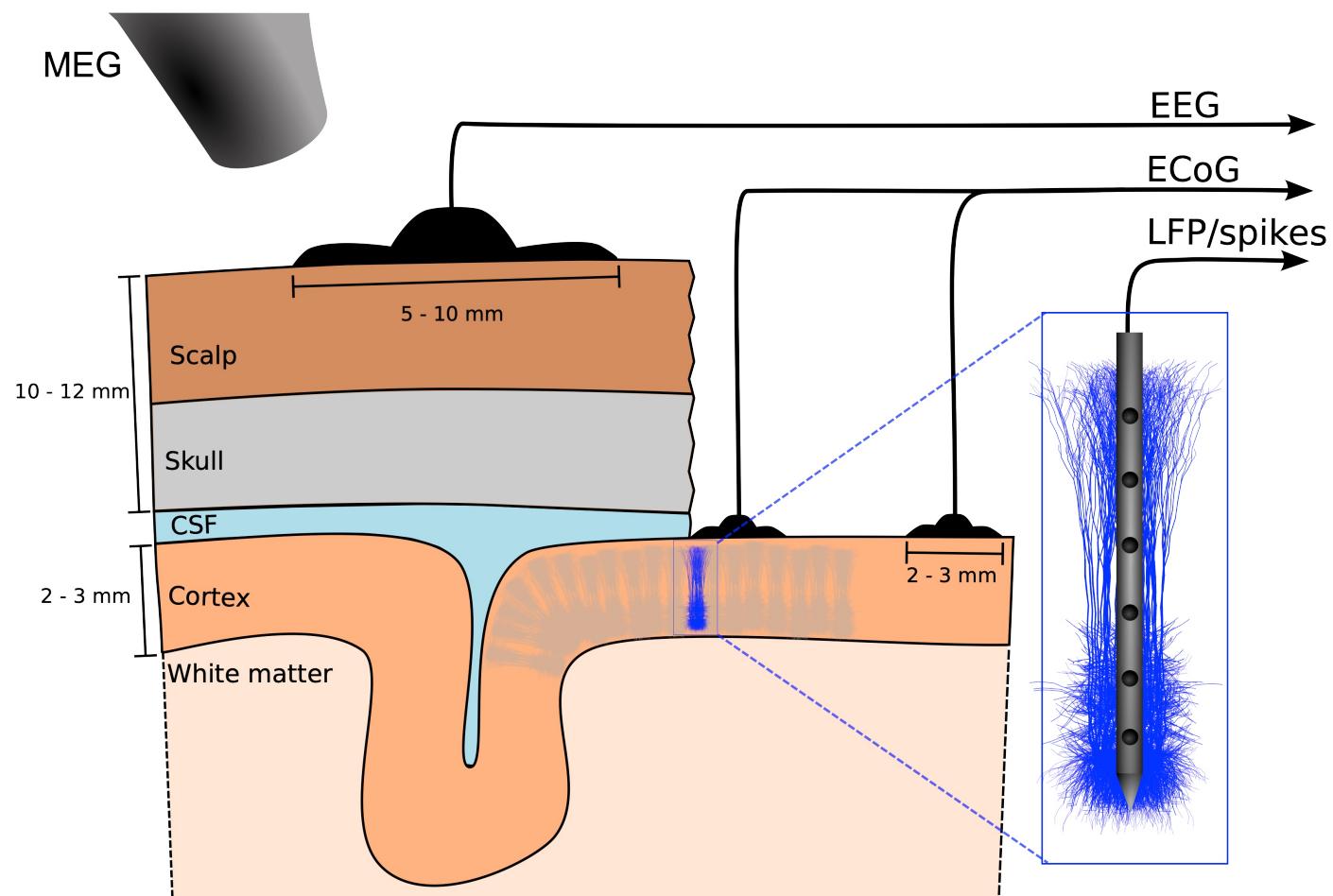
¹²Blue Brain Project, École Polytechnique Fédérale de Lausanne (EPFL), Campus Biotech, 1202 Geneva, Switzerland

*Correspondence: gaute.einevoll@nmbu.no

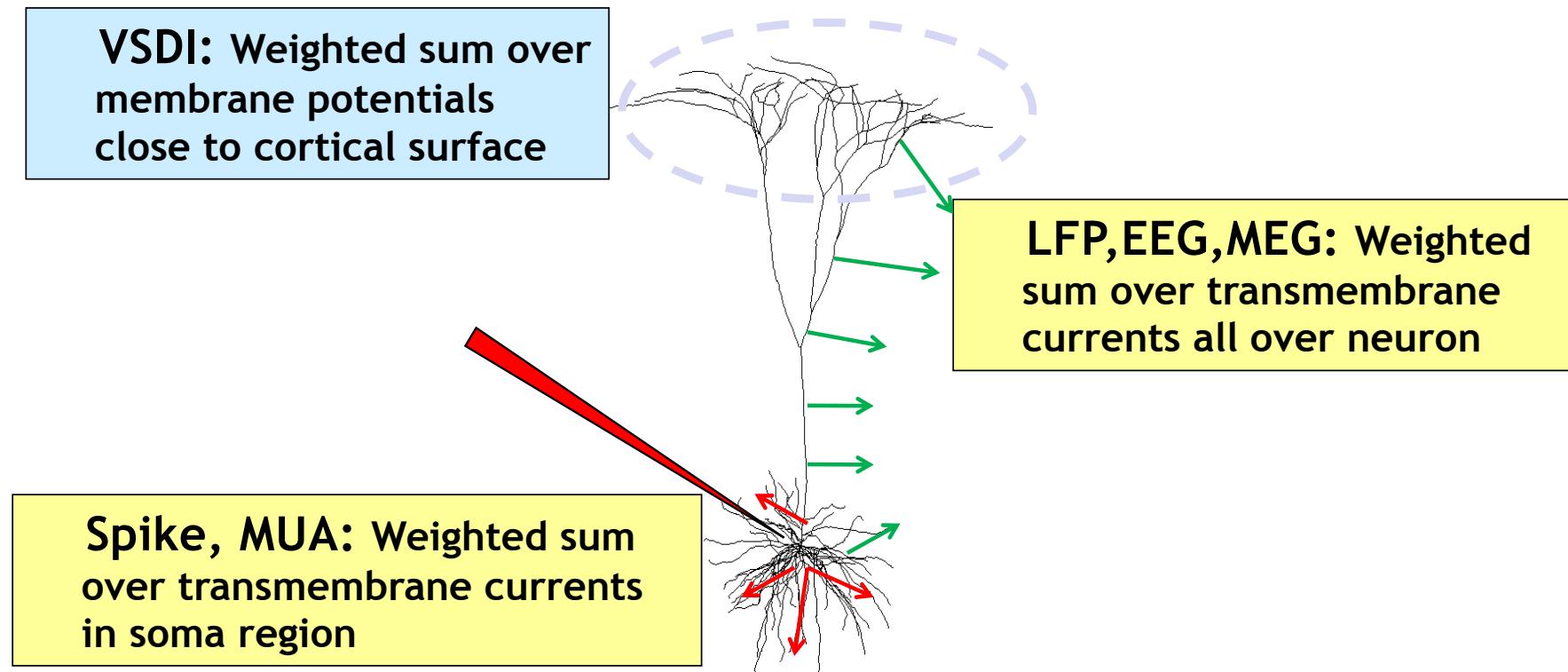
<https://doi.org/10.1016/j.neuron.2019.03.027>

A key element of the European Union's Human Brain Project (HBP) and other large-scale brain research projects is the simulation of large-scale model networks of neurons. Here, we argue why such simulations will likely be indispensable for bridging the scales between the neuron and system levels in the brain, and why a set of brain simulators based on neuron models at different levels of biological detail should therefore be developed. To allow for systematic refinement of candidate network models by comparison with experiments, the simulations should be multimodal in the sense that they should predict not only action potentials, but also electric, magnetic, and optical signals measured at the population and system levels.

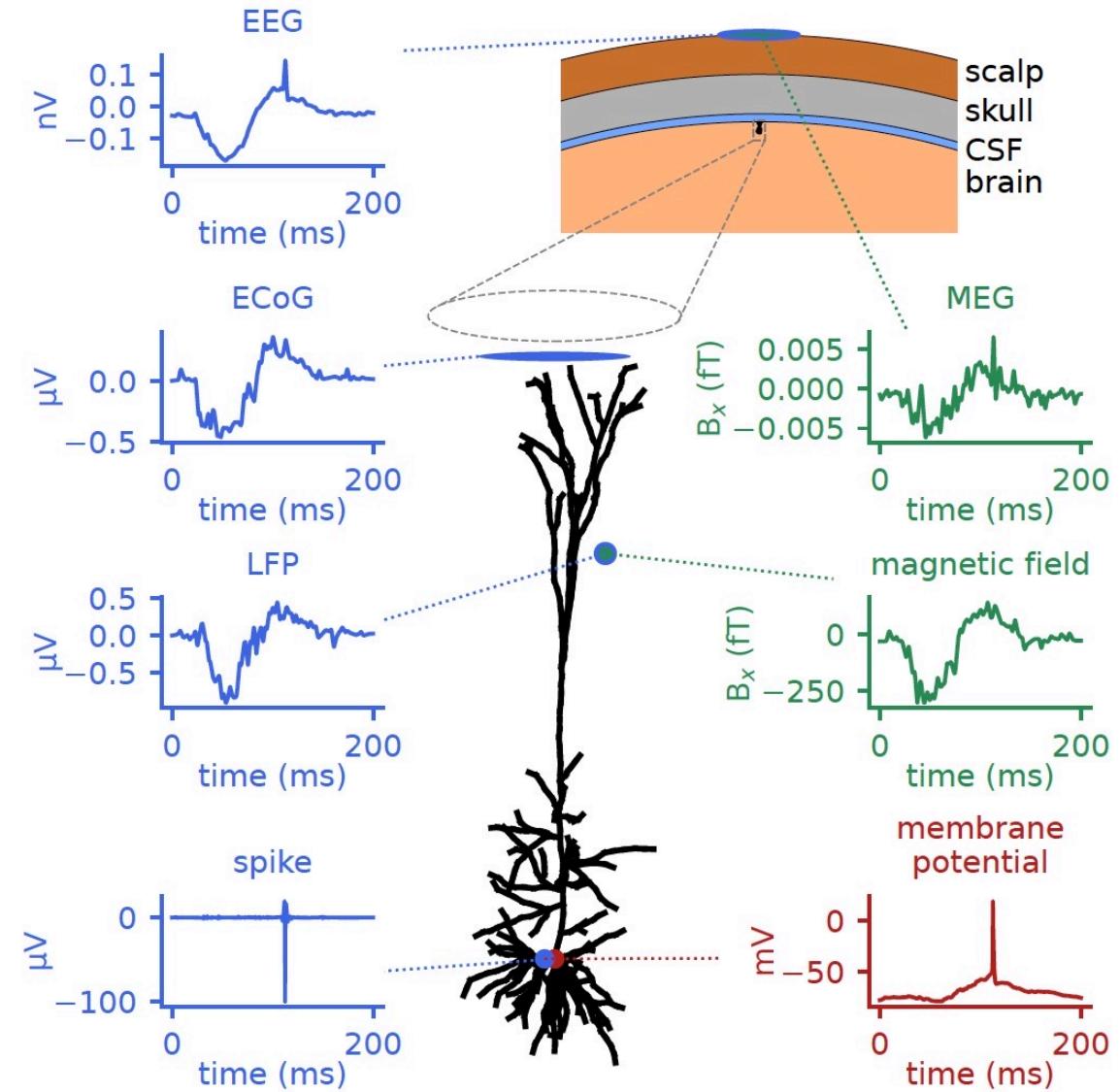
Systems level measurements of neural activity



Mechanistic modeling of brain signals



Modeled brain signals from single neuron firing action potential following synaptic inputs



From “Electric Brain Signals” (2024)

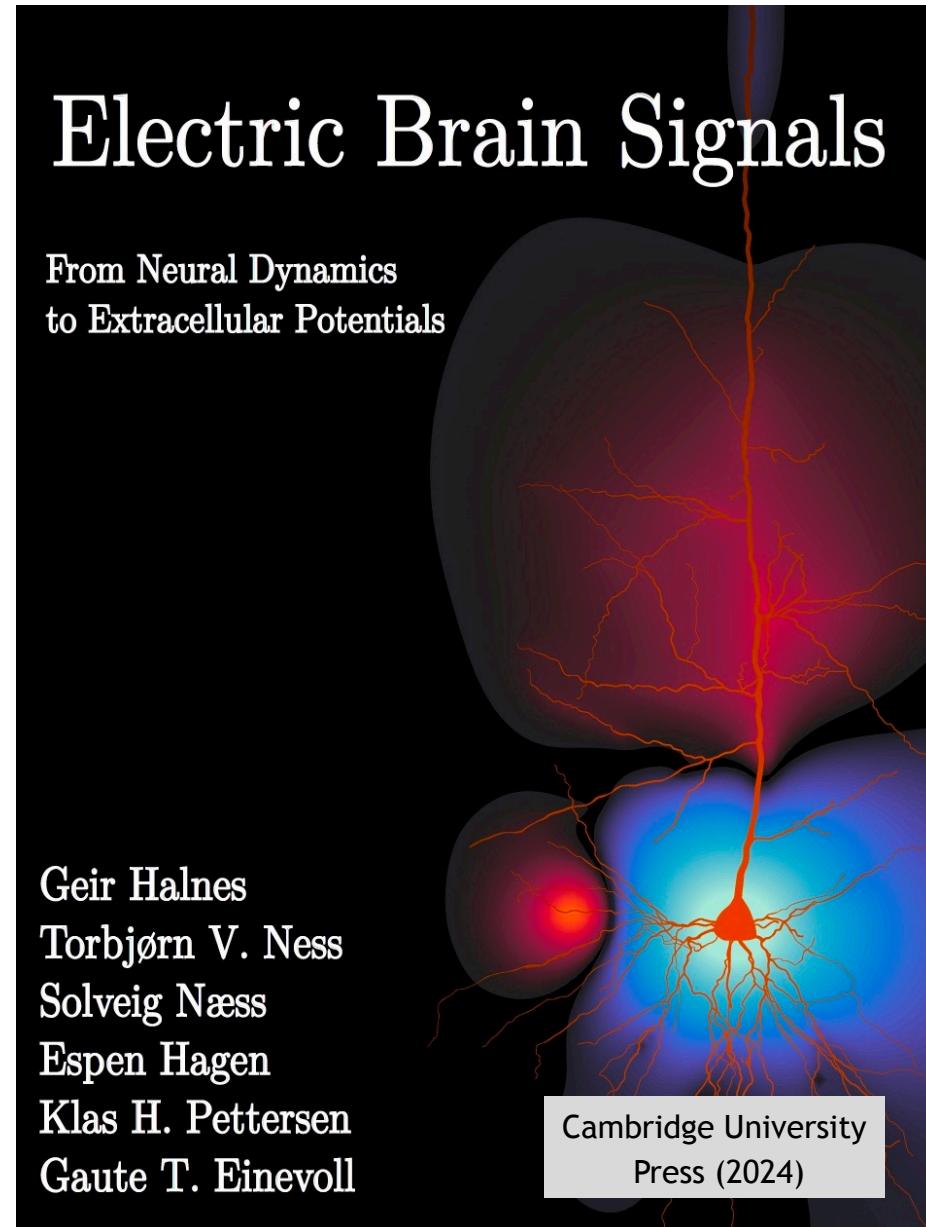
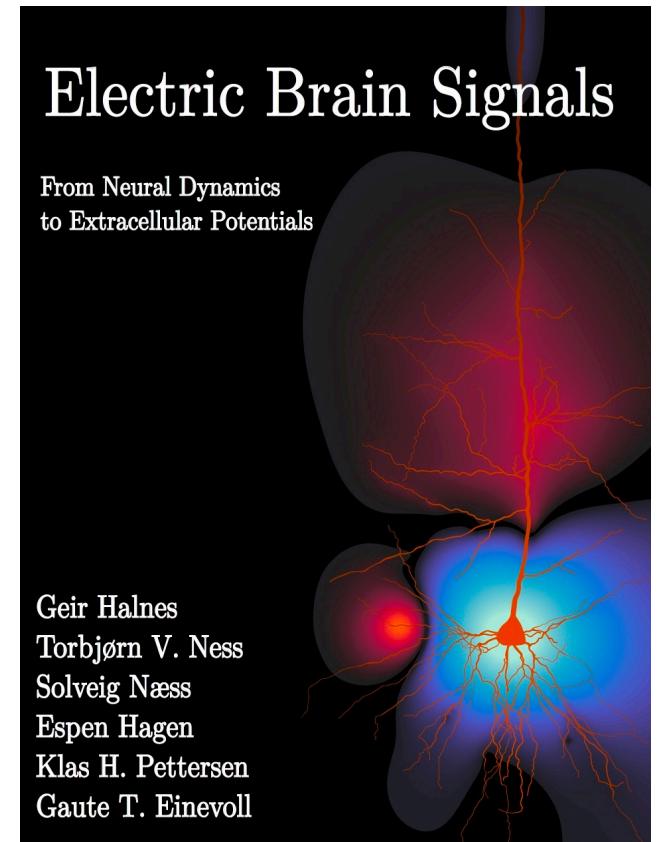
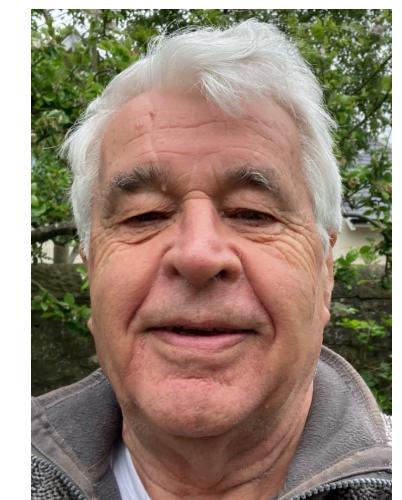
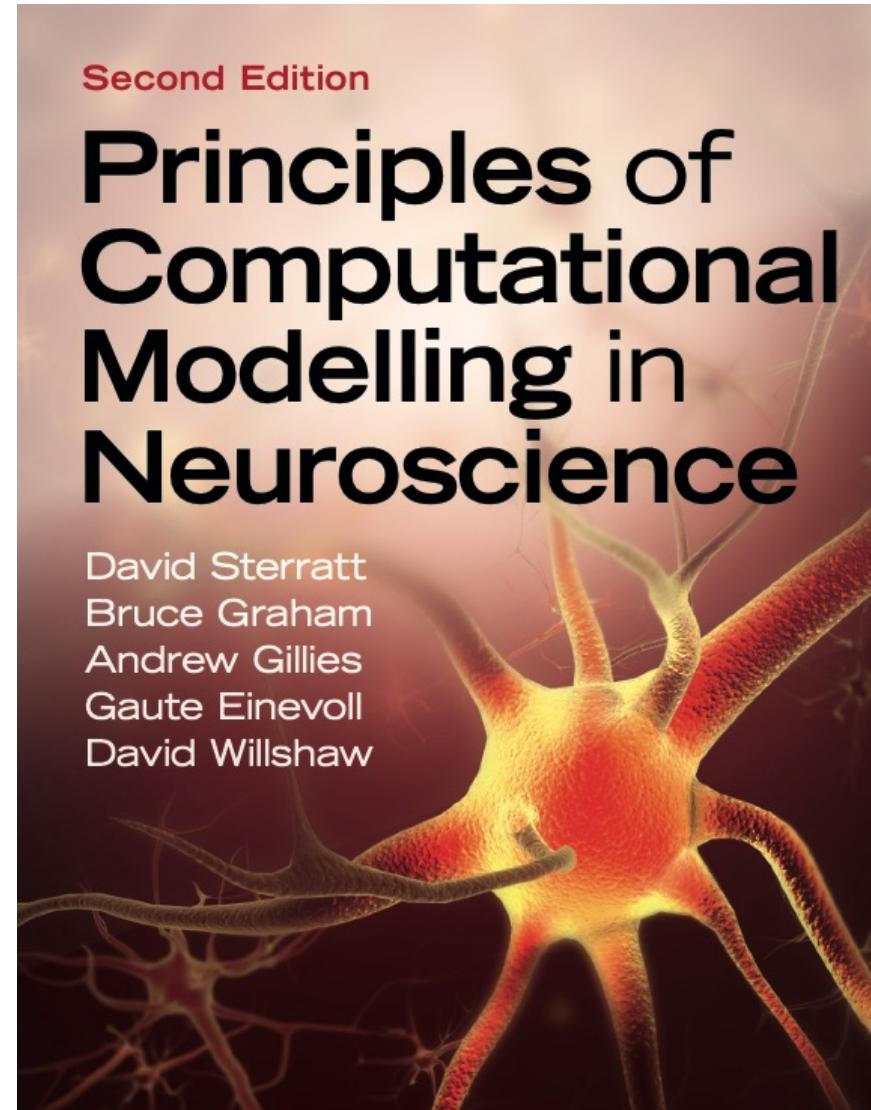


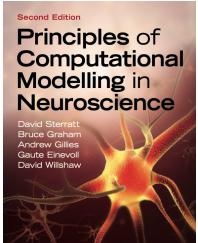
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7. Spikes
8. Local field potentials (LFPs)
9. Electroencephalography (EEG)
10. Electrocorticography (ECoG)
11. Magnetoencephalography (MEG)
12. Diffusion potentials in brain tissue
13. Final comments and outlook

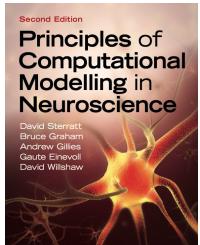




Cambridge University Press (2023)



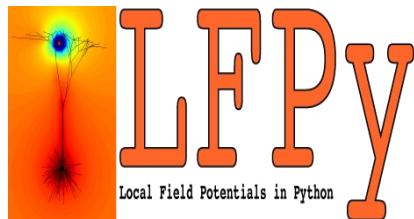
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Multimodal Modeling of Neural Network Activity: Computing LFP, ECoG, EEG, and MEG Signals With LFPy 2.0

Espen Hagen^{1,2*†}, Solveig Næss^{3†}, Torbjørn V. Ness² and Gaute T. Einevoll^{1,2*}

¹ Department of Physics, University of Oslo, Oslo, Norway, ² Faculty of Science and Technology, Norwegian University of Life Sciences, Ås, Norway, ³ Department of Informatics, University of Oslo, Oslo, Norway

Recordings of extracellular electrical, and later also magnetic, brain signals have been the dominant technique for measuring brain activity for decades. The interpretation of such signals is however nontrivial, as the measured signals result from both local and distant neuronal activity. In volume-conductor theory the extracellular potentials can be calculated from a distance-weighted sum of contributions from transmembrane currents of neurons. Given the same transmembrane currents, the contributions to the magnetic field recorded both inside and outside the brain can also be computed. This allows for the development of computational tools implementing forward models grounded in the biophysics underlying electrical

OPEN ACCESS

Edited by:

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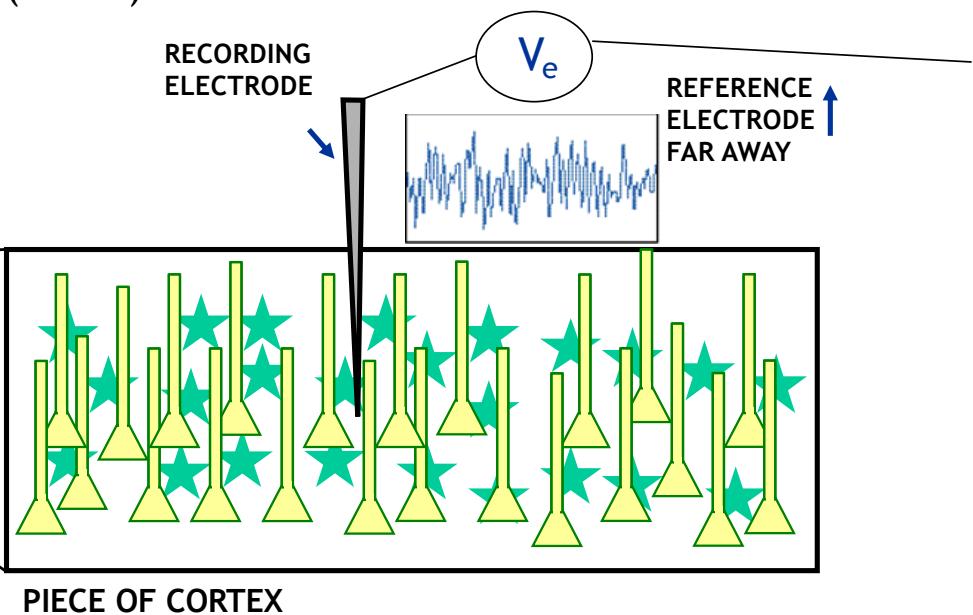
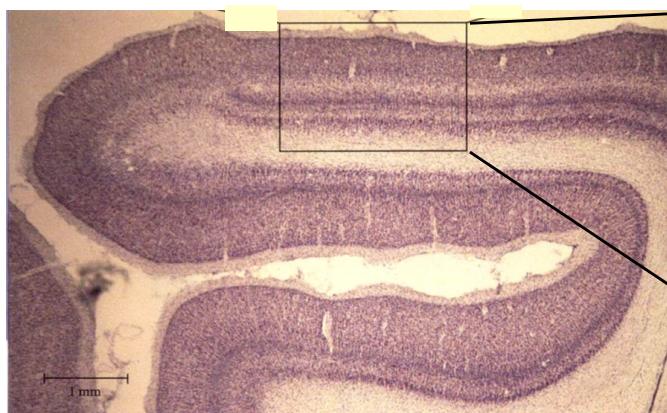
Why mechanistic modeling of brain signals?

- Exploration of brain signals stemming from different kinds of neural activity
Ex: What does LFP generated by a population of neurons look like?
- Constraining neural network models
Ex: Use spikes and LFP data to fit model parameters in cortical network model
- Development and validation of data analysis methods
Ex: iCSD method for current-source density (CSD) analysis of LFP signals
Ex: Generation of model-based benchmarking spike data for development and validation of automatic spike-sorting methods

Measuring electrical potentials in the brain

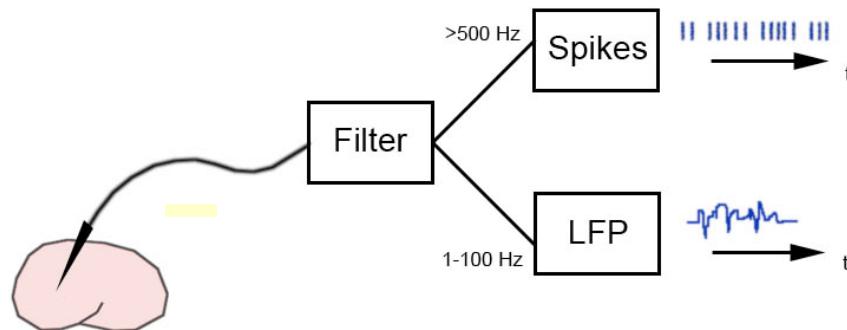


- Among the oldest and (conceptually) simplest measurements of neural activity
- Richard Caton (1875): Measures electrical potentials from surfaces of animal brains (ECoG)

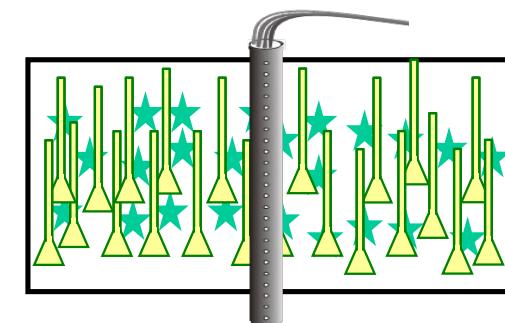


Typical analysis for extracellular recordings inside brain

- Recorded signal split into two frequency bands:
 - High-frequency band ($>\sim 500$ Hz): **Multi-unit activity (MUA)**,
measures spikes in neurons surrounding electrode tip
 - Low-frequency band ($<\sim 300$ Hz): **Local field potential (LFP)**,
measures subthreshold activity

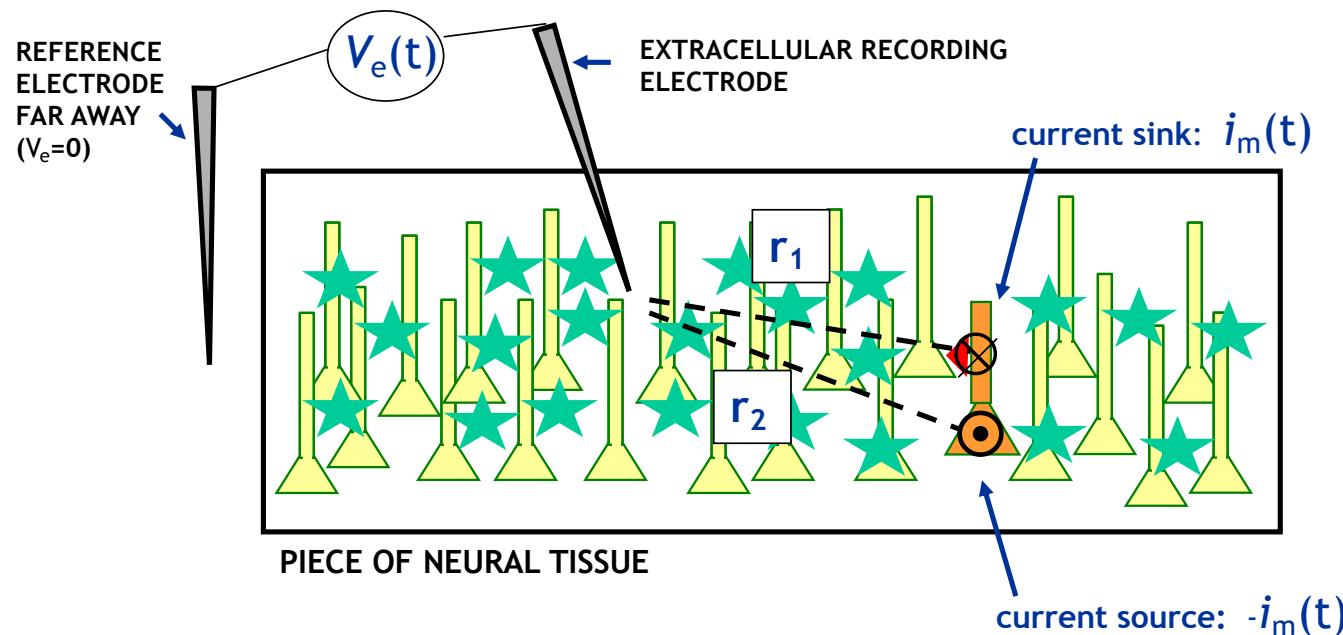


- LFP often discarded
- Sometimes used for current-source density (CSD) analysis with laminar-electrode recordings spanning cortical layers



Physical origin of spikes, LFP, ECoG, EEG and MEG

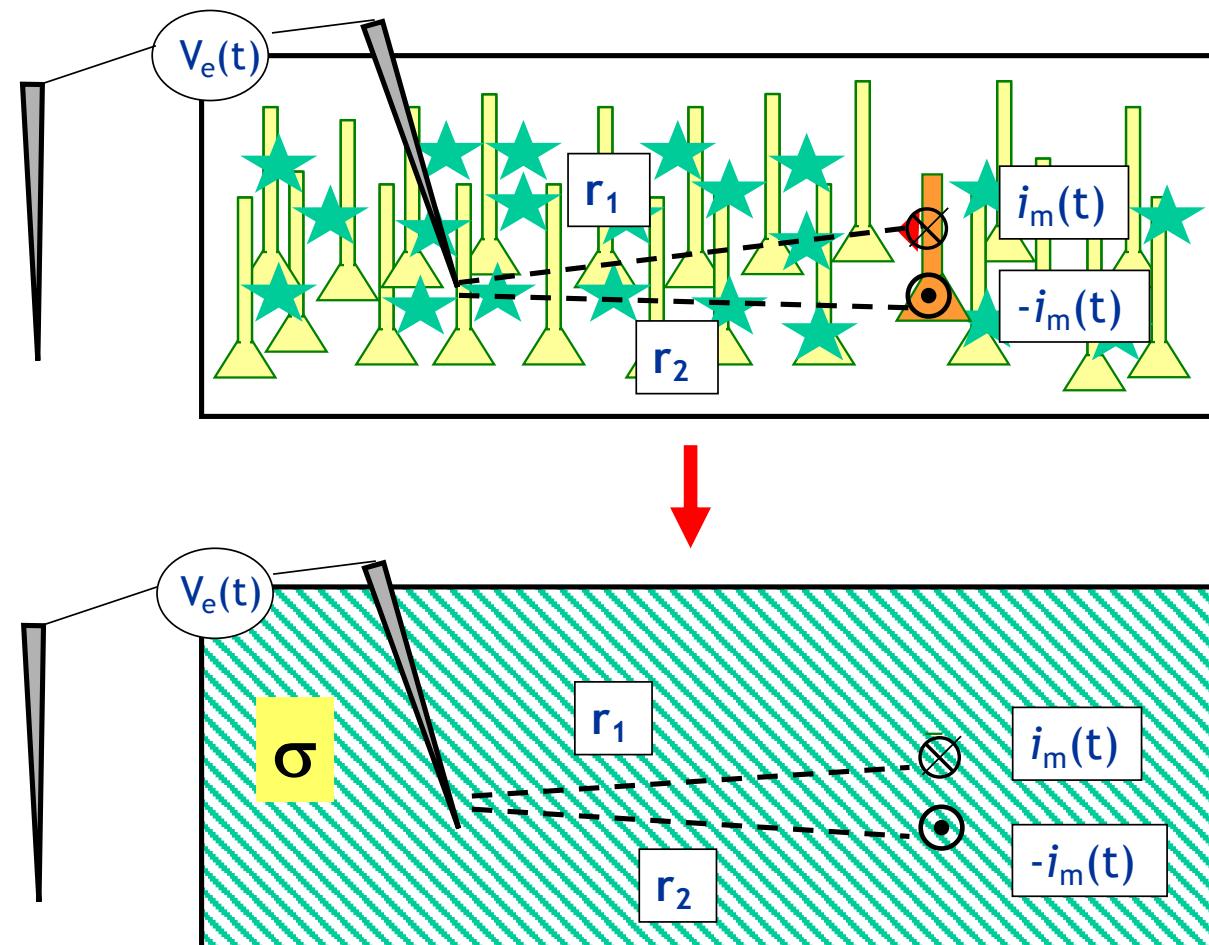
- Source of extracellular potentials (and MEG): Transmembrane currents



FORWARD SOLUTION FOR V_e
(2-COMP. NEURON MODEL):

$$V_e(t) = \frac{i_m(t)}{4\pi\sigma r_1} - \frac{i_m(t)}{4\pi\sigma r_2}$$

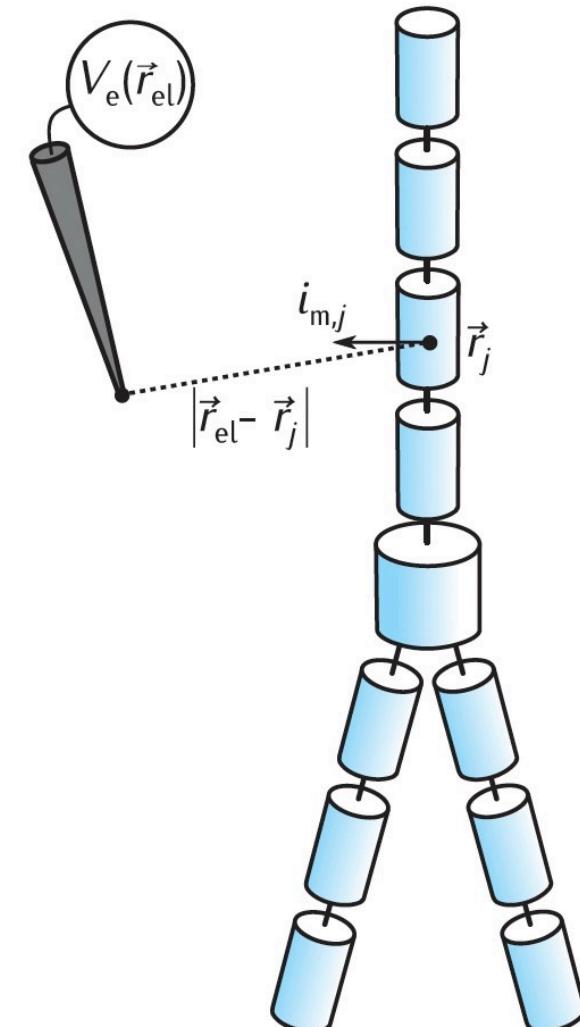
σ : extracellular conductivity



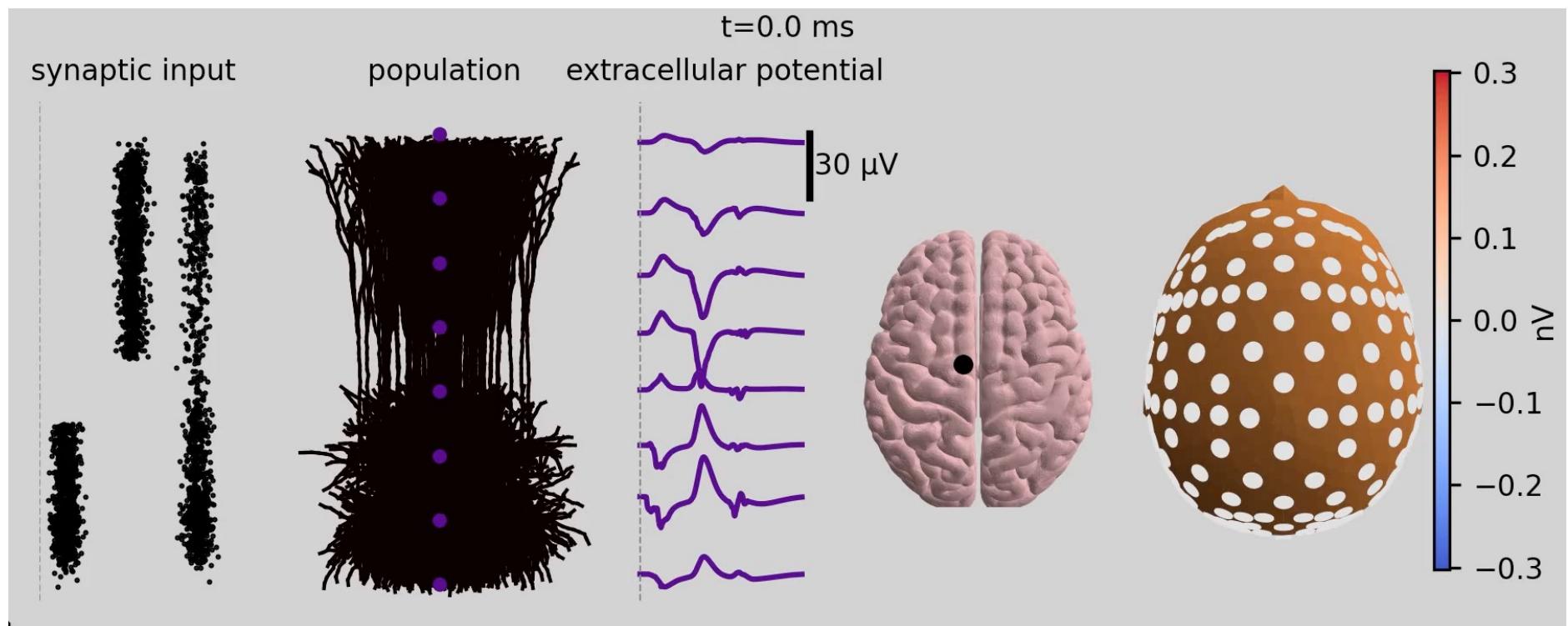
Forward-modeling formula for multicompartment neuron model

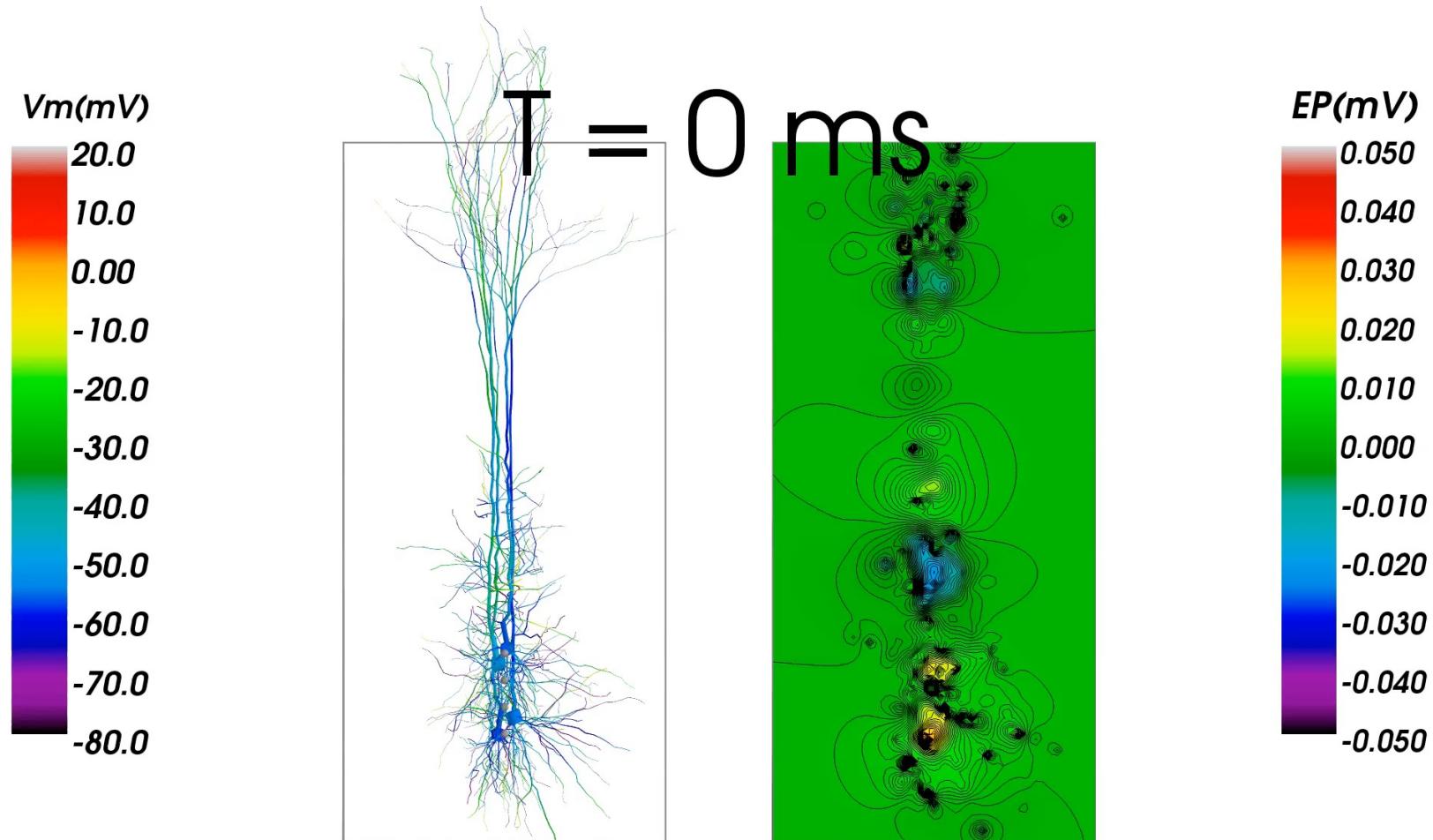
$$V_e(\mathbf{r}) = \frac{1}{4\pi\sigma} \sum_{j=1}^N \frac{i_{m,j}}{|\mathbf{r} - \mathbf{r}_j|}$$

- Forward-modeling scheme can be generalised to situations where:
 - conductivity σ varies with position
 - conductivity σ is anisotropic
 - conductivity σ is frequency dependent
(if it turns out to be warranted)
- Contributions from many neurons sum up



Example: LFP and EEG signal from 10000 biophysically detailed neuron models



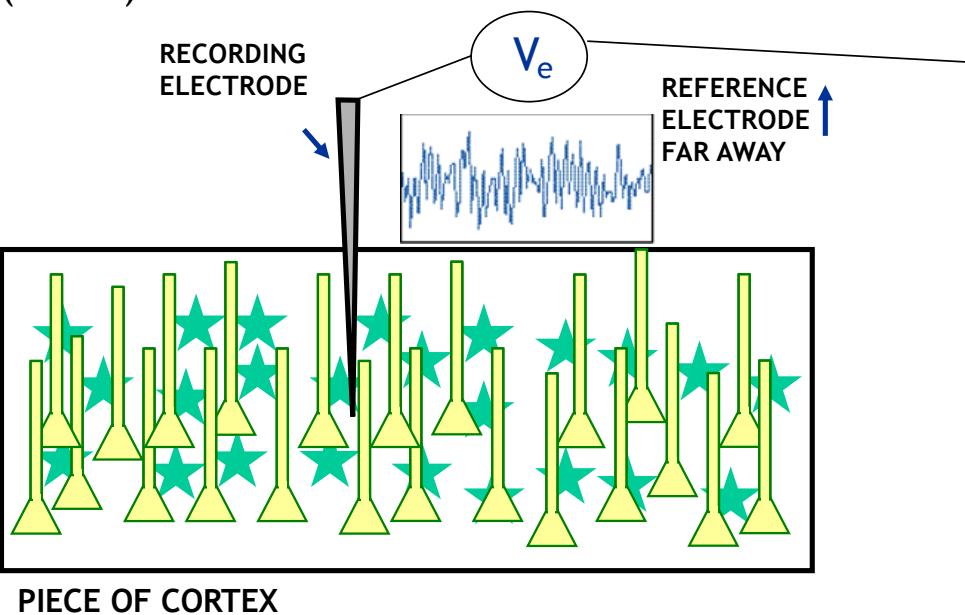
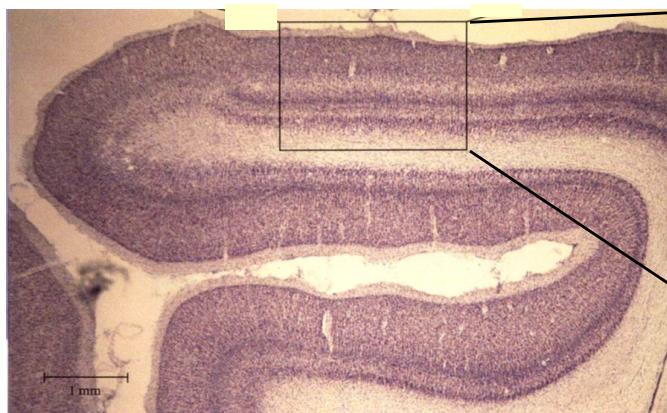


END - part 1

Measuring electrical potentials in the brain

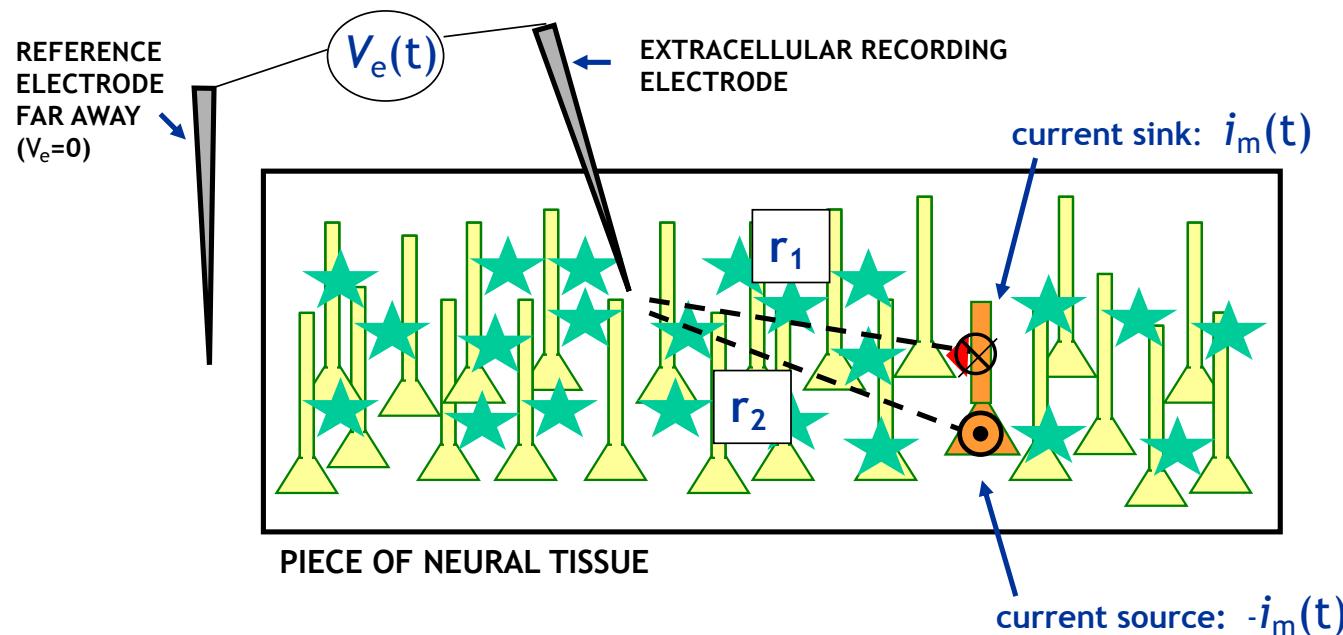


- Among the oldest and (conceptually) simplest measurements of neural activity
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Physical origin of spikes, LFP, ECoG, EEG and MEG

- Source of extracellular potentials (and MEG): Transmembrane currents

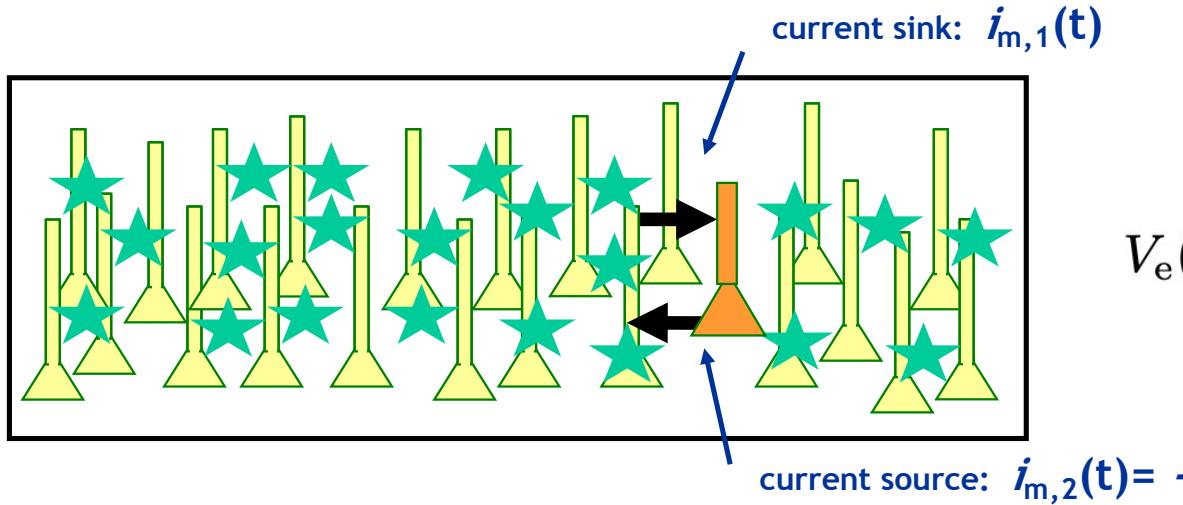


FORWARD SOLUTION FOR V_e
(2-COMP. NEURON MODEL):

$$V_e(t) = \frac{i_m(t)}{4\pi\sigma r_1} - \frac{-i_m(t)}{4\pi\sigma r_2}$$

σ : extracellular conductivity

Current monopoles do not exist



$$V_e(t) = \frac{i_{m,1}(t)}{4\pi\sigma r_1} + \frac{i_{m,2}(t)}{4\pi\sigma r_2}$$

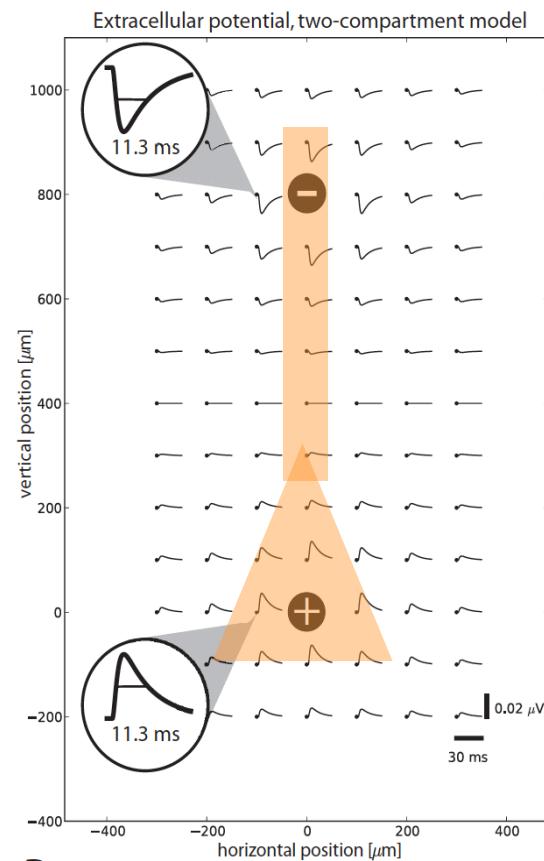
- Conservation of electric charge requires (capacitive currents included!):

$$i_{m,1} + i_{m,2} = 0$$

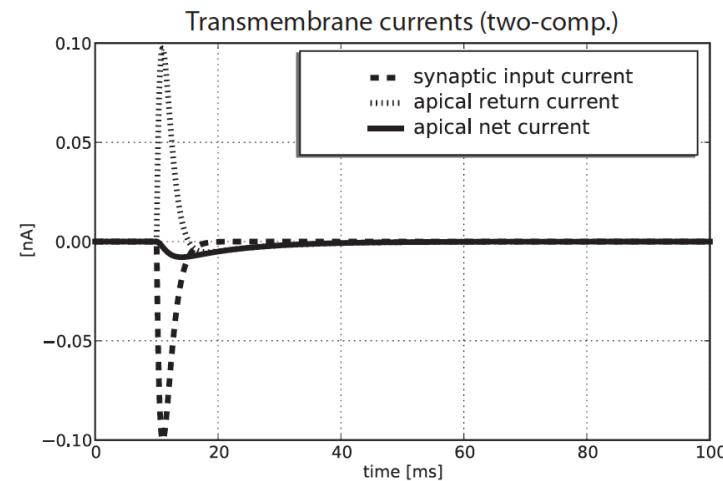
$$V_e(t) = \frac{i_{m,1}(t)}{4\pi\sigma r_1} - \frac{i_{m,1}(t)}{4\pi\sigma r_2}$$

- From far away it looks like a current dipole

LFP from two-compartment neuron



$$V_e(t) = \frac{i_m(t)}{4\pi\sigma r_1} - \frac{i_m(t)}{4\pi\sigma r_2}$$



Assumptions

$$V_e(t) = \frac{i_m(t)}{4\pi\sigma r_1} - \frac{i_m(t)}{4\pi\sigma r_2}$$

I. Quasistatic approximation to Maxwell's equations

$$\begin{aligned}\nabla \cdot \mathbf{E} &= \frac{\rho}{\epsilon_0} \\ \nabla \cdot \mathbf{B} &= 0 \\ \nabla \times \mathbf{E} &= -\cancel{\frac{\partial \mathbf{B}}{\partial t}} \\ \nabla \times \mathbf{B} &= \mu_0 \mathbf{j} + \cancel{\frac{1}{c^2} \frac{\partial \mathbf{E}}{\partial t}}\end{aligned}$$

- sufficiently low frequencies so that electrical and magnetic fields are decoupled (OK for $f < \sim 10$ kHz)

- here: focus on electrical fields

- then:

$$\nabla \times \mathbf{E} = 0$$

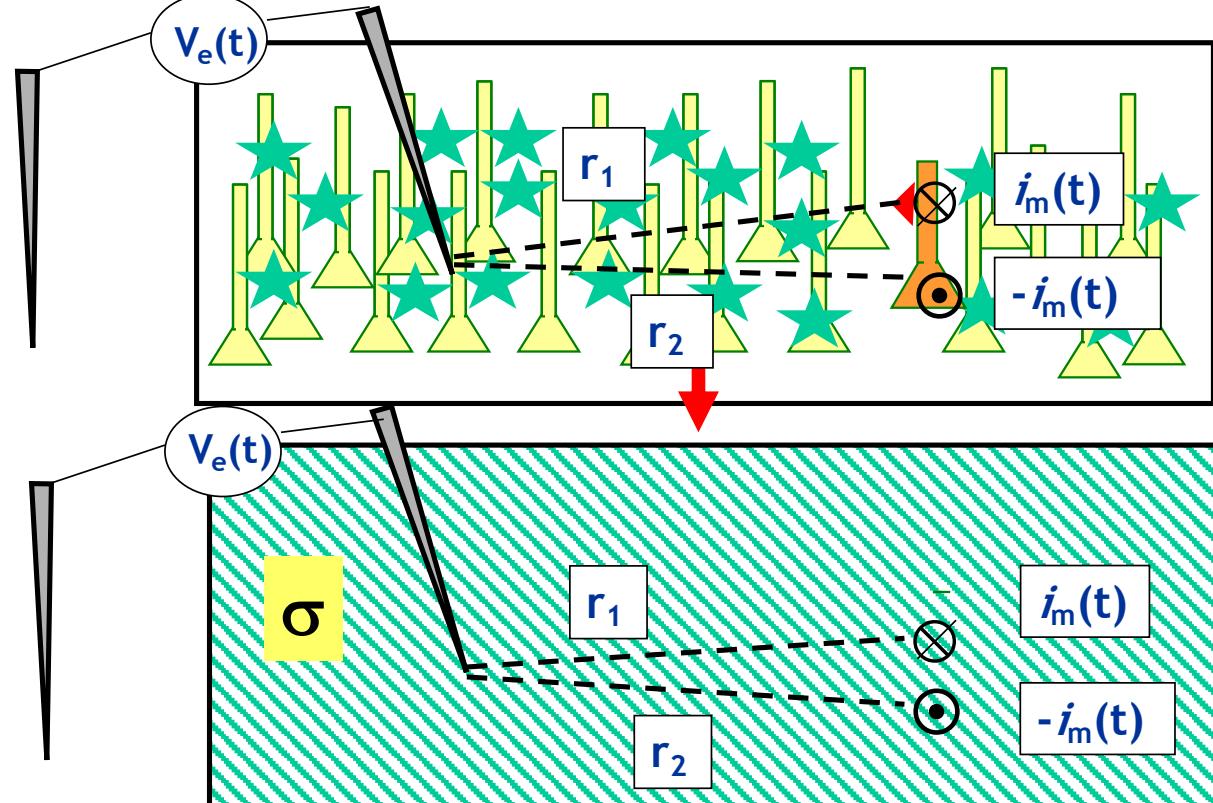
\Rightarrow

$$\mathbf{E} = -\nabla V_e$$

Assumptions underlying:

$$V_e(t) = \frac{i_m(t)}{4\pi\sigma r_1} - \frac{i_m(t)}{4\pi\sigma r_2}$$

II. Coarse-grained extracellular medium described by conductivity σ



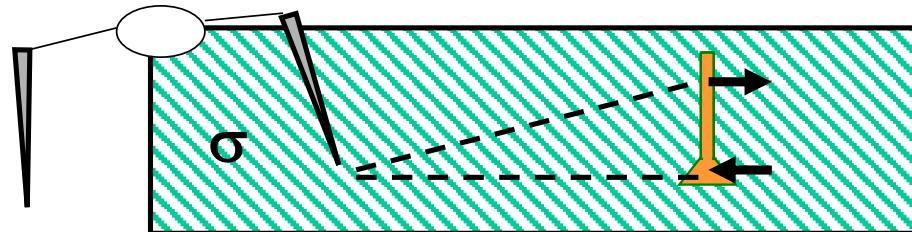
Assumptions underlying:

$$V_e(t) = \frac{i_m(t)}{4\pi\sigma r_1} - \frac{i_m(t)}{4\pi\sigma r_2}$$

III. Linear extracellular medium (with no net charge, that is, $\rho=0$)

$$\mathbf{j} = \sigma \mathbf{E}$$

j : current density (A/m^2) E : electric field (V/m)



IV. Extracellular medium is

1. Ohmic
2. homogeneous
3. frequency-independent
4. isotropic

Formula for potential from current source

1. Assumption I:

$$\mathbf{E} = -\nabla V_e$$

2. Assumptions II+III+IV:

$$\mathbf{I}_{\text{density}} = \sigma \mathbf{E}$$

3. Conservation
of current
around source:

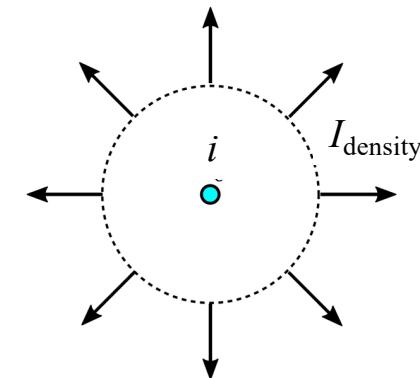
$$i = 4\pi r^2 I_{\text{density}}$$

• 1+2+3+math give:

$$V_e(r) = \frac{i}{4\pi\sigma r}$$

• Source and sink
pair:

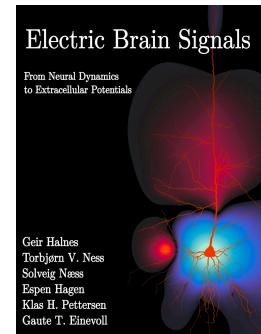
$$V_e(\mathbf{r}) = \frac{i}{4\pi\sigma r_1} - \frac{i}{4\pi\sigma r_2}$$

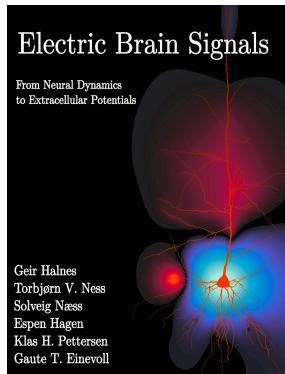


Electromagnetic foundations

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Conductivity σ

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Assumptions regarding σ

$$V_e(t) = \frac{i_m(t)}{4\pi\sigma r_1} - \frac{i_m(t)}{4\pi\sigma r_2}$$

IV.1: Ohmic: σ is real, that is, extracellular medium is not capacitive

- OK

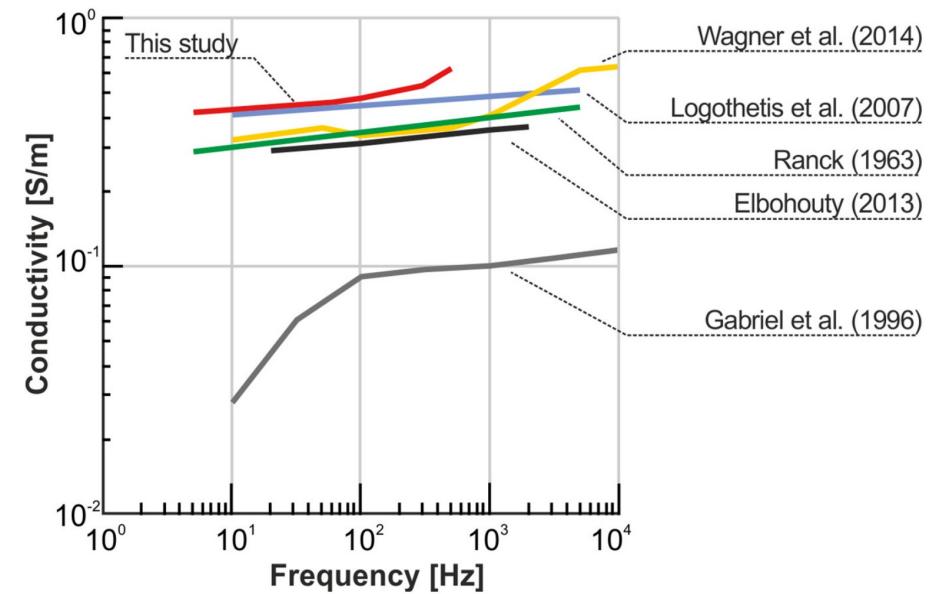
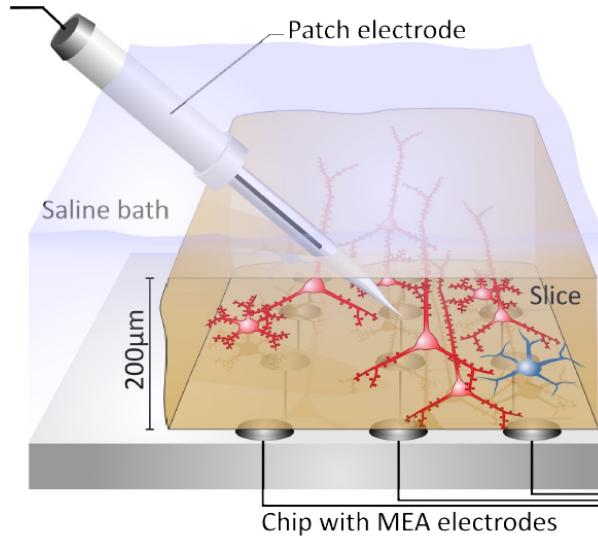
IV.2: Homogeneous: σ is the same at all positions

- OK inside cortex, but lower σ in white matter
- Formula can be modified by means of «method of images» from electrostatics

IV. 3: Frequency-independent: σ is same for all frequencies

- Probably OK (I think), but still somewhat debated
- But if frequency dependence is found, formalism can easily be adapted

Frequency-dependence of conductivity σ ?

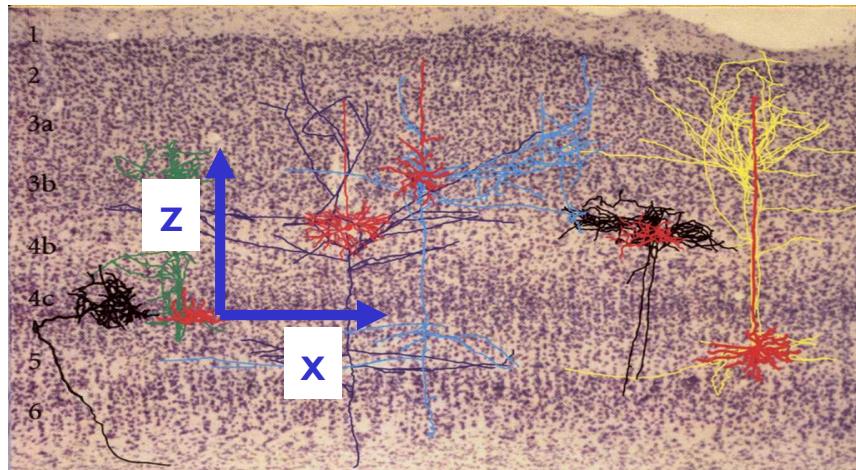


Miceli, Ness, Einevoll & Schubert, eNeuro (2017)

Assumptions underlying:

$$V_e(t) = \frac{i_m(t)}{4\pi\sigma r_1} - \frac{i_m(t)}{4\pi\sigma r_2}$$

IV.4 Isotropic: σ is the same in all directions



- σ is in general a tensor ($\sigma_x, \sigma_y, \sigma_z$)
- Easier to move along apical dendrites than across ($\sigma_z > \sigma_x$ and σ_y)
- Cortex: $\sigma_z \sim 1-1.5 \sigma_{x,y}$

- Generalized formula:

$$V_e(t) = \frac{i_m(t)}{4\pi\sqrt{\sigma_y\sigma_z x_1^2 + \sigma_z\sigma_x y_1^2 + \sigma_x\sigma_y z_1^2}} - \frac{i_m(t)}{4\pi\sqrt{\sigma_y\sigma_z x_2^2 + \sigma_z\sigma_x y_2^2 + \sigma_x\sigma_y z_2^2}}$$

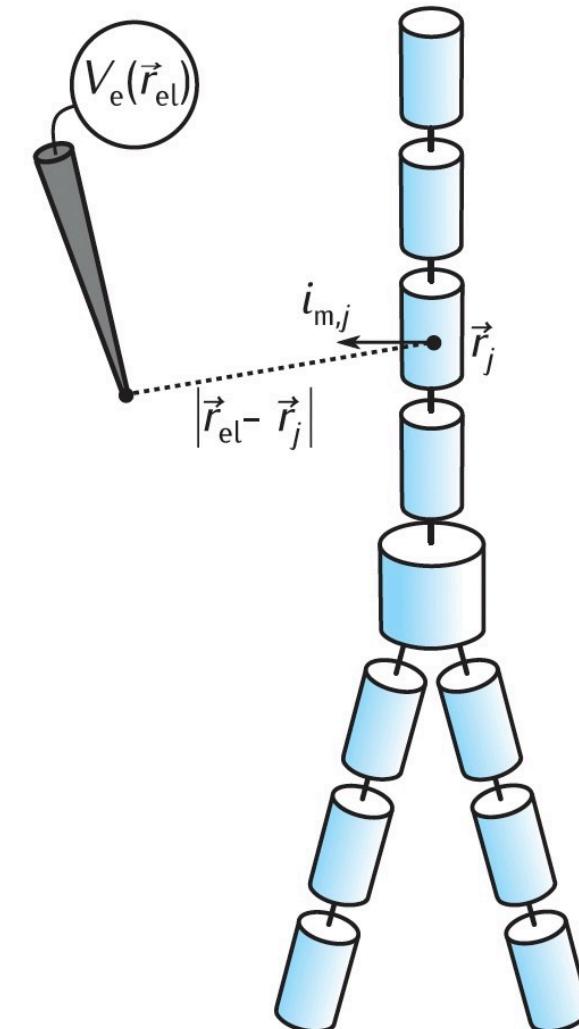
Forward-modeling formula for multicompartment neuron model

$$V_e(\mathbf{r}) = \frac{1}{4\pi\sigma} \sum_{j=1}^N \frac{i_{m,j}}{|\mathbf{r} - \mathbf{r}_j|}$$

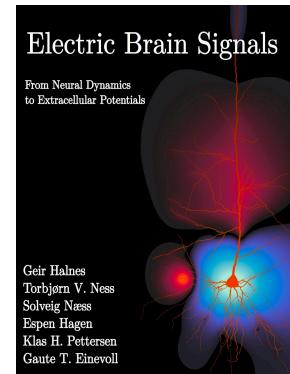
- Current conservation

$$\sum_{j=1}^N i_{m,j} = 0$$

- Contributions from many neurons sum up

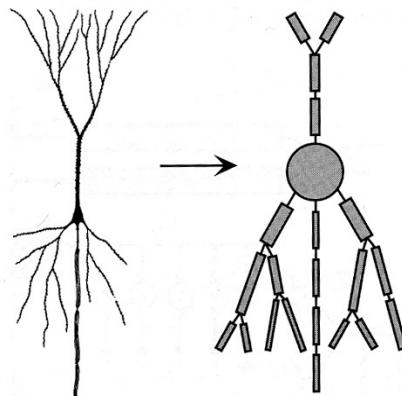


Volume conductor theory

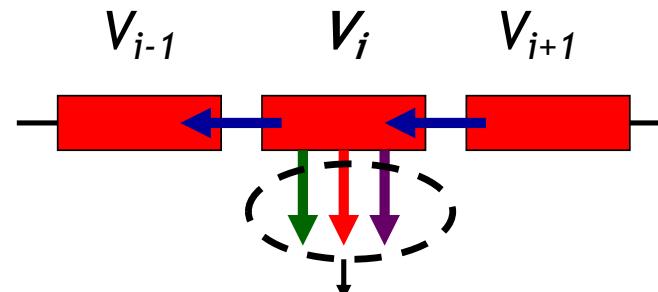


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Multicompartmental modeling scheme



- Example dendritic segment [non-branching case]:



- Kirchhoff's current law ("currents sum to zero"):

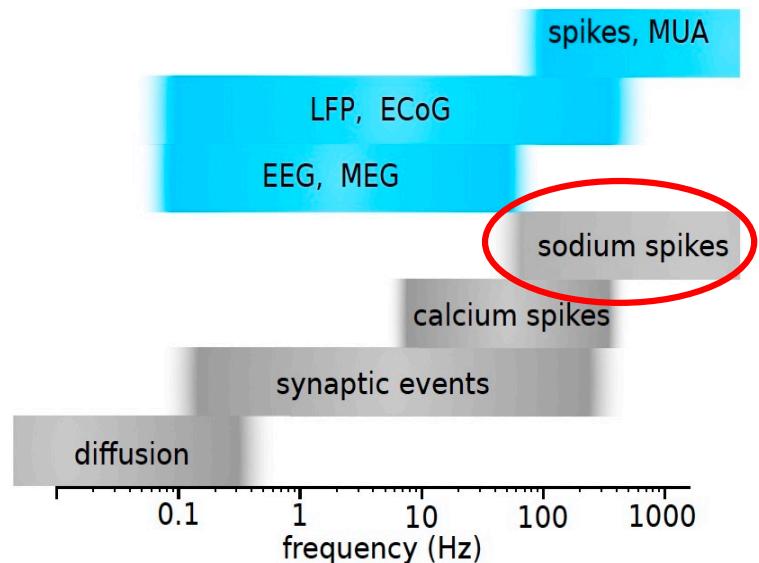
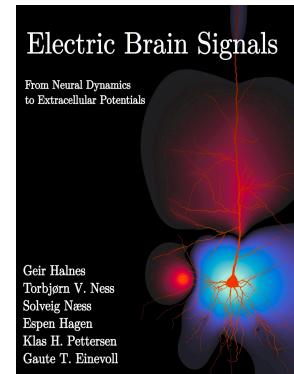
$$g_{i,i+1}(V_{i+1}-V_i) - g_{i-1,i}(V_i-V_{i-1}) = c_i \frac{dV_i}{dt} + g_i^m(V_i - V_r) + \sum_j I_i^j + \sum_s I_i^s$$

CURRENTS TO NEIGHBOURING SEGMENTS **PASSIVE MEMBRANE CURRENT** **ACTIVE MEMBRANE CURRENTS** **SYNAPTIC CURRENTS**

Spikes

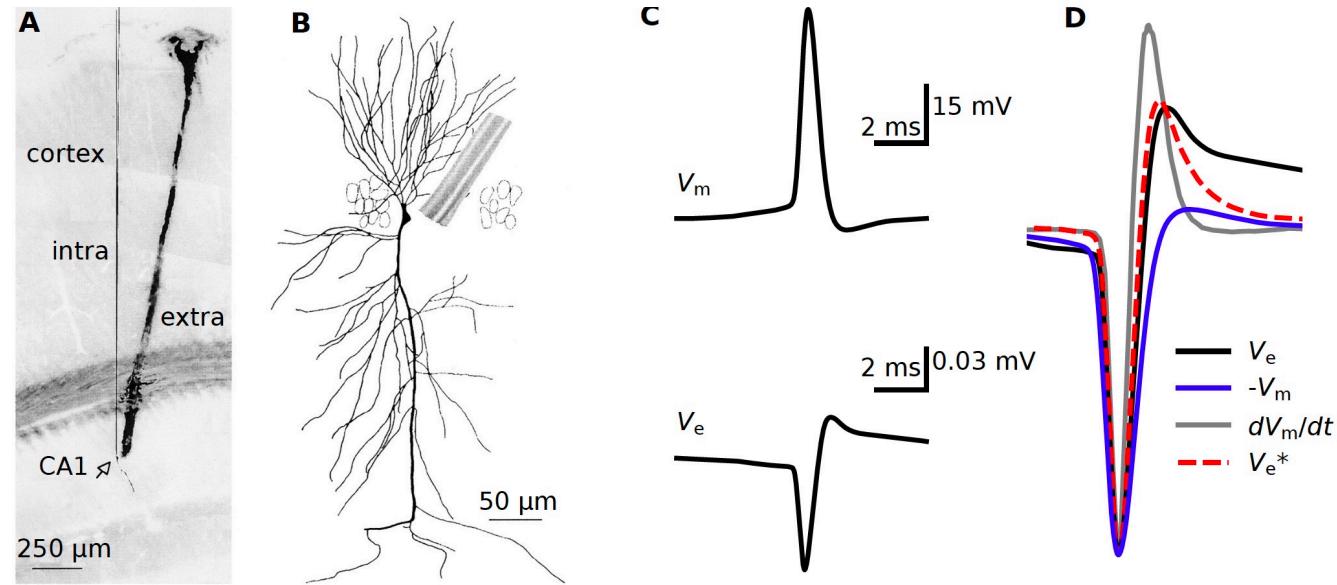
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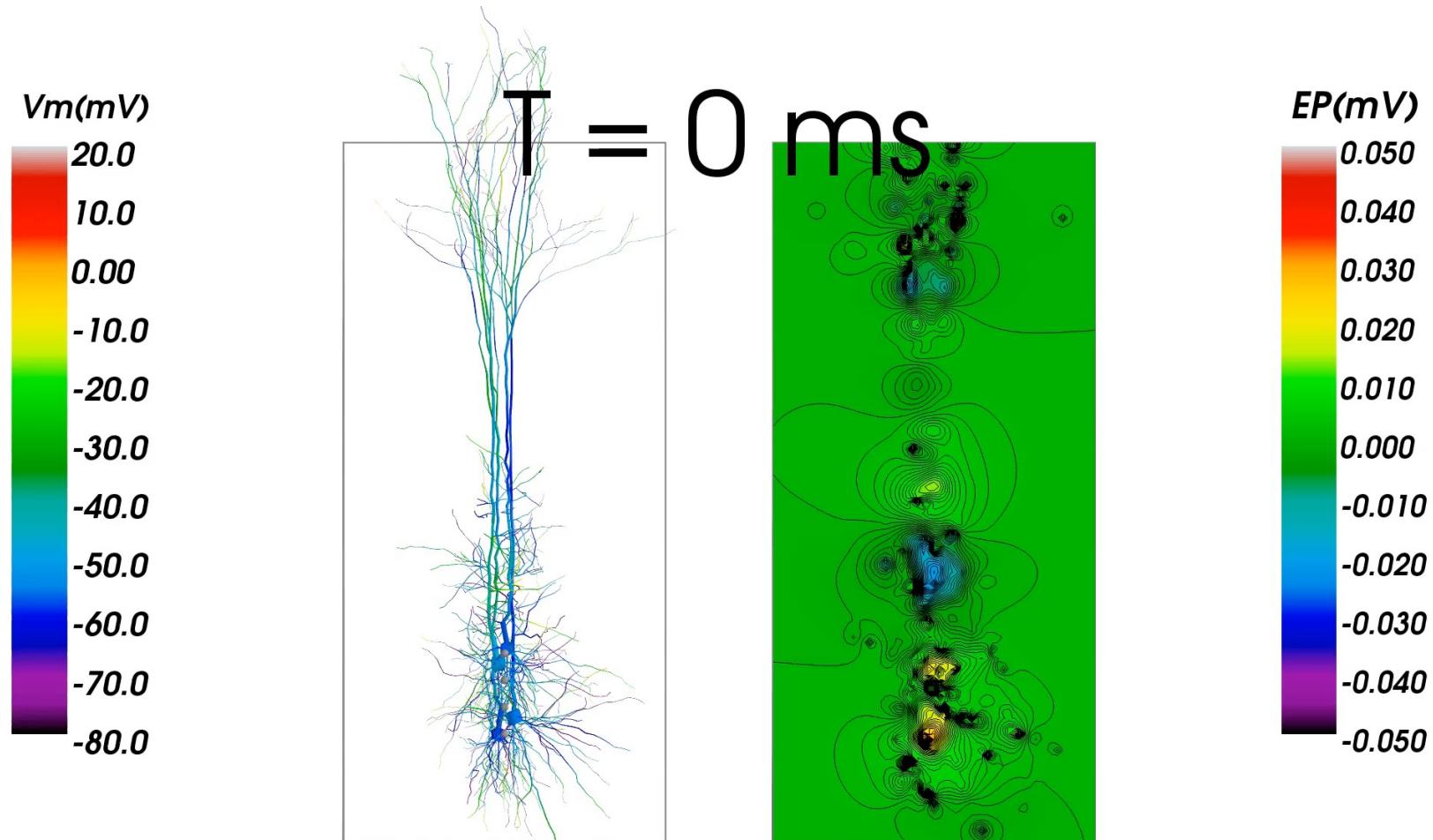


Extracellular vs. intracellular spikes

Experimental data from Henze et al (2000)

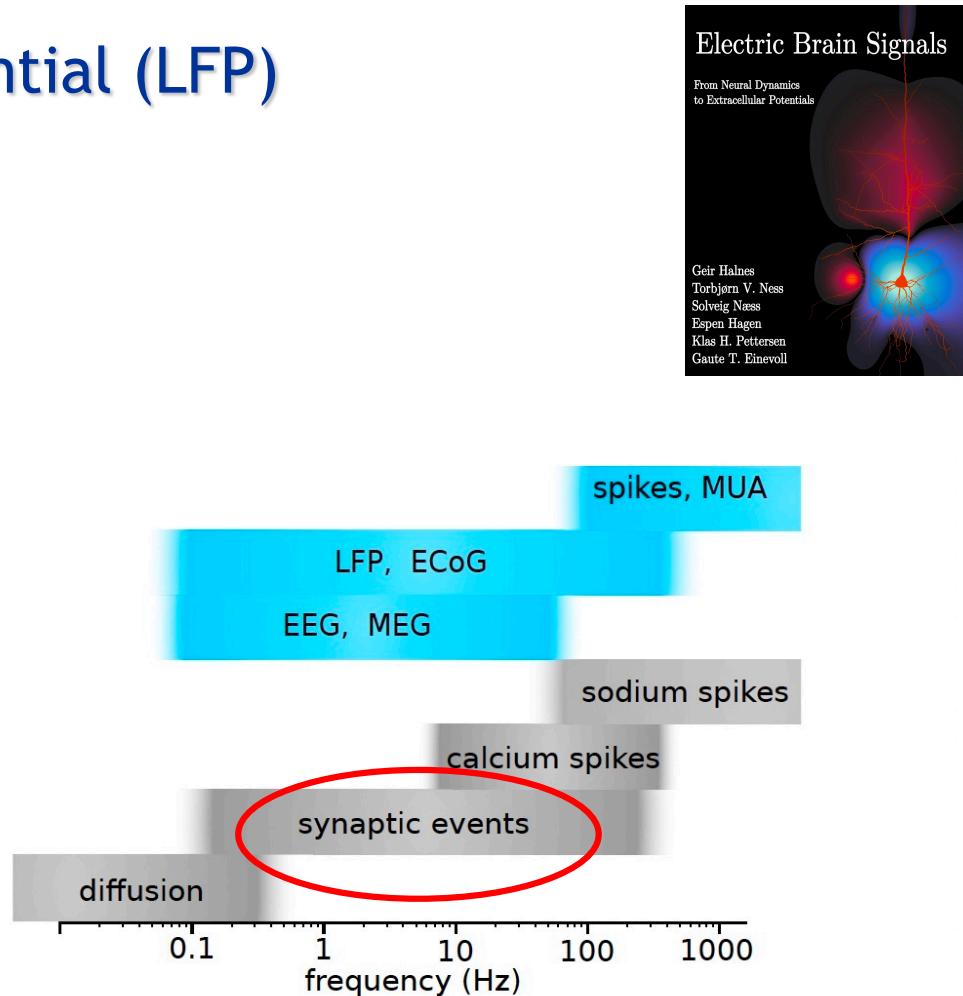


- Spike (V_e) is sharper than intracellular AP (V_m), but less sharp than the derivative (dV_m/dt)
- In frequency space: $V_e(f) \sim \sqrt{f} V_m(f)$



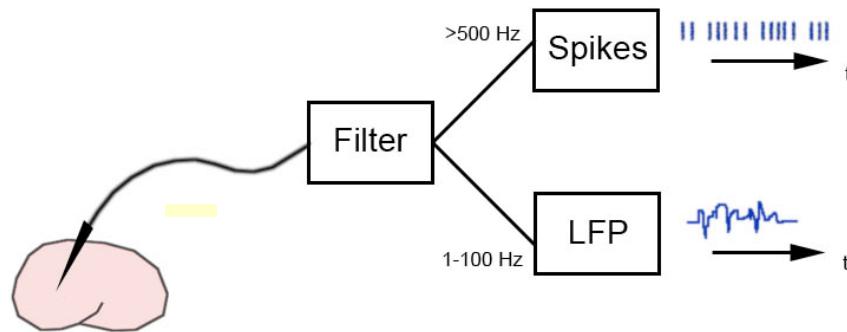
Local field potential (LFP)

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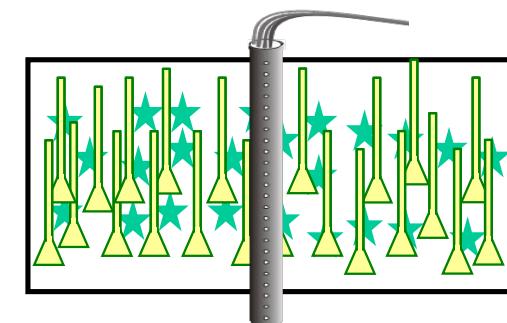


Typical analysis for extracellular recordings inside brain

- Recorded signal split into two frequency bands:
 - High-frequency band ($>\sim 500$ Hz): **Multi-unit activity (MUA)**,
measures spikes in neurons surrounding electrode tip
 - Low-frequency band ($<\sim 300$ Hz): **Local field potential (LFP)**,
measures subthreshold activity

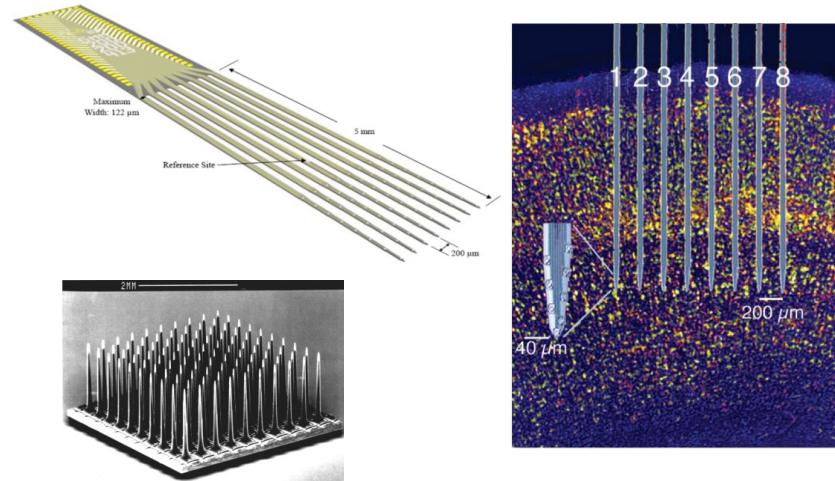


- LFP often discarded
- Sometimes used for current-source density (CSD) analysis with laminar-electrode recordings spanning cortical layers

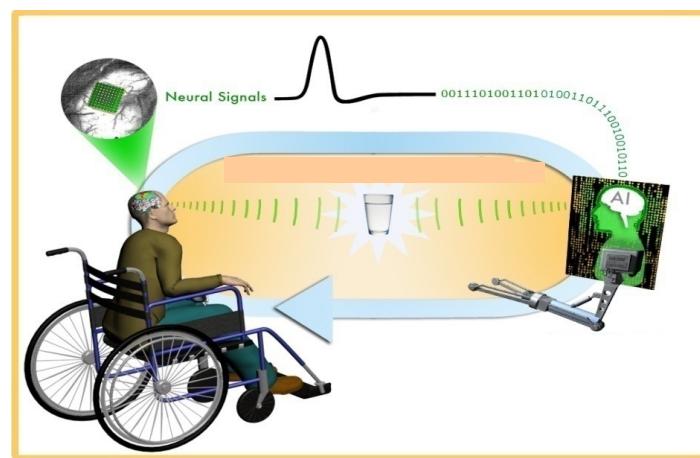


Revival of LFP in last decades

- LFP is unique window into activity in *populations* (thousands) of neurons
- New generation of silicon-based multielectrodes with up to thousands of contacts offers new possibilities

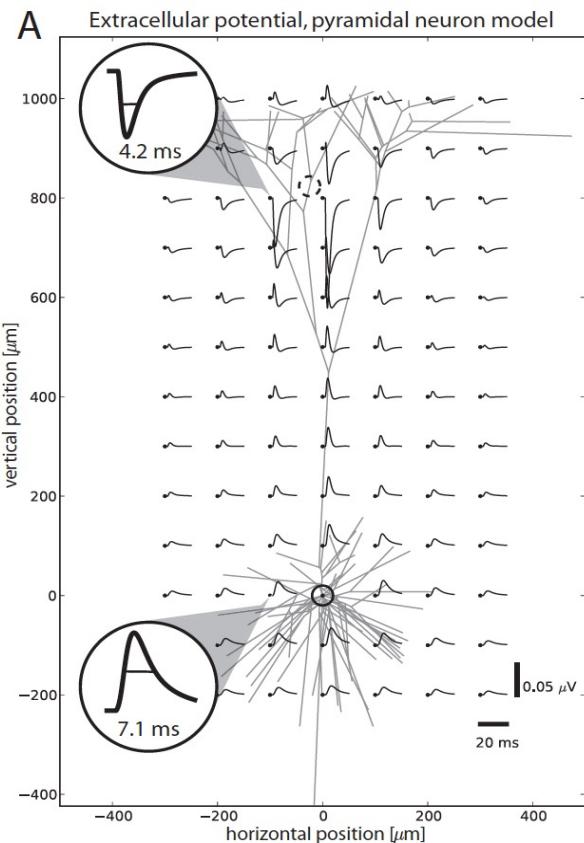


- Candidate signal for brain-computer interfaces (BCI); more stable than spikes

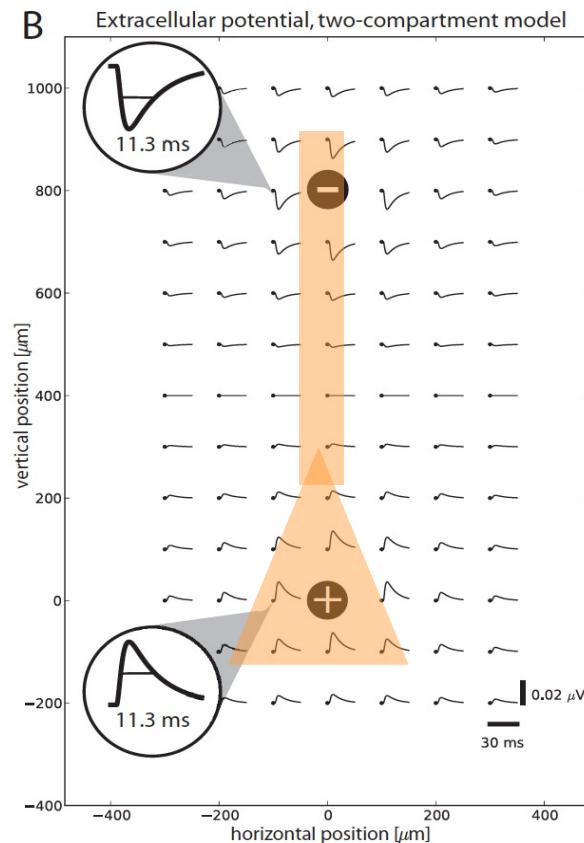


LFPs from different neuron models

Multi-compartment model



Two-compartment model



From Pettersen et al., in Handbook of Neural Activity Measurements, 2012

END - part 2

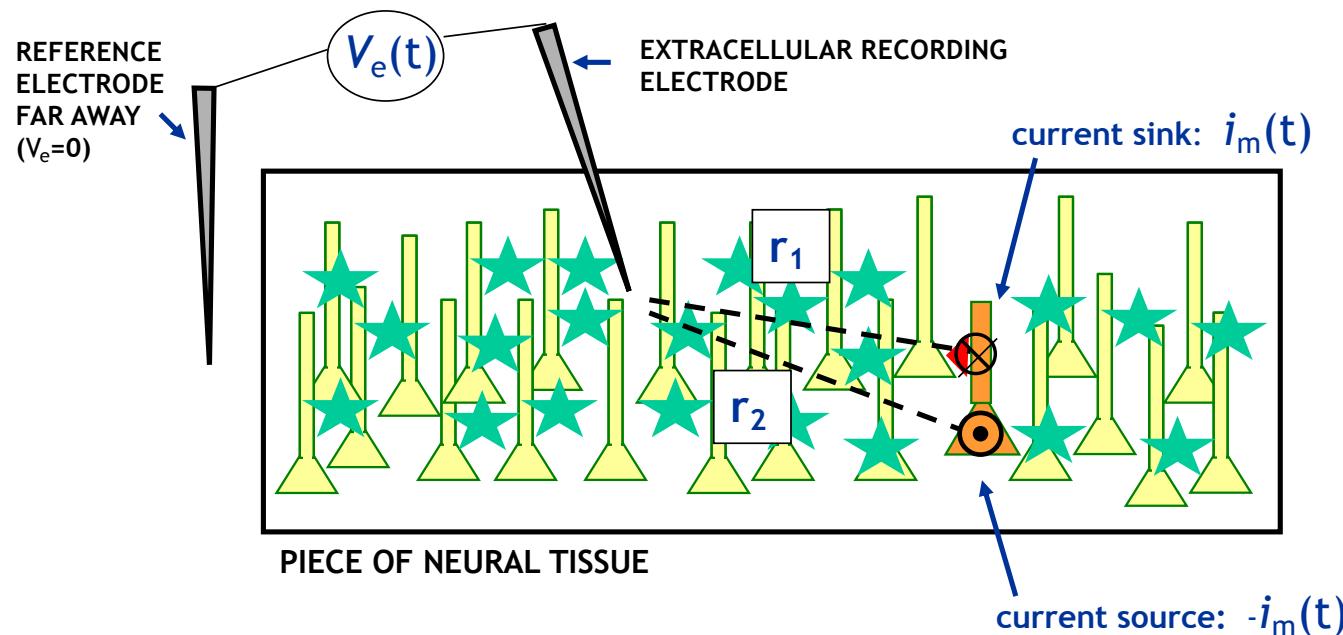
PhD and postdoc position available in Germany

- Group of Prof. Sacha van Albada at Jülich Research Center
- Large-scale spiking network simulations (NEST)
- Postdoc via Henriette Herz Scouting Programme → Humboldt Research Fellowship for female candidate
- Up to 24 months for researchers within 4 years of their defence
- Up to 18 months for researchers within 4-12 years of their defence
- Cannot have done studies or research in Germany or have German citizenship
- Embedding in vibrant institute with international collaborations
- Links to University of Cologne → teaching/tutoring opportunities
- Send motivation letter, CV, and university transcripts to s.van.albada@fz-juelich.de and m.reske@fz-juelich.de



Physical origin of spikes, LFP, ECoG, EEG and MEG

- Source of extracellular potentials (and MEG): Transmembrane currents



FORWARD SOLUTION FOR V_e
(2-COMP. NEURON MODEL):

$$V_e(t) = \frac{i_m(t)}{4\pi\sigma r_1} - \frac{-i_m(t)}{4\pi\sigma r_2}$$

σ : extracellular conductivity

Two-compartment neuron model

- Simplest model giving an extracellular potential
- From current conservation inherent in cable equation:

$$i_{m,s} = -i_{m,d}$$

- No current monopoles!

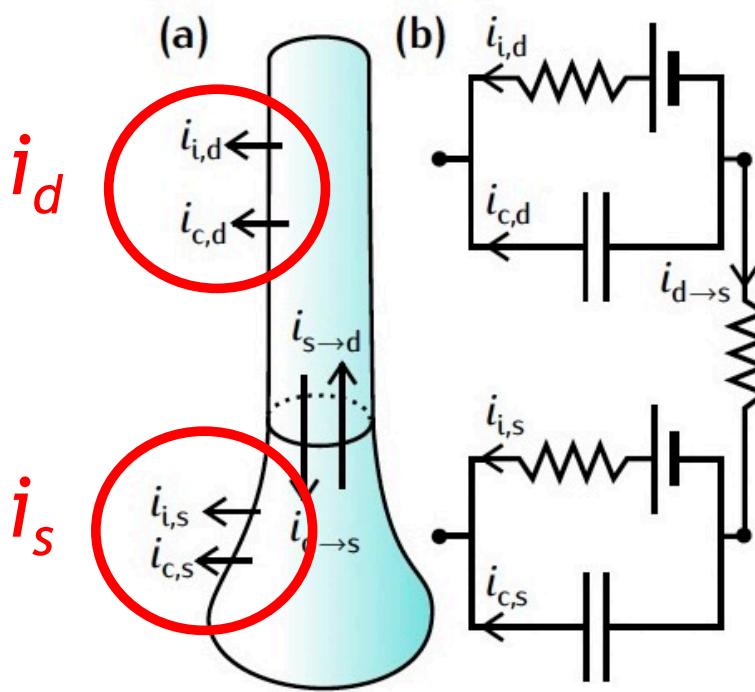


Fig 13.5 Source and sink currents in a two-compartment neuron with a dendrite and soma compartment (a) and its associated circuit diagram (b).

Box 13.2 Source and sink currents are balanced

The source and sink membrane currents across the surface of a neuron always sum to zero. This can be shown by considering a two-compartment neuron with a dendrite and soma compartment (Figure 13.5a) and its associated circuit diagram (Figure 13.5b).

For this simple neuron, Kirchhoff's current law introduced in Chapter 2 gives:

$$i_{c,d} + i_{i,d} + i_{d \rightarrow s} = 0 \quad (a)$$

$$i_{c,s} + i_{i,s} + i_{s \rightarrow d} = 0. \quad (b)$$

Equation (a) is for the dendrite compartment, Equation (b) is for the soma compartment, and i_c and i_i represent the capacitive and ionic currents across the membrane, respectively. Furthermore, $i_{d \rightarrow s}$ is the axial current from the dendrite to the soma compartment, and $i_{s \rightarrow d}$ is the axial current the other way. These axial currents are obviously the same, but have opposite signs, so that $i_{s \rightarrow d} = -i_{d \rightarrow s}$.

Since the total membrane current i_m is the sum of the capacitive and ionic currents, we have:

$$i_{m,d} = -i_{d \rightarrow s} \quad (c)$$

$$i_{m,s} = -i_{s \rightarrow d}. \quad (d)$$

By summing each side of this equation set, we find:

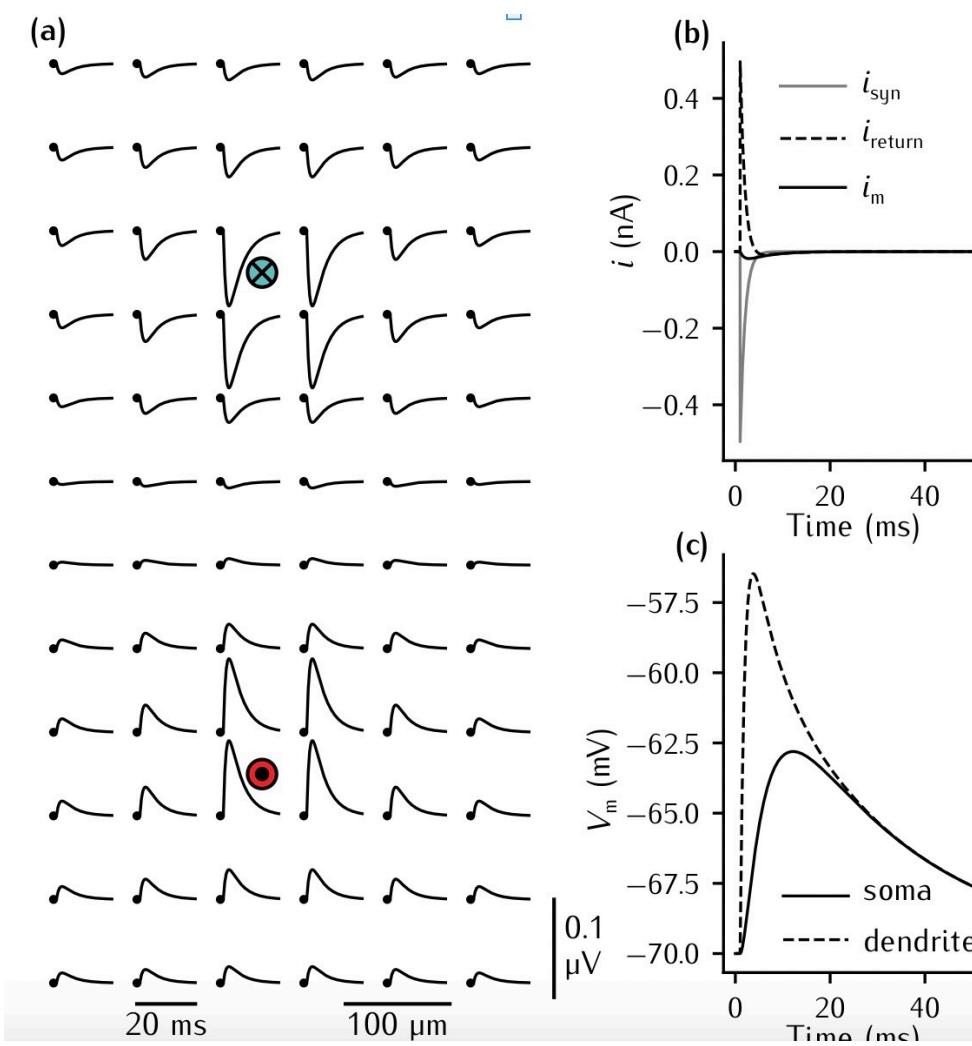
$$\sum_{j=d,s} i_{m,j} = i_{m,d} + i_{m,s} = -(i_{d \rightarrow s} + i_{s \rightarrow d}) = -i_{d \rightarrow s} + i_{d \rightarrow s} = 0, \quad (e)$$

demonstrating that the total membrane current across the neuronal surface sums to zero.

This argument demonstrates that current monopoles cannot exist for two-compartment neuron models. The same reasoning can be used to show that it also applies for multi-compartment neuron models with any number N compartments, i.e., $\sum_{j=1}^N i_{m,j} = 0$ (Equation 13.5).

“Principles of Computational Modeling in Neuroscience”, 2023

Two-compartment neuron model receiving excitatory synaptic input in apical (top) compartment



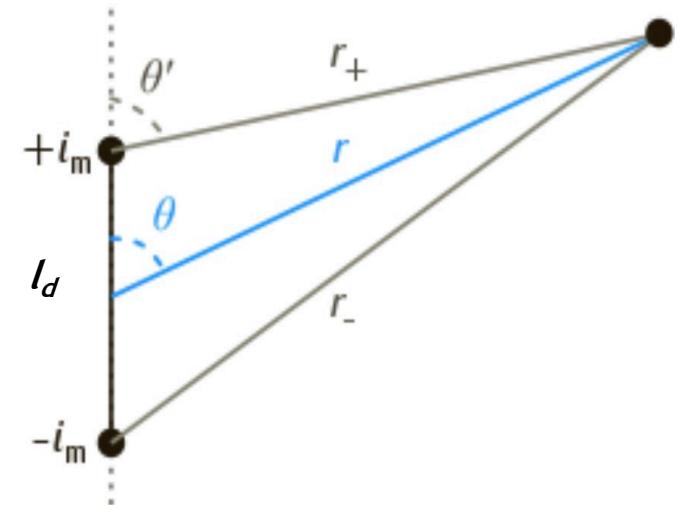
“Principles of Computational Modeling in Neuroscience, 2023

Dipole approximation of extracellular potential

$$V_e(\mathbf{r}) = \frac{i_m}{4\pi\sigma r_+} - \frac{i_m}{4\pi\sigma r_-}$$

- Far away ($l_d \ll r$):

$$V_e(\mathbf{r}) \approx \frac{\mathbf{p} \cdot \mathbf{e}_r}{4\pi\sigma r^2} = \frac{i_m l_d \cos \theta}{4\pi\sigma r^2}$$



Current dipole moment:

$$\mathbf{p} = i_m l_d \mathbf{e}_p$$

Box 13.3 | Dipolar EP around the two-compartment neuron

Far away from the cell, the EP set up by the two-compartment neuron gives a characteristic dipolar pattern. In this regime, the EP pattern can be described by a current dipole moment \vec{p} . This is illustrated in Figure 13.8, where the computation of the EP around such a neuron is depicted.

As described in Equation 13.1, the EP generated by two such balanced currents is given by (Figure 13.8a):

$$V_e(\vec{r}) = \frac{i_m}{4\pi\sigma_t r_+} - \frac{i_m}{4\pi\sigma_t r_-} = \frac{i_m(r_- - r_+)}{4\pi\sigma_t r_+ r_-}. \quad (\text{a})$$

From trigonometry, it follows that: $r_-^2 = r_+^2 + l_d^2 + 2r_+l_d \cos\theta'$ or $r_- - r_+ = l_d(l_d + 2r_+ \cos\theta')/(r_- + r_+)$ so that:

$$V_e(\vec{r}) = \frac{i_m l_d (l_d + 2r_+ \cos\theta')}{4\pi\sigma_t r_+ r_- (r_- + r_+)} \approx \frac{i_m l_d \cos\theta}{4\pi\sigma_t r_-^2}. \quad (\text{b})$$

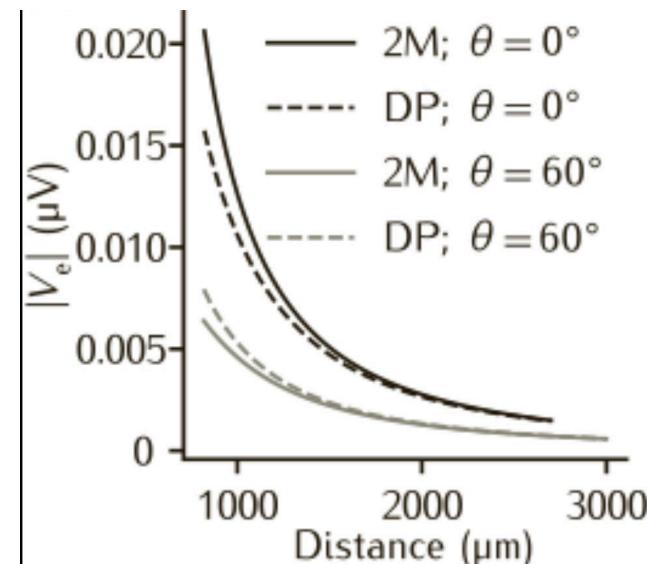
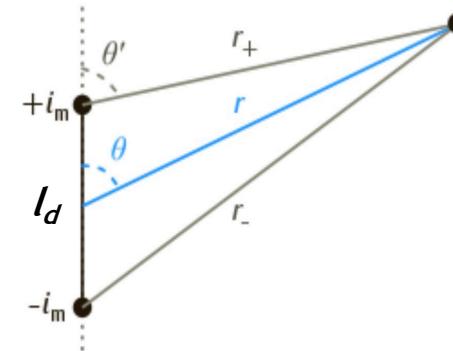
In the final step, the far-field limit $l_d \ll r$ has been assumed so that $r_- \rightarrow r$, $r_+ \rightarrow r$, and $\theta' \rightarrow \theta$.

The current dipole moment is defined as $\vec{p} = i_m l_d \vec{e}_p$, where \vec{e}_p is a unit vector pointing from the sink current ($-i_m$) to the source current ($+i_m$). Then the dipole EP is given by:

$$V_e(\vec{r}) = \frac{\vec{p} \cdot \vec{e}_r}{4\pi\sigma_t r^2}, \quad (\text{c})$$

where \vec{e}_r is a unit vector pointing in the radial direction towards the electrode tip.

This dipole formula is only applicable far away from the neuron. This is illustrated in Figure 13.8b comparing the EPs predicted by the dipolar formula (Equation c) with the two-monopole formula (Equation a). In the present example, a dipole length $l_d = 0.8$ mm is assumed and the two formulae are seen to give very similar results for distances larger than 1–2 mm. The upper pair of curves corresponds to $\theta = 0^\circ$, which is in the vertical direction where the EP is maximal, whilst the lower pair of curves corresponds to $\theta = 60^\circ$. A current $i_m = 0.05$ nA is used, roughly the maximum magnitude of the net membrane current in Figure 13.6.





1. Go to <https://wiki.ebrains.eu/bin/view/Main/>, log in, and click "Collabs" on the top right
2. Click the button "Create a collab"
3. Make up some personal collab name ("Mary_testing_LFPy"), and set visibility to "Private". Click "Create Collab"
4. Press "Lab" on the left, and choose Execution Site. Which site you chose should mostly be irrelevant.
5. In the Jupyter Notebook, press the button on the leftmost bar that is named "Git" (hover over with the mouse to see the name).
6. Press the button "Clone a Repository", and give the URL https://github.com/LFPy/tutorial_at_EBRAINS/
7. Under the folder "tutorial_at_EBRAINS", you should now find examples and exercises. Find and click on a Jupyter Notebook
8. When it opens, make sure the Jupyter Notebook kernel (top right on the Jupyter notebook) is set to "EBRAINS-23.09" or newer



File Edit View Run Kernel Git Tabs Settings Help | Mem: 923 / 2048 MB

+ Filter files by name

/ ... / gaute-LFPTutorial / gaute_test /

Name	Last Modified
exercise_pot_decay_mono...	2 minutes ago
exercise_pot_decay_three...	2 minutes ago
exercise_pot_decay_two-...	2 minutes ago
Exercise01_solution.ipynb	seconds ago
Exercise01.ipynb	2 minutes ago

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Exercise 01: Extracellular potentials from simple neuron models

As described in PCMN [1] Section 13.2, a single-compartment (point) neuron does not generate any extracellular signal. The simplest neuron model generating an extracellular potential is the two-compartment model where, for example, one compartment represents the soma and the other the dendrite. In this exercise we will explore the extracellular potential set up by various simple neuron models.

For the case of a single static (constant) current source i in an infinite homogeneous and isotropic volume conductor with conductivity σ , the potential around the position of the current source is given by (PCMN Equation 10.15):

$$V_e(r) = \frac{i}{4\pi\sigma r}.$$

In the present exercise we will assume the value $\sigma = 0.3 \text{ S/m}$.

[1] Sterratt, Graham, Gillies, Einevoll, & Willshaw (2023). Principles of Computational Modelling in Neuroscience (2nd ed.) doi:10.1017/9781108672955

Task 1: Current monopoles

While single-compartment neurons do not produce any extracellular potential, the potential set up by a thin and sharp

Simple 0 \$ 6 E BRAINS-23.09 | Idle Mem: 818.48 / 2048.00 MB Mode: Command Ln 1, Col 1 Exercise01.ipynb

Task 1: Current monopoles

While single-compartment neurons do not produce any extracellular potential, the potential set up by a thin and sharp electrode injecting a current into the extracellular space will resemble the potential described by the equation above.

- Write the Python code to make a 2D plot of the extracellular potential around the electrode tip set up by a constant current sink with a current of -1.0 nA.
- Make a double-logarithmic plot showing how the potential varies with distance from the neuron, from 10 μm to 5000 μm . Can you read out the characteristic $1/r$ -decay with distance from the plot?

Task 2: Two-compartment neuron

Next we consider a two-compartment model with a 100 μm distance between the top apical compartment and the bottom soma compartment. There is a constant membrane current sink of -1.0 nA in the apical compartment. This could mimic the effect of a (really) long-lasting excitatory input to the apical compartment.

- What is the membrane current in the basal compartment?
- What is the axial current between the two compartments?
- Write the Python code to make a 2D plot of the extracellular potential around the two-compartment neuron.
- Make a double-logarithmic plot of how the potential varies with distance from the neuron when moving in the vertical direction, that is, along the line connecting the two compartments, starting from 10 μm below the soma compartment. Can you from the plot read out the characteristic $1/r^2$ dipolar decay expected for large distances?
- Why doesn't the potential decay as $1/r^2$ close to the neuron?

Task 3: Three-compartment neuron

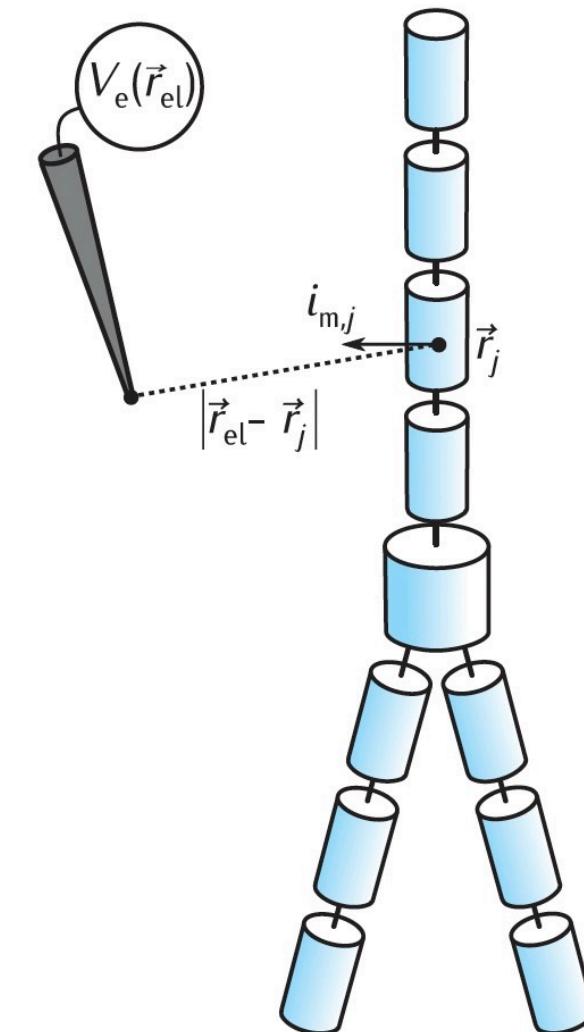
We now consider a three-compartment model with three vertically aligned compartments where the lowest compartment corresponds to the soma, while the middle and top compartments correspond to dendritic compartments. The distance between neighbouring compartments is 50 μm . The middle compartment is a current sink with constant amplitude -1 nA, while the bottom and top compartments are current sources, both with 0.5 nA amplitudes. This could (maybe) mimic the effect of a (really) long-lasting excitatory input to the middle of an apical dendritic compartment.

- Write the Python code to make a 2D plot of the extracellular potential around the three-compartment neuron.
- Make a double-logarithmic plot of how the potential varies with distance from the neuron when moving in the vertical direction, that is, along the line connecting the two compartments? How does the potential decay with distance far away from the neuron? Why?

END - tutorial 1

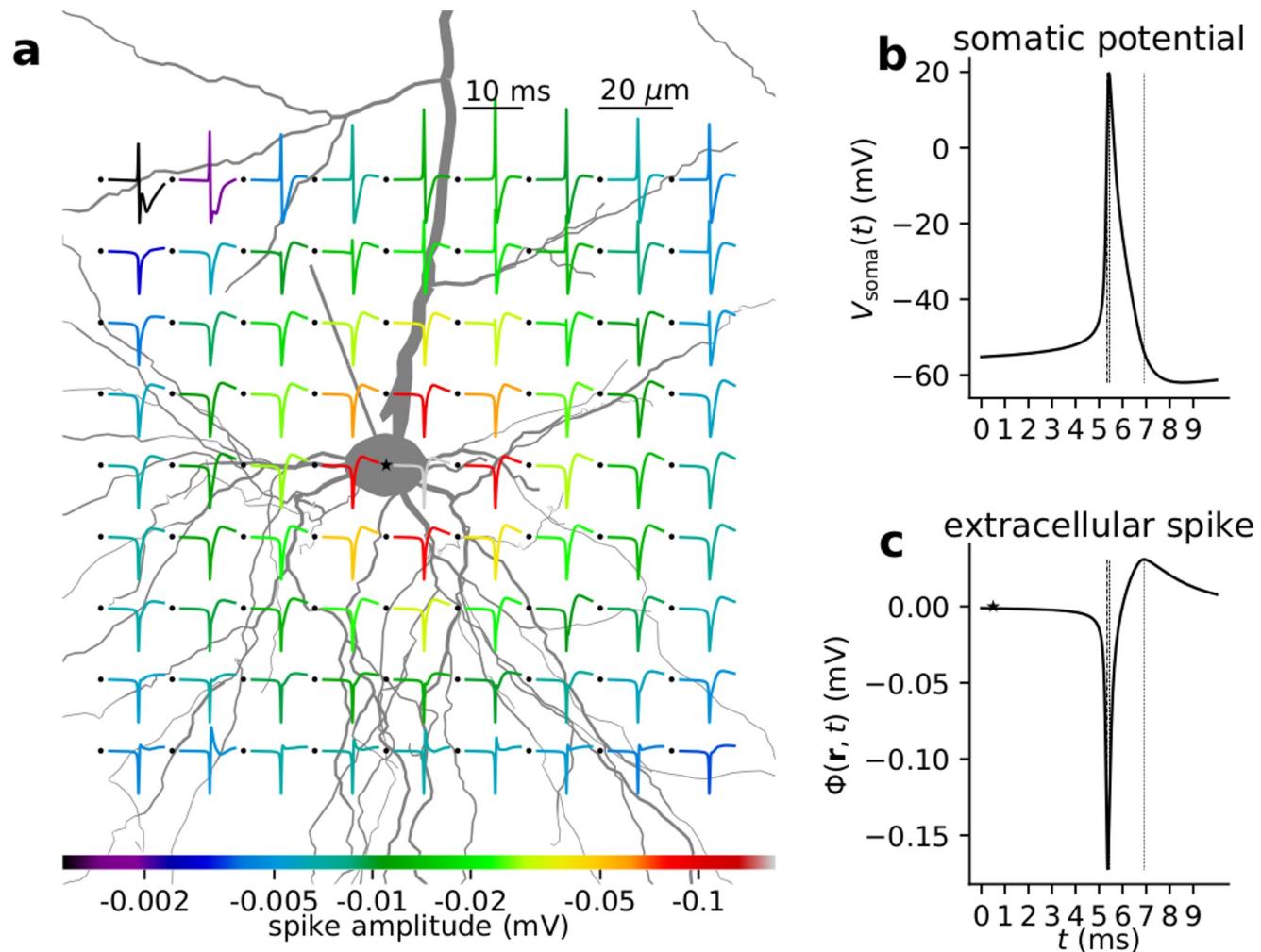
Forward-modeling formula for multicompartment neuron model

$$V_e(\mathbf{r}) = \frac{1}{4\pi\sigma} \sum_{j=1}^N \frac{i_{m,j}}{|\mathbf{r} - \mathbf{r}_j|}$$



Extracellular spike

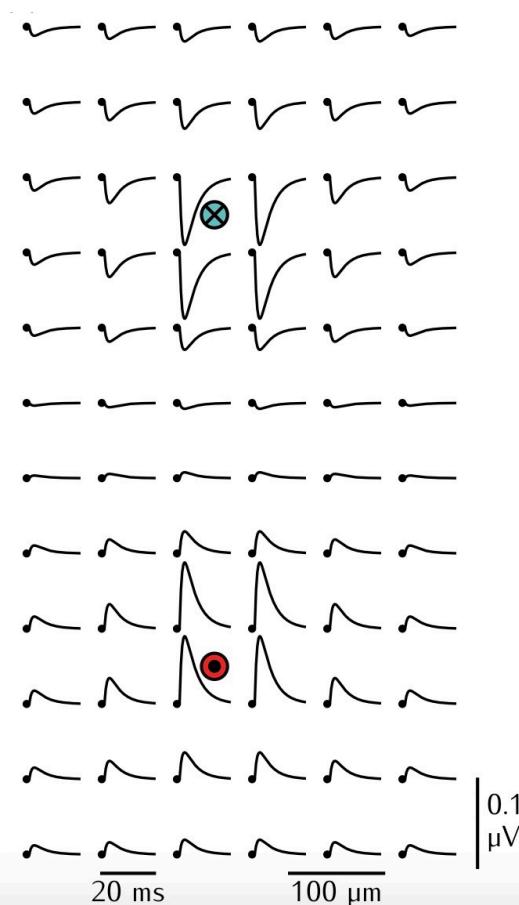
LFPy_examples/LFPy-example-04-spike1.ipynb



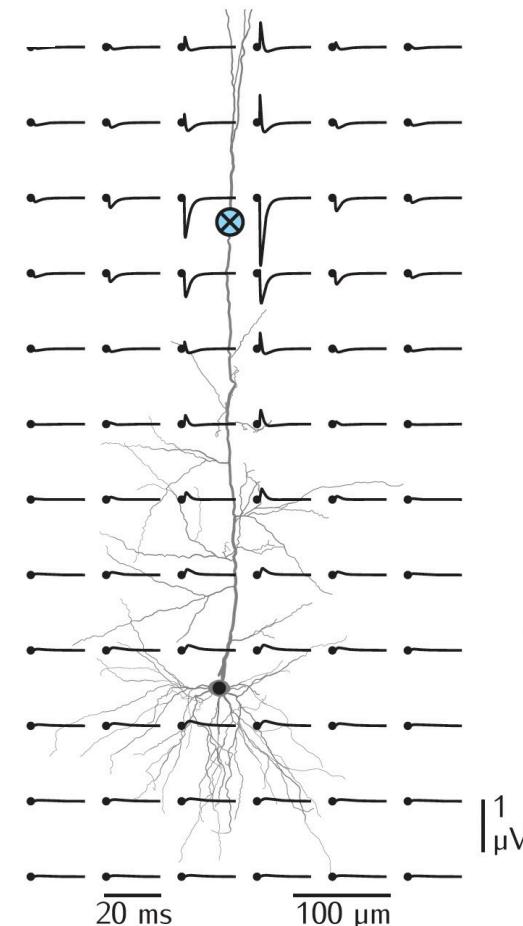
Hay et al. (2011) PLOS Comput Biol 7:e1002107

LFP from excitatory synaptic input in apical (top) compartment

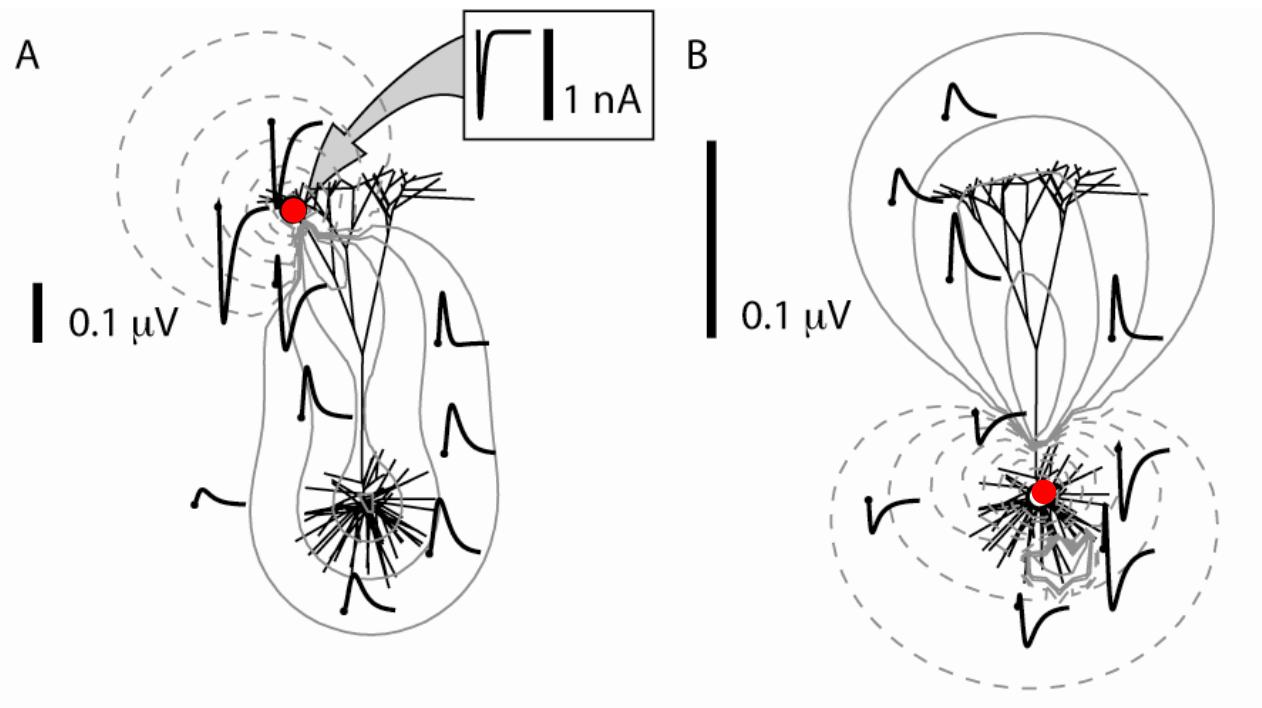
Two-compartment model



Multi-compartment model



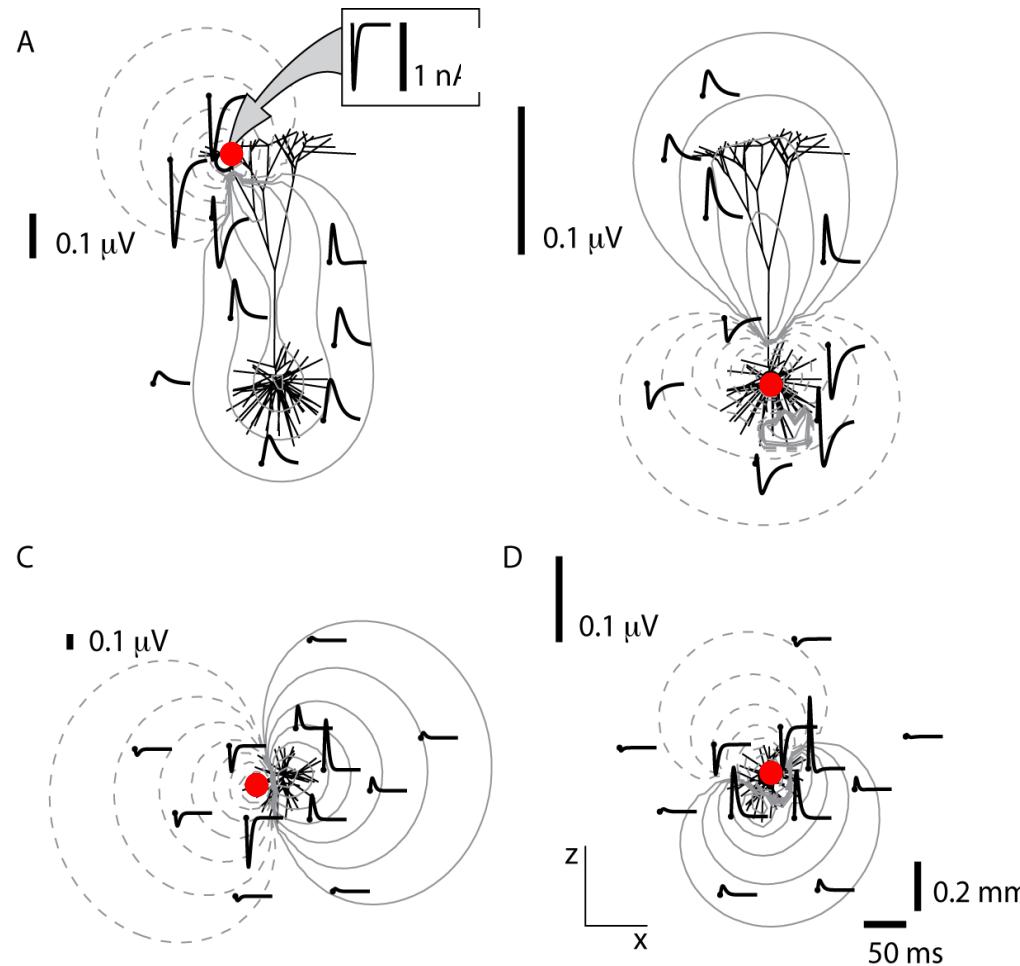
Example LFP from multicompartiment model



Basal excitation gives "inverted" LFP pattern compared to apical excitation

Generated LFP depend on morphology

Pyramidal
(L5 cat V1):



Stellate
(L4 cat V1):



- Tool for calculating brain signals from simulated neural activity
- Relies on **NEURON** for simulating multi-compartment neuron models
- For single cells to large neuronal networks
- Can calculate:
 - local field potential (LFP)
 - extracellular action potentials (spike/MUA)
 - electrocorticography (ECoG)
 - electroencephalography (EEG)
 - magnetoencephalography (MEG)

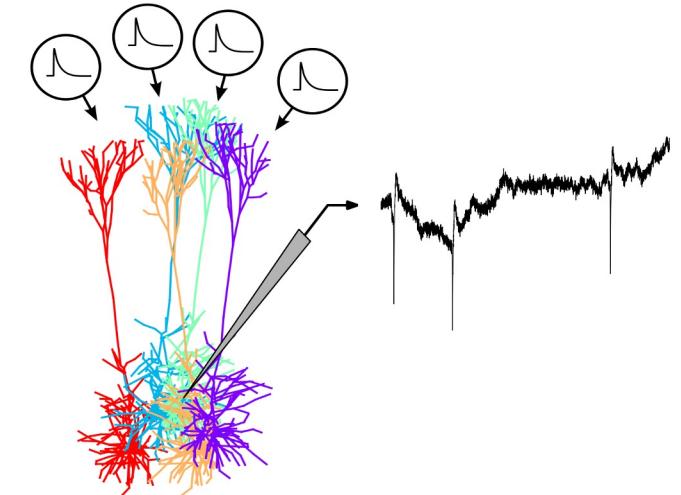


Figure from Carnevale & Hines (2006). The NEURON Book



 **frontiers**
in Neuroinformatics

ORIGINAL RESEARCH
published: 18 December 2018
doi: 10.3389/fninf.2018.00092

Multimodal Modeling of Neural Network Activity: Computing LFP, ECoG, EEG, and MEG Signals With LFPy 2.0

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lfp.readthedocs.io/en/latest/

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models

Current Source Density (CSD)

Misc.

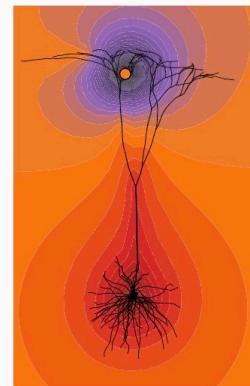


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🏠 / Welcome to LFPy's documentation!

Edit on GitHub

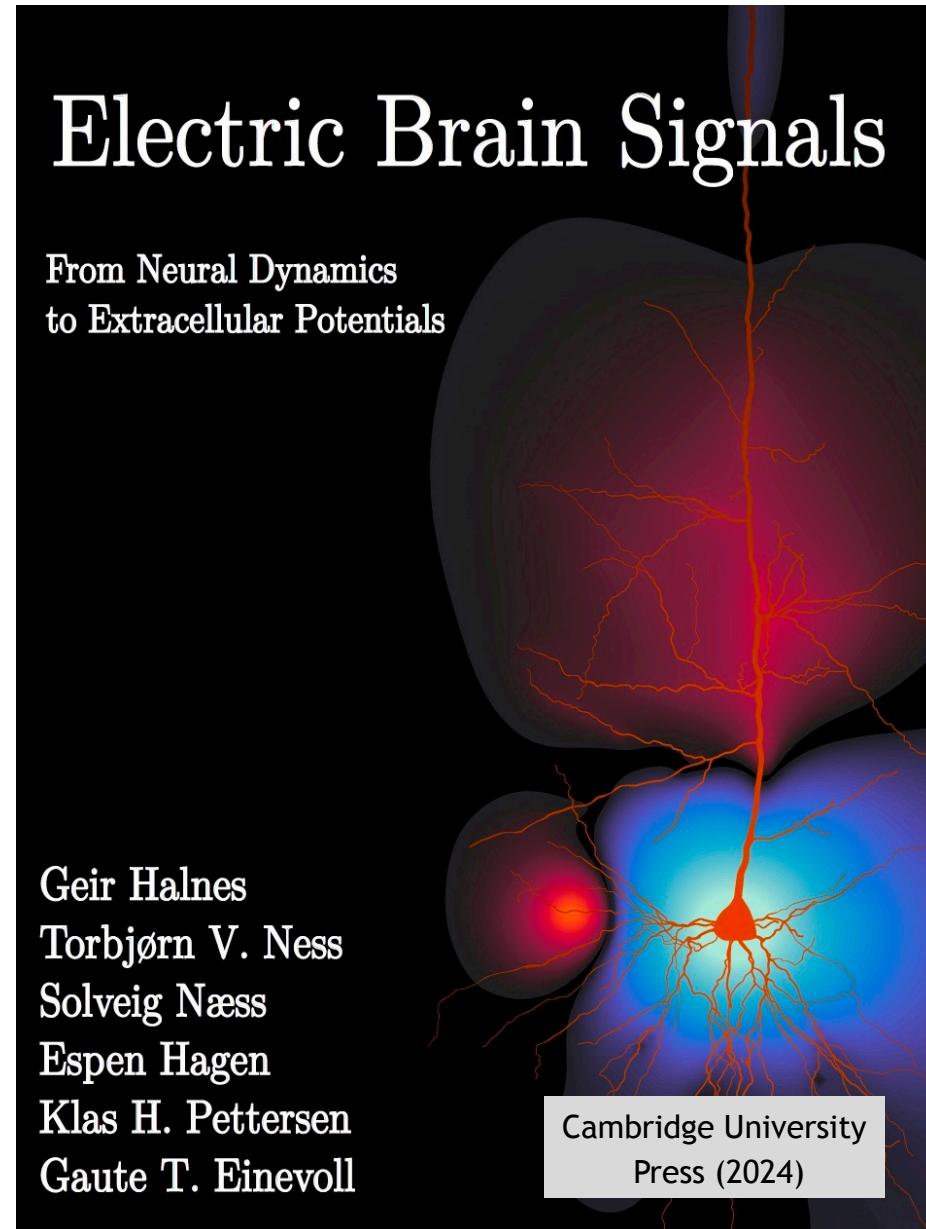


LFPY

Welcome to LFPy's documentation!

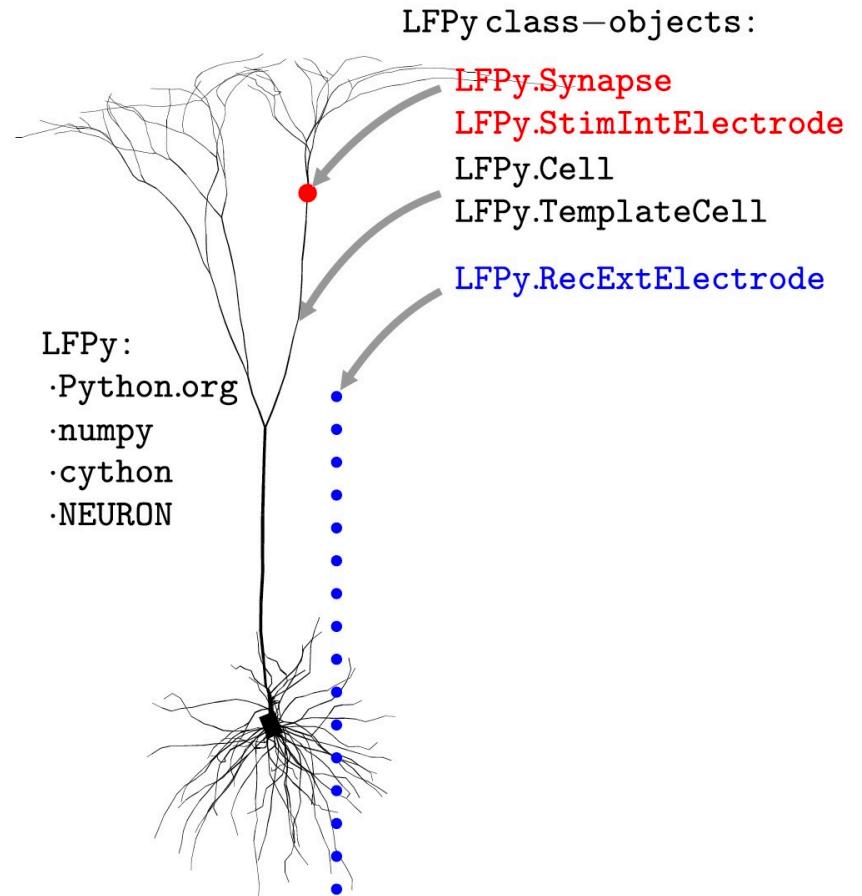
A brief video tutorial on LFPy is available here:







- ▶ Implemented in Python
- ▶ Uses NEURON under the hood
- ▶ Class objects represent:
 - ▶ cells, populations, networks
 - ▶ synapses
 - ▶ intracellular electrodes
 - ▶ extracellular electrodes
- ▶ Homepages w. documentation:
<http://LFPy.rtfd.io>
<https://github.com/LFPy/LFPy>





Summary

- LFPy is an open-source python tool for calculating measurable brain signals
- Can help researchers compare simulation results with experimental data in a multimodal manner
- Applicable for single cells and large networks
- Can calculate LFP, spike, ECoG, EEG and MEG
- EEG/MEG calculation:
 - Current dipole moments are extracted from arbitrary simulated neural activity
 - Can be used with both simple and complex head models
- Is also a convenient NEURON wrapper
- Can be tested without installation (link on github)
- Well-tested and documented: <https://lfpy.readthedocs.io>

File Edit View Run Kernel Git Tabs Settings Help

Mem: 1.28 / 2.00

+ Filter files by name

Untitled.ipynb Exercise_03.ipynb Exercise_03_solution.ipynb

EBRAINS-23.09

Exercise 03 Forward modelling of extracellular potentials using LFPy

In this exercise you will work with forward modelling of extracellular potentials, based on the Hay model (Hay et al. (2011) PLoS Comput Biol 7: e1002107, doi:10.1371/journal.pcbi.1002107).

You will be given example code below, based on *LFPy* and *NEURON*, which you can adapt to solve this exercise.

```
[1]: # TO IMPORT LFPY, SELECT THE KERNEL EBRAINS-23.02
import os
retval = os.getcwd()
print("Current working directory %s" % retval)
os.chdir("hay_model/mod/")
!nrnivmodl
os.chdir(retval)

%matplotlib inline
from os.path import join
import numpy as np
import matplotlib.pyplot as plt
import neuron
import LFPy
from hay_model.hay_active_declarations import active_declarations
nrn = neuron.h
```

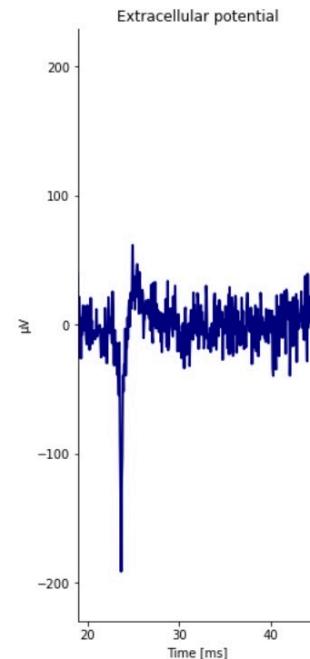
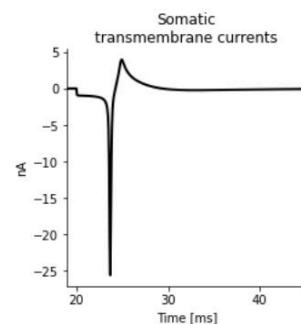
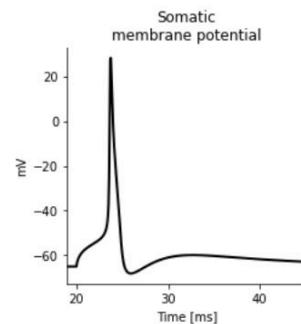
Task 1

Given a noise level on the virtual extracellular electrode corresponding to white noise with a Root-Mean-Square of 15 μV , roughly how far away from soma will a spike from the Hay model be visible on an electrode?

Note: The soma of the cell is in origo, and you can change the distance to the electrode by for example changing the x position of the electrode (elec_x)

```
3]: cell = return_cell(conductance_type="active")
insert_synapse(cell, synaptic_y_pos=0, weight=0.018)
cell.simulate(rec_imem=True, rec_vmem=True)
elec_x = np.array([20.])
elec_y = np.array([0.0])
elec_z = np.array([0.0])
electrode = make_extracellular_electrode(cell, elec_x, elec_y, elec_z)
plot_extracellular_potential(cell, electrode, xlim=[19, 45])
```

active ion-channels inserted.

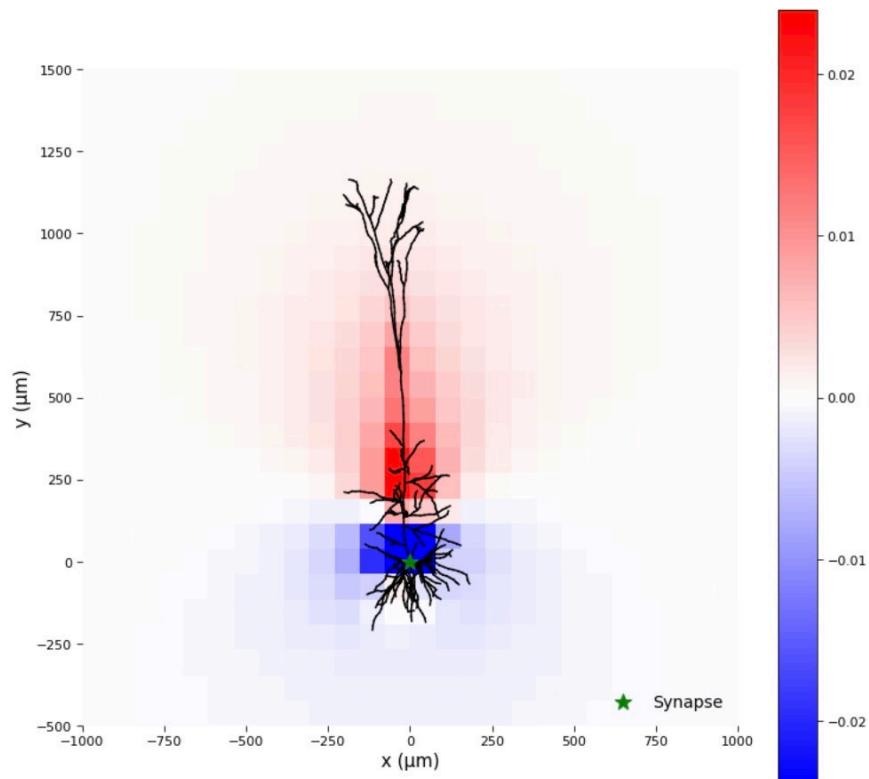


Task 2:

We will now look at the origin of the Local Field Potential (LFP), which is typically assumed to be caused by synaptic input to large populations of cells.

Decrease the synaptic weight so that the cell does not fire an action potential, and plot the extracellular amplitude on a dense 2D grid around the cell at the time corresponding to the maximum deflection in the membrane potential at the position of the synapse. A plotting function for this is already implemented below.

- What shape does the LFP around the cell have for a somatic synapse ($y=0$)?
- What shape does the LFP around the cell have for a synapse arriving at the center of the apical dendrite of the cell ($y = 600 \mu\text{m}$)? How about at the distal apical dendrite ($y = 1200 \mu\text{m}$)?
- Can you, based only on the shape of the LFP, predict which of the three that will fall off most rapidly with distance from the cell? Hint: Distance decay of a dipole versus higher order multipoles.

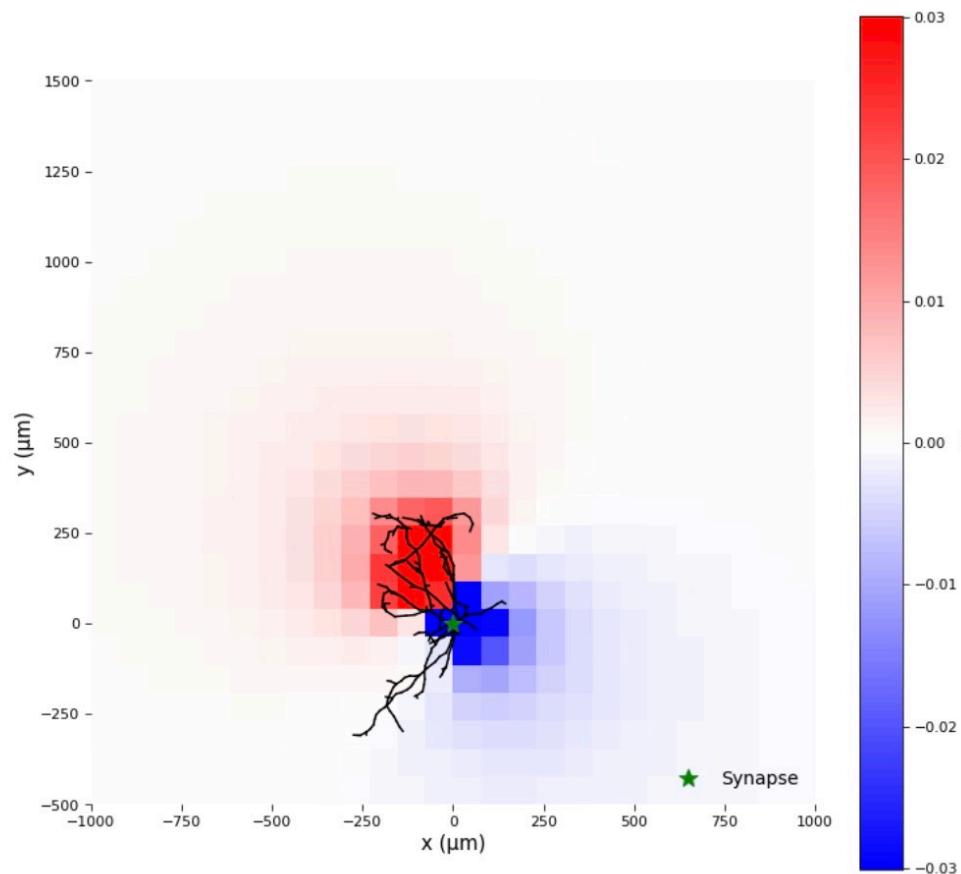


Task 3

Compare the LFP from this pyramidal cell model, with the LFP from an interneuron cell model (code below). Are there differences that might be important?

Hint: The LFP is expected to result from many synaptic inputs to many different cells, and the LFP is not expected to sum in the same way for these two different cell types.

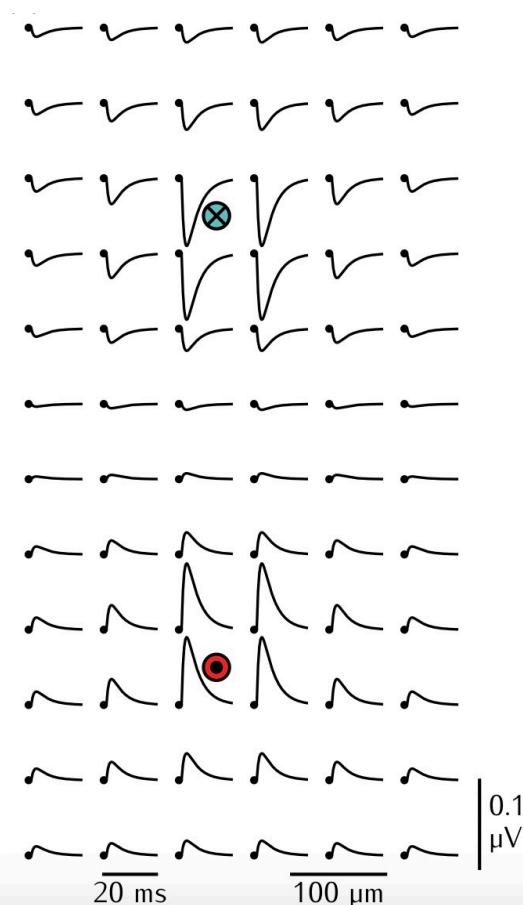
Based on the results from Task 2 and Task 3 in this exercise, it is possible to make quite strong claims about which neuronal processes that will dominate the LFP. For more information on this, see: Lindén et al. (2010) Intrinsic dendritic filtering gives low-pass power spectra of local field potentials. *J Comput Neurosci* 29: 423–444. <http://www.ncbi.nlm.nih.gov/pubmed/20502952>



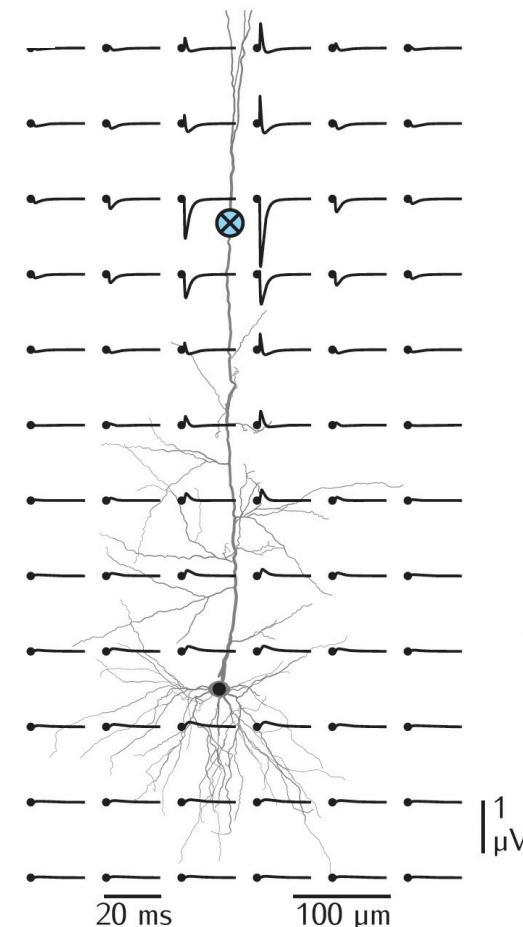
END - tutorial 2

LFP from excitatory synaptic input in apical (top) compartment

Two-compartment model

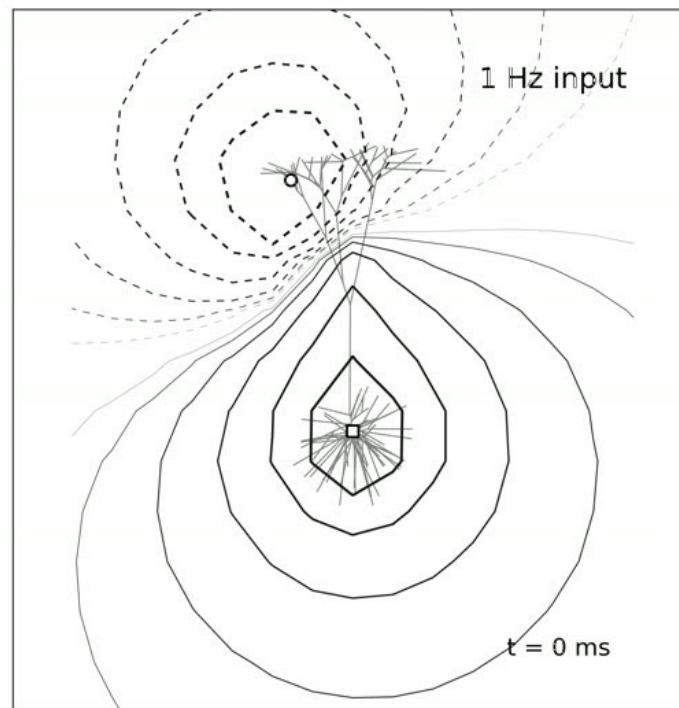


Multi-compartment model



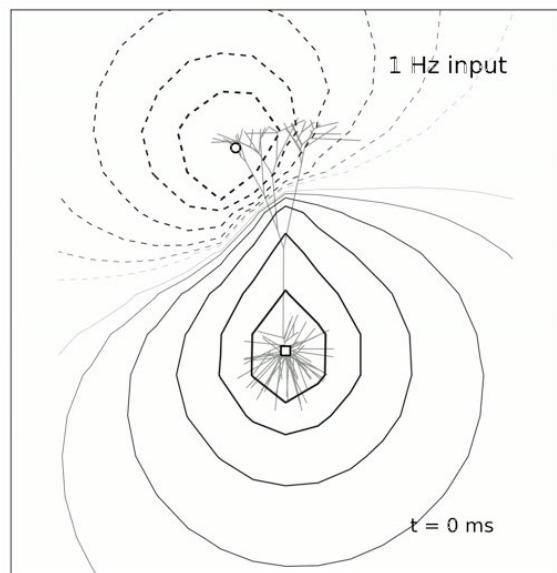
LFP dipole from single L5 pyramidal neuron

1 Hz oscillatory current into apical synapse:

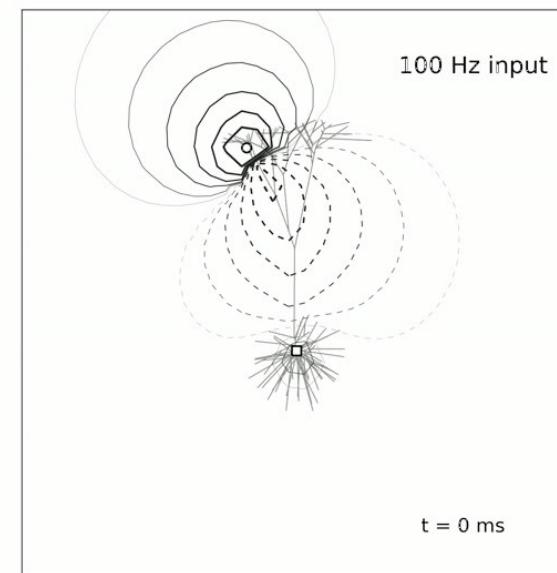


Frequency dependence of LFP "dipole"

1 Hz



100 Hz



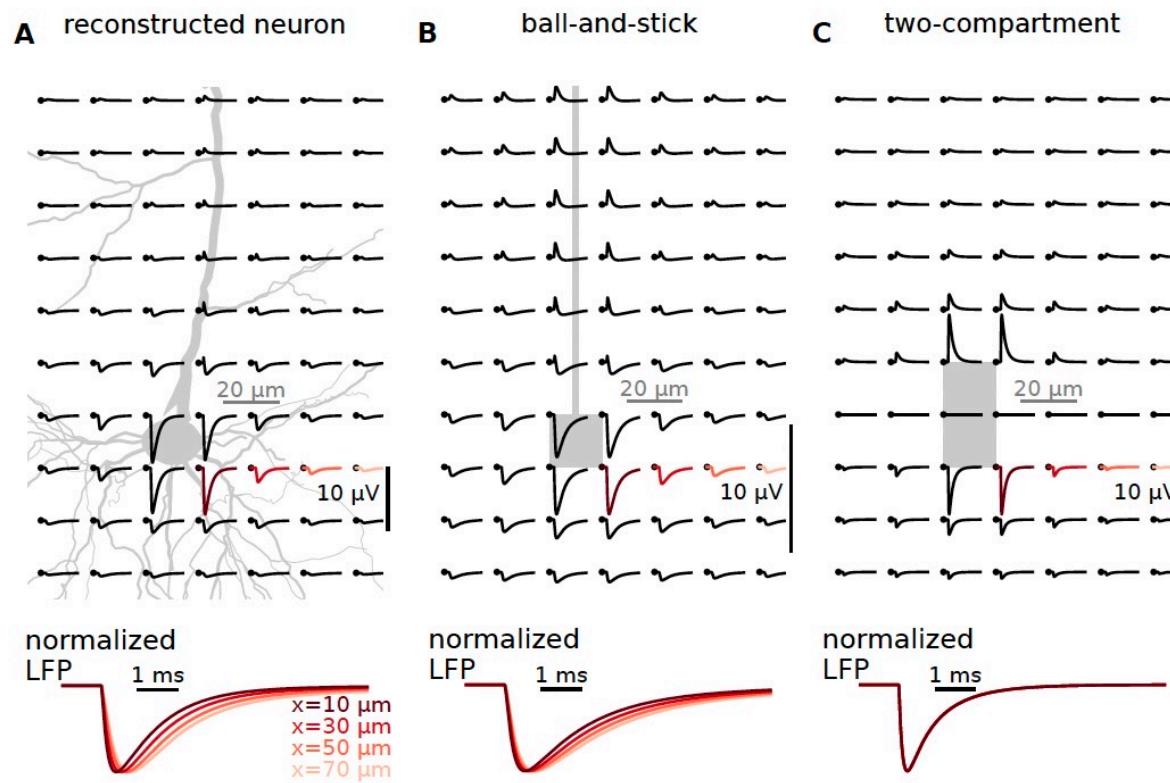
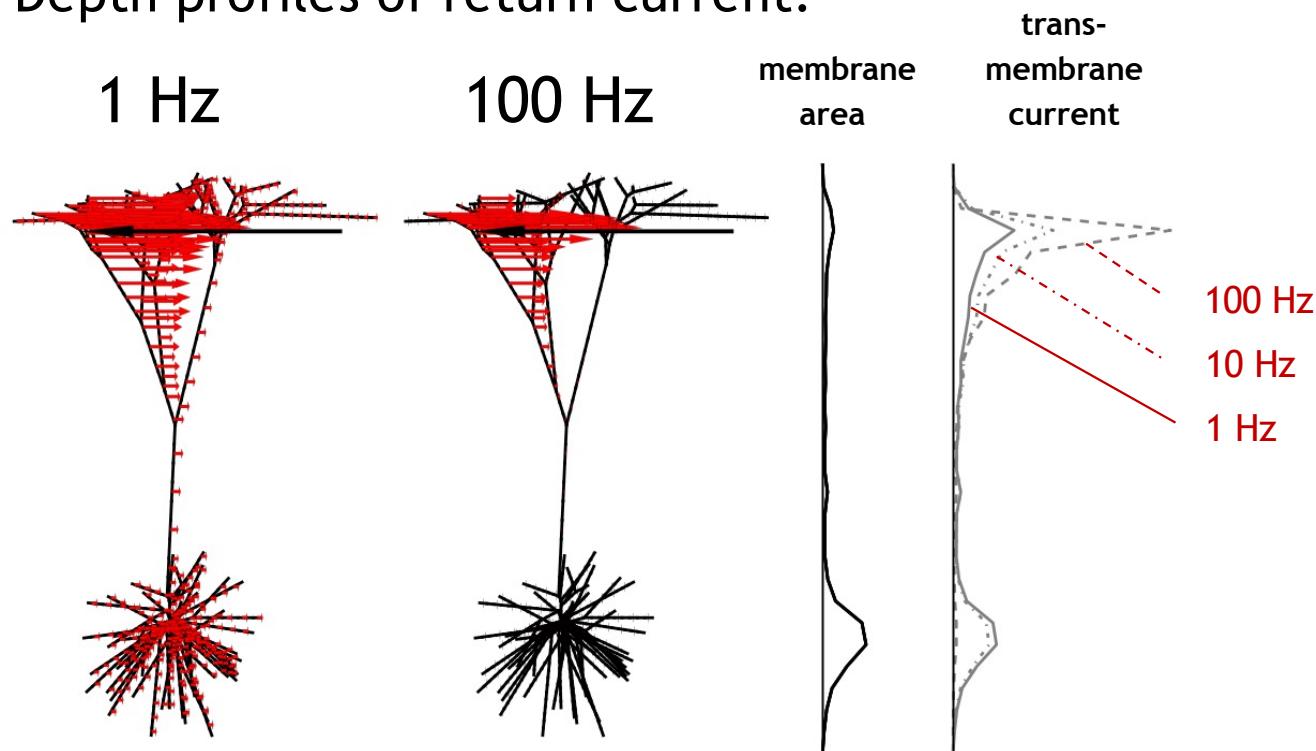


Figure 8.3 Shape of LFP signal is dependent on the morphology. **A:** LFP around the Hay model neuron from a single excitatory synaptic input in the soma. The lower panel shows LFP signal shapes at different lateral positions from the soma, as indicated by the color coding. **B:** Same as panel A for a ball-and-stick neuron model. **C:** Same as panel C for a two-compartment neuron model.

Code: [Ch-8/compare_Hay_bns_2comp.ipynb](#)

Origin of low-pass filtering effect of LFP

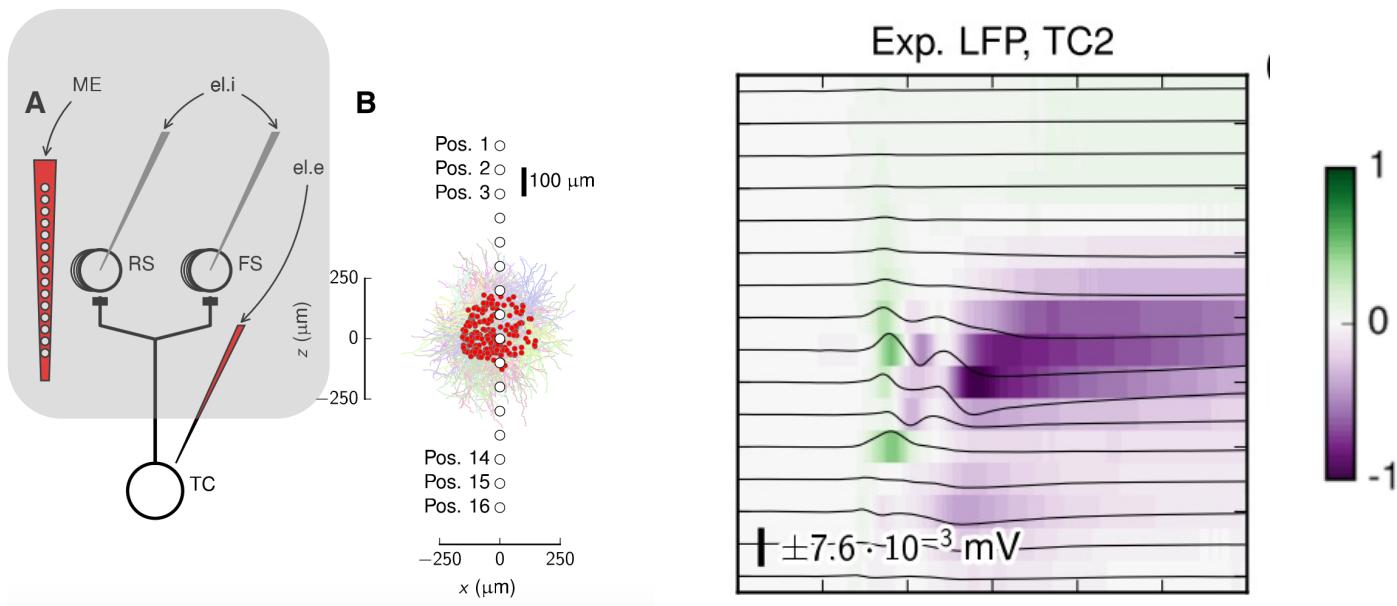
- Depth profiles of return current:



Effective current-dipole moment decreases with increasing frequency due to cable properties of dendrites

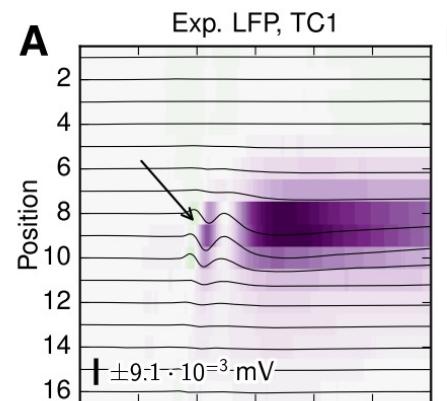
LFP signature of thalamocortical projection

- Spike-triggered LFP (Swadlow et al, 2002):

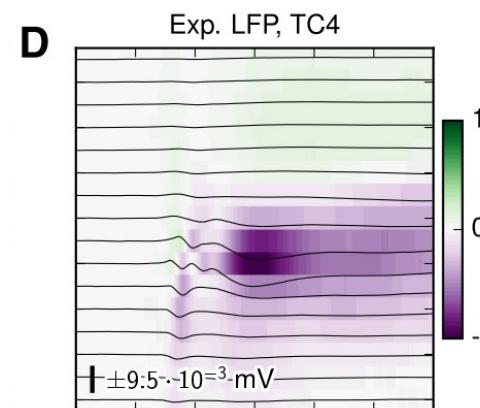


Experiments

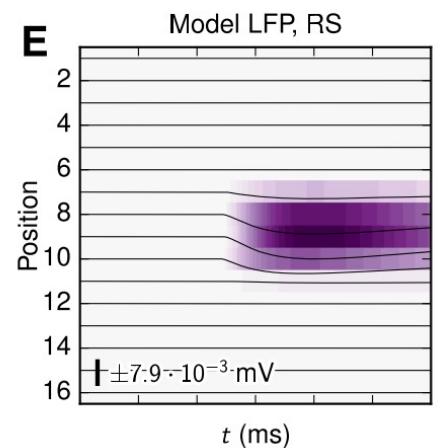
Example 1



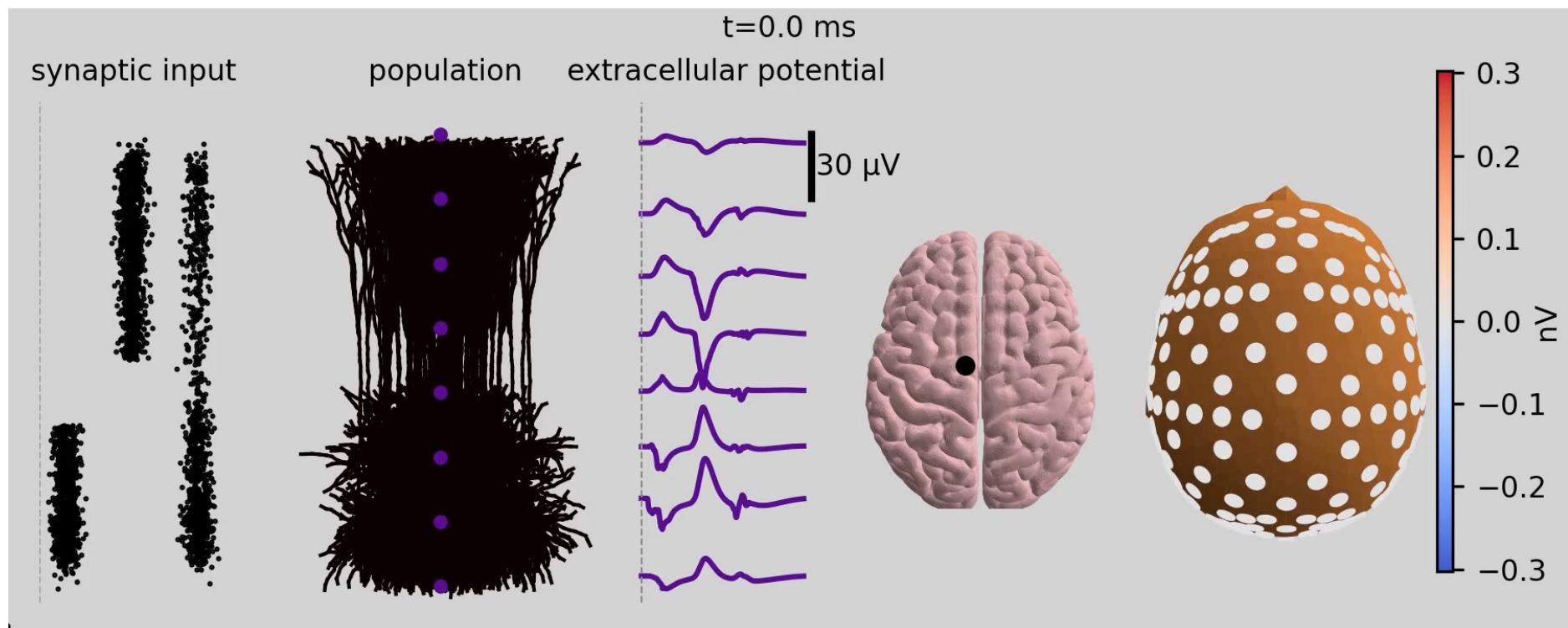
Example 2



Model



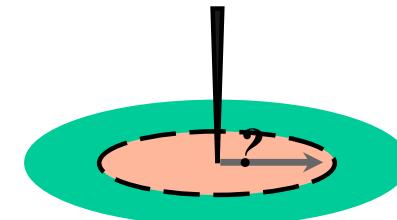
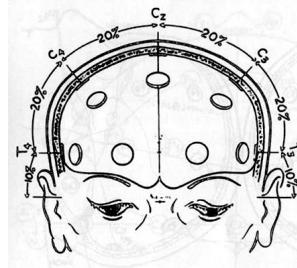
Example: LFP and EEG signal from 10000 biophysically detailed neuron models



How local is the local field potential?

Linden et al, Neuron 2011

- More local than EEG where sources are further away!

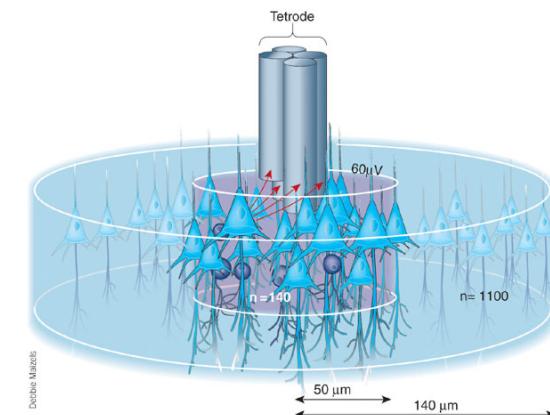


- Analogous question for high frequency part:

How many neurons can an electrode record spikes from?

Can be answered since:

- spikes are spatially very local (< 100 µm)
- spikes don't last long (~1 ms) [just say 'beep']



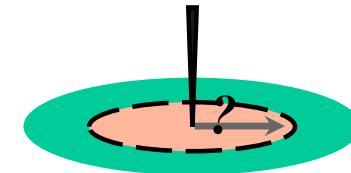
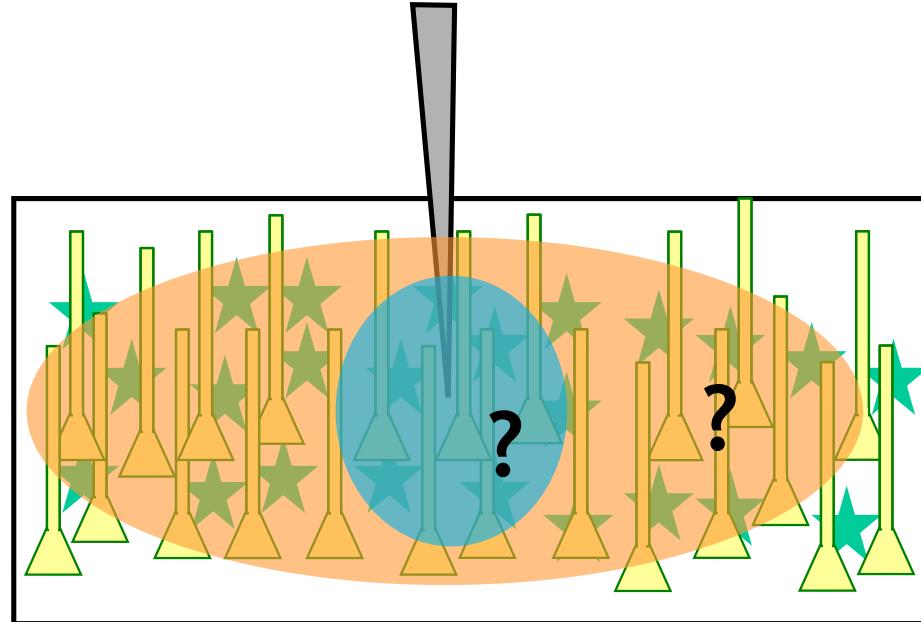
How many people can a microphone record from?



- It depends!

LFP is (unlike spikes) non-local in time and space, and thousands of neurons will typically contribute to the LFP

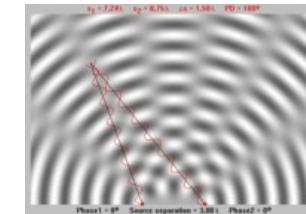
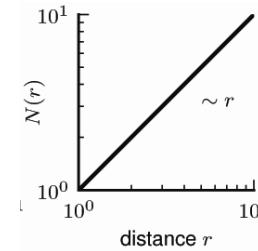
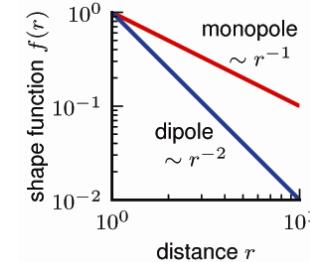
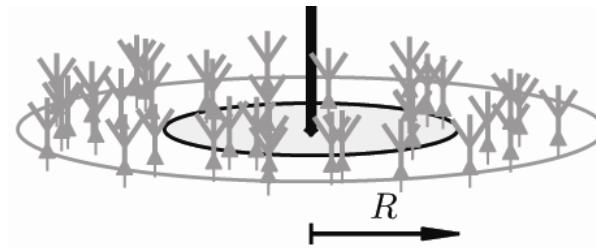
How large is the LFP-generating region?



- Different reports on spatial extent on this spatial reach:
from ~200-300 μm to 1-10 mm

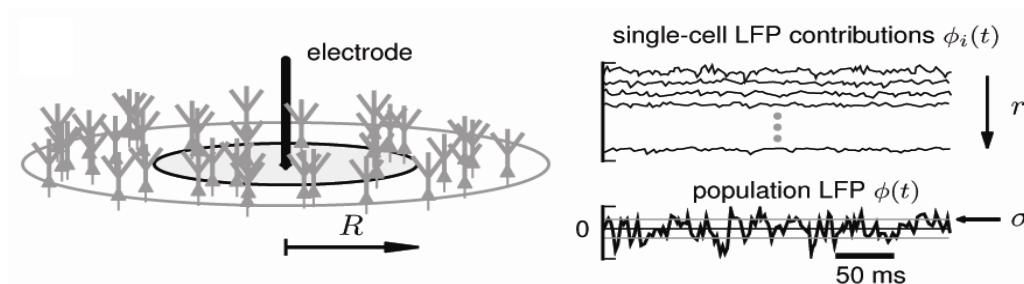
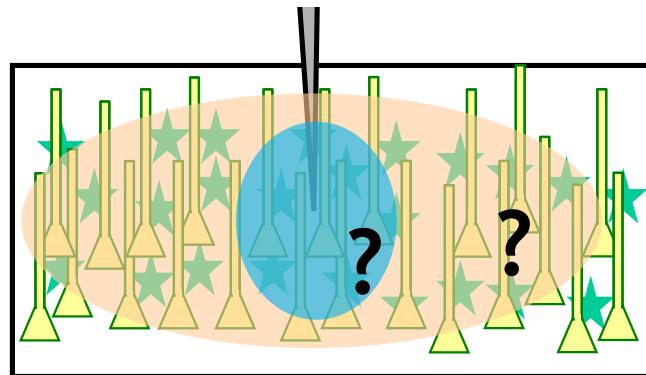
What determines the spatial reach?

1. How far does the contribution from a single neuronal LFP source extend?
2. How does the number of contributing LFP sources change with distance from the electrode?
3. How synchronized are the LFP sources?



Result from modeling study

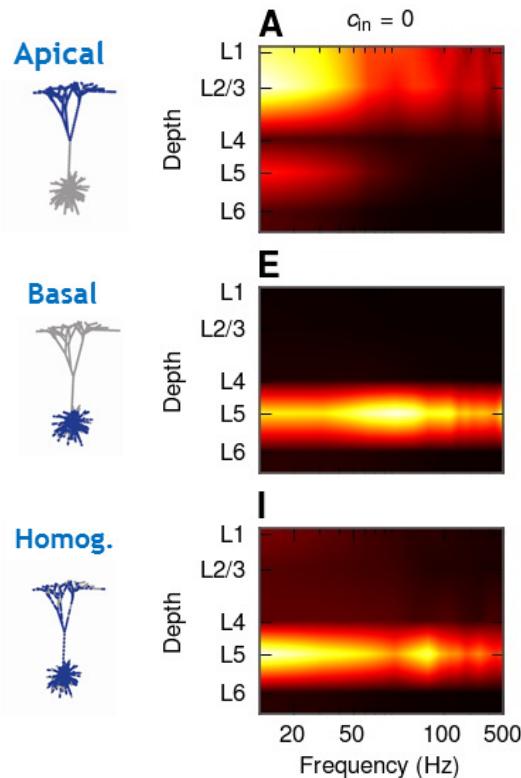
- Modeling study for populations of neurons:



- Uncorrelated neuronal LFP sources: spatial reach ~ 0.2 mm
- Correlated neuronal LFP sources:
 - spatial reach set by spatial range of correlations of synaptic input
 - effect of correlations depends sensitively on synaptic input distribution

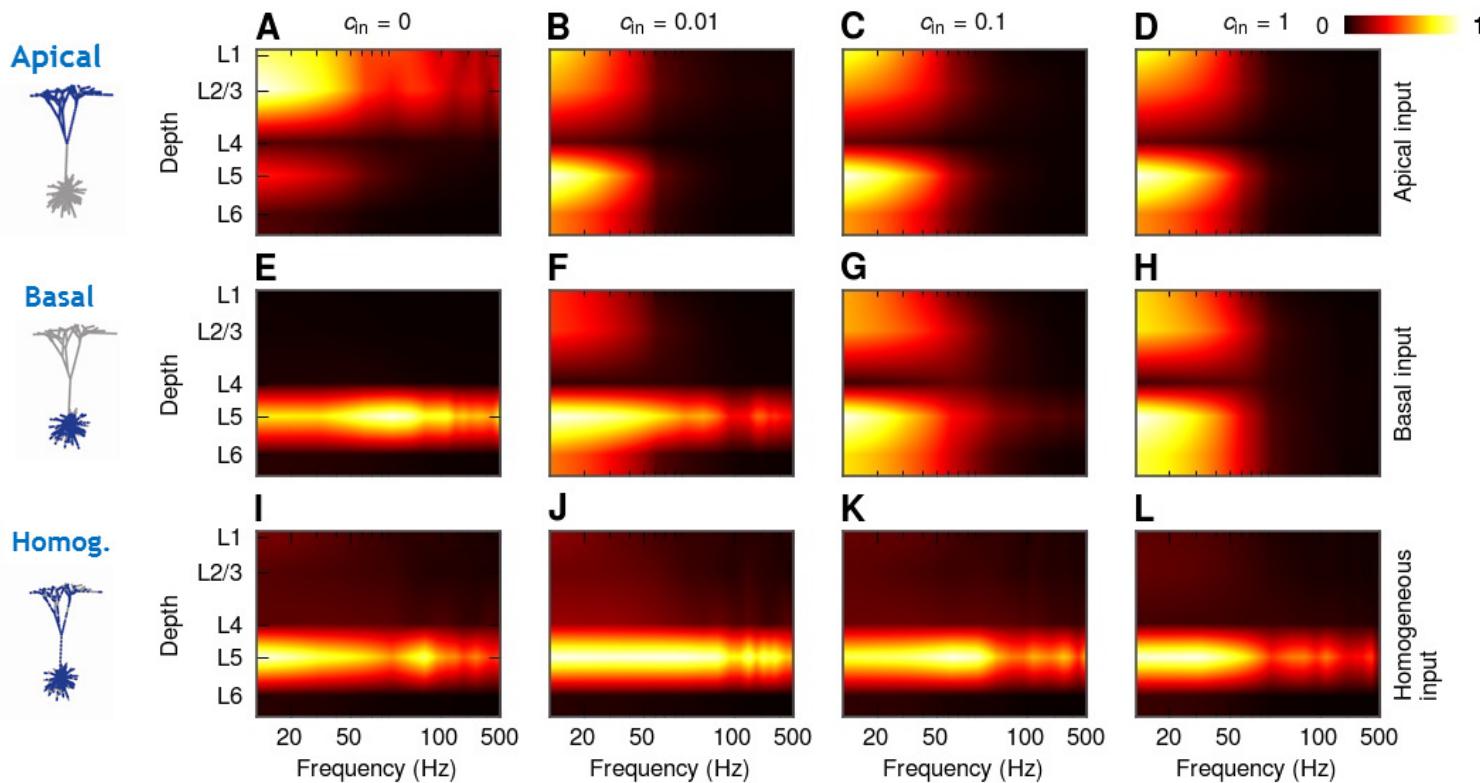
Conditions for 'dipolar' LFP

- Correlated and spatially asymmetric synaptic input
- Low frequencies



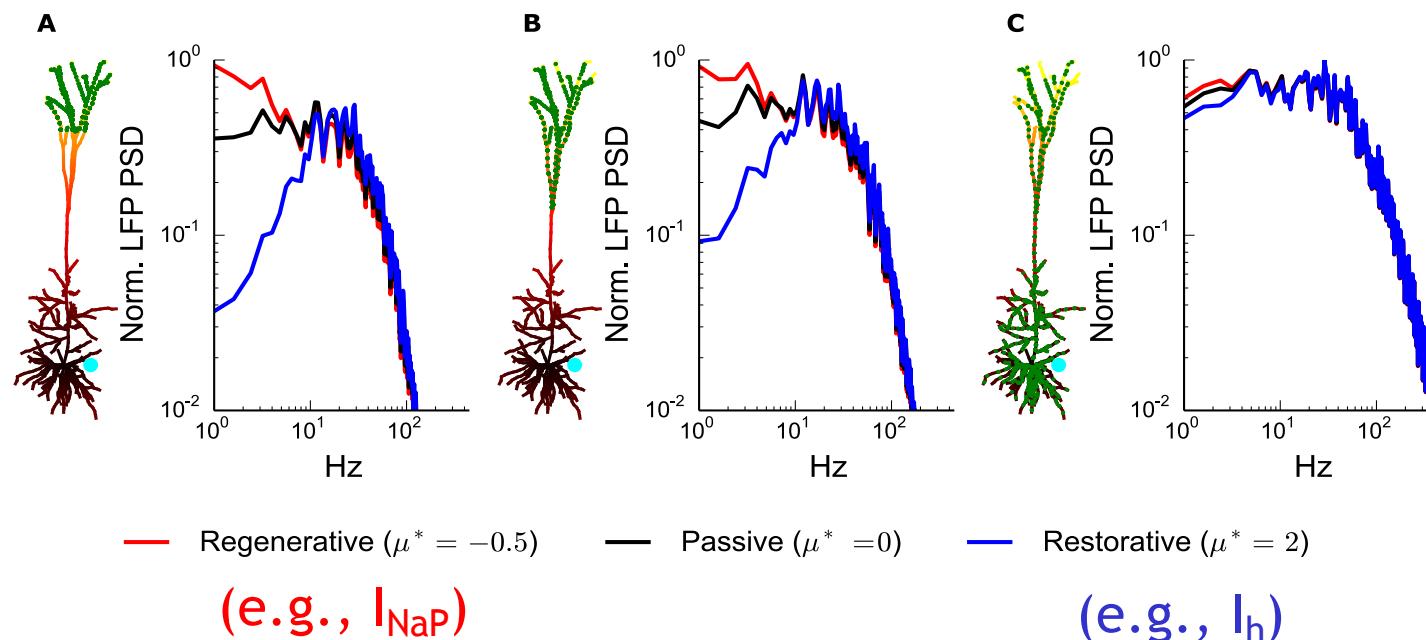
Conditions for 'dipolar' LFP

- Correlated and spatially asymmetric synaptic input
- Low frequencies



What about active dendritic conductances?

- Layer 5b pyramidal cell model (Hay et al, 2011)
 - Linearly increasing active density up from soma



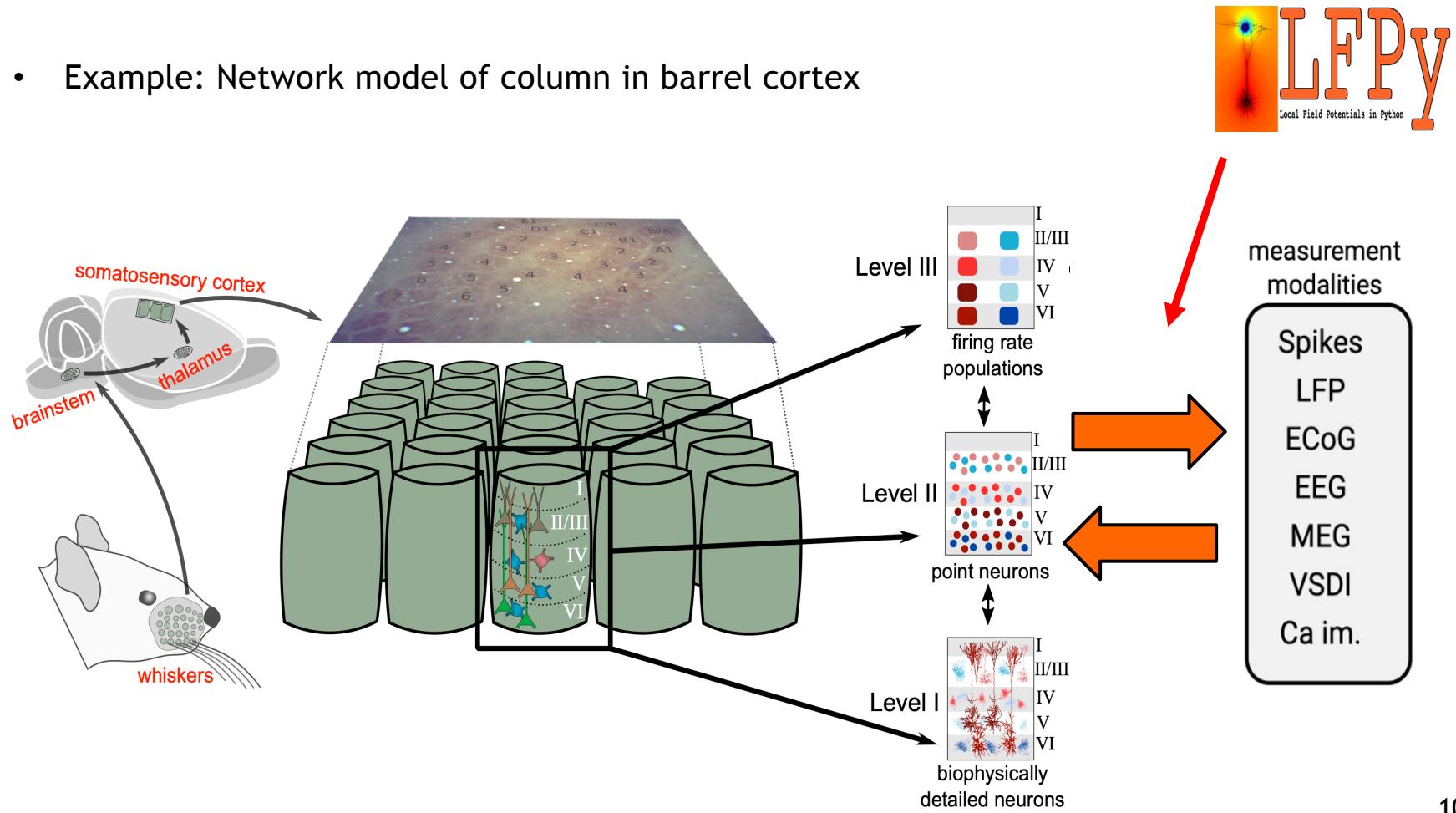
Ness, Remme & Einevoll, J Physiol, 2016

Ness, Remme & Einevoll, J Neurosci, 2018



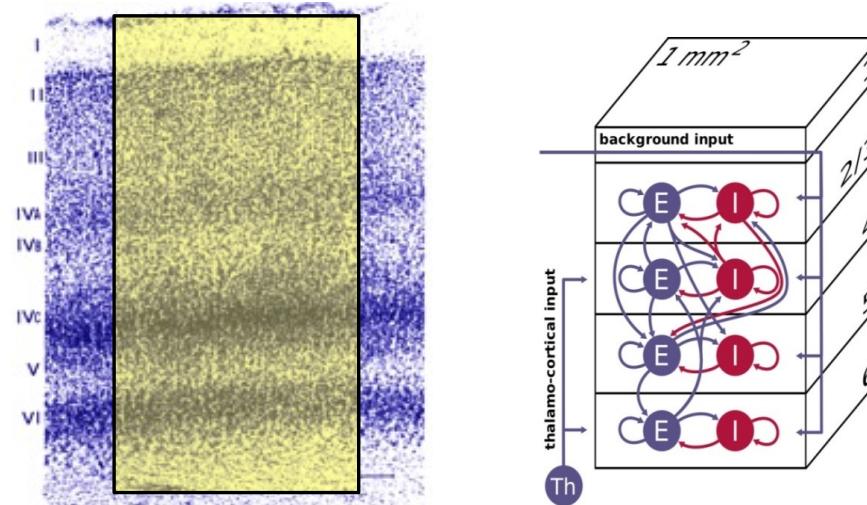
Multilevel + multimodal network modeling

- Example: Network model of column in barrel cortex



Example: LFP & EEG from point neurons (level II)

- Potjans-Diesmann model for cortical column

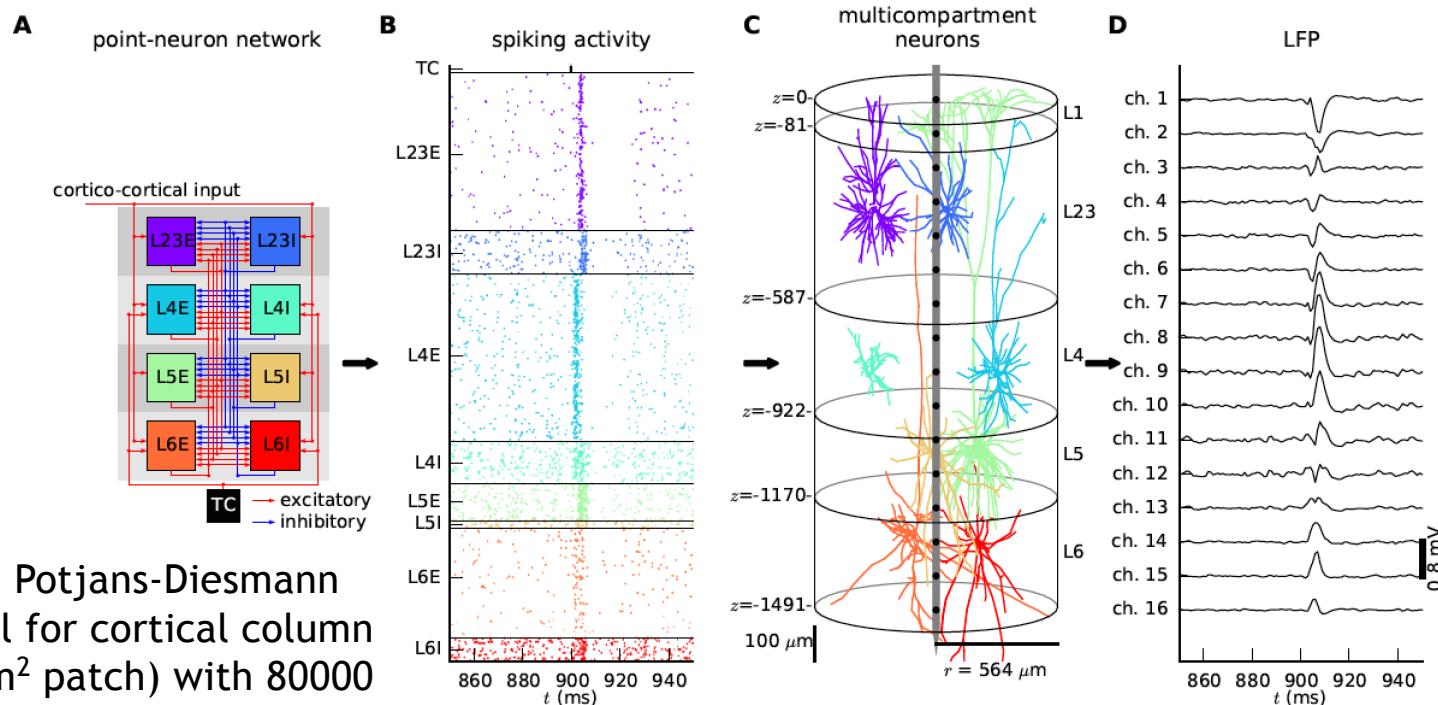


- 80,000 IF neurons, ~1 mm² of cortex
- 4 layers, 2 neuron populations (E,I) per layer
- Synaptic connection rules taken from experiments

nest::
simulated()

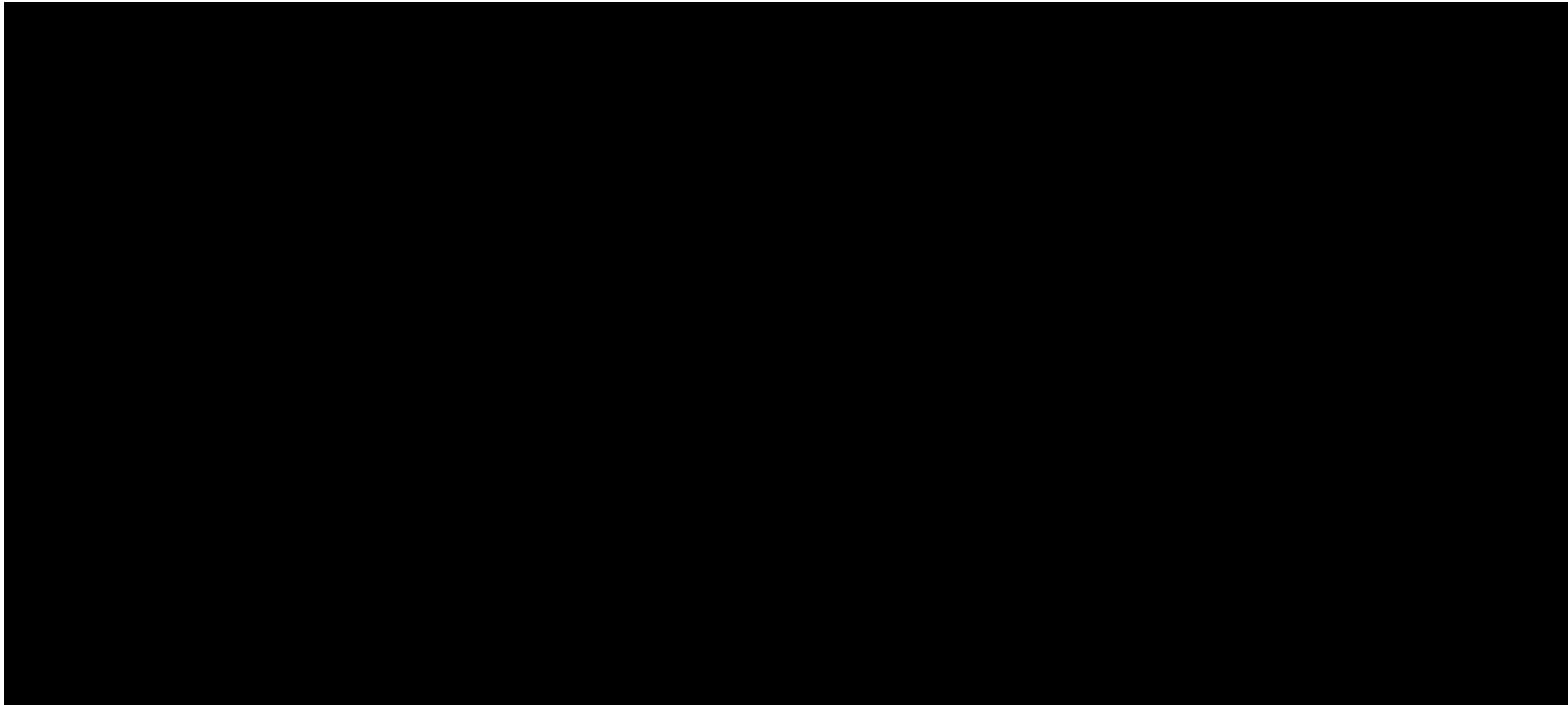
Hybrid scheme for computing network LFPs

- Point-neurons (integrate-and-fire neurons) do not generate LFPs. Trick required!



Here: Potjans-Diesmann
model for cortical column
(1 mm^2 patch) with 80000
neurons

Example: Potjans-Diesmann model for visual cortex column (80000 integrate-and-fire neurons)

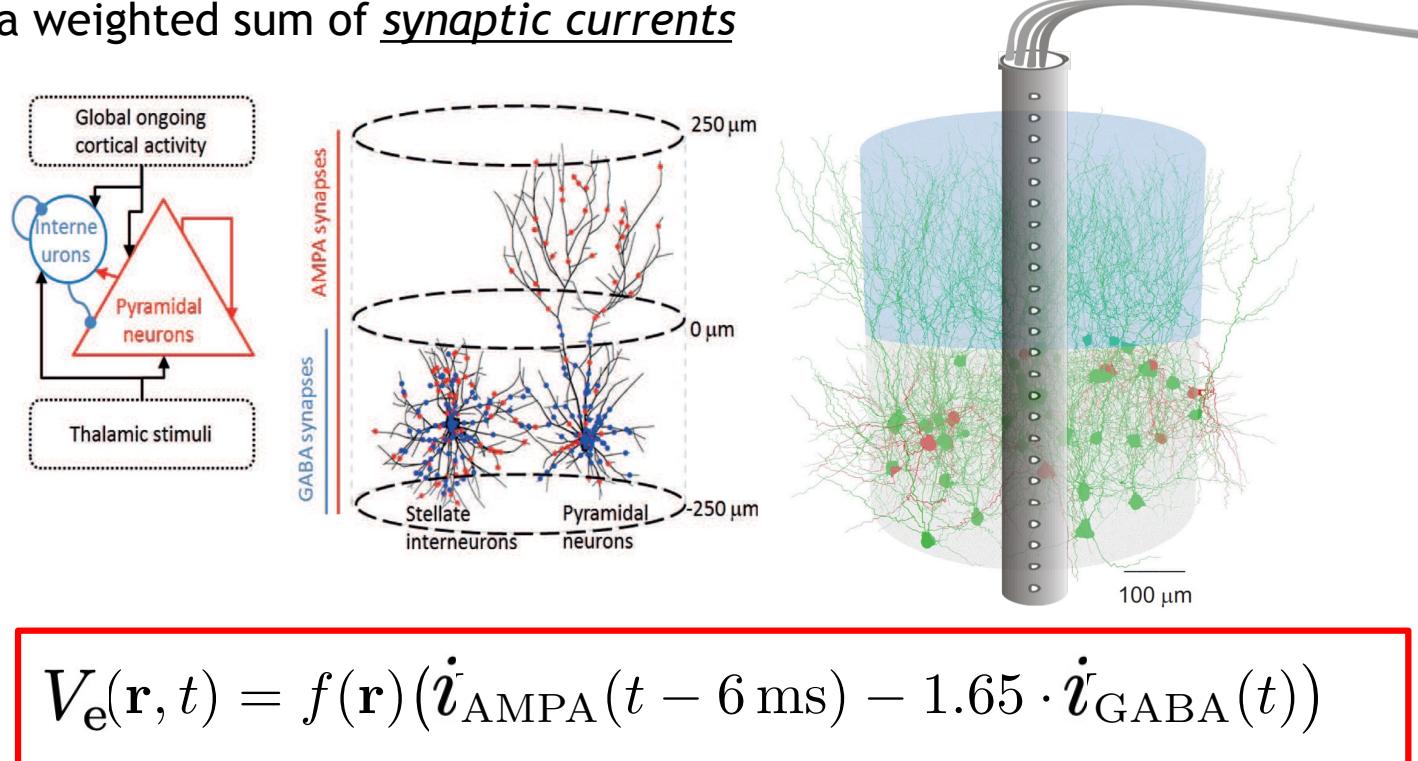


Hagen et al, Cerebral Cortex, 2016

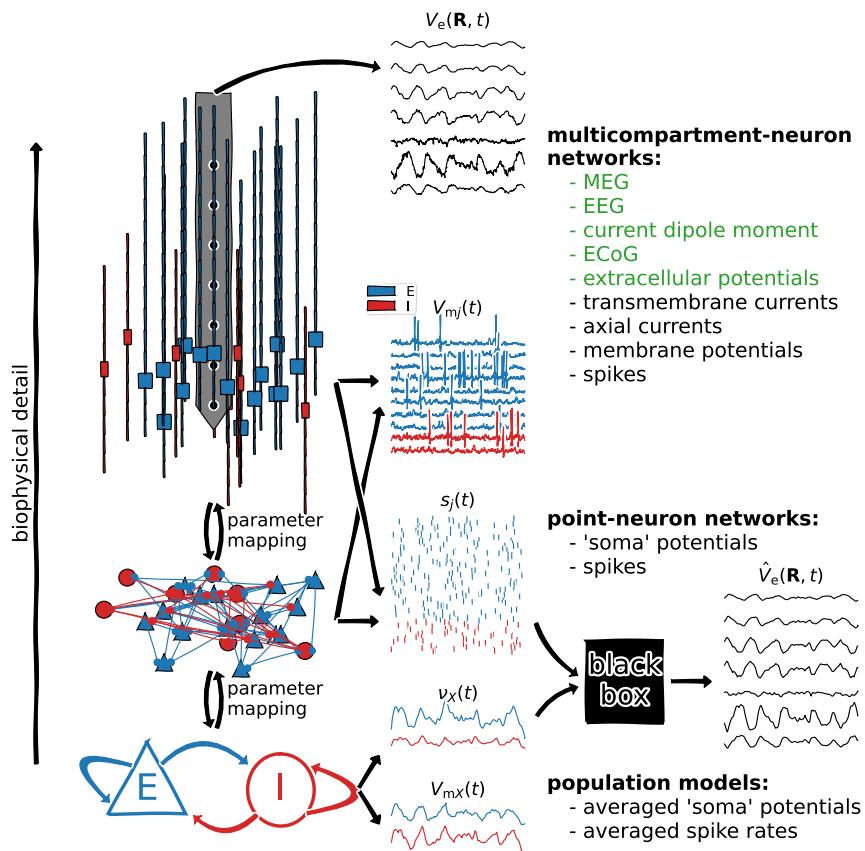
Hagen et al, Frontiers in Neuroinformatics, 2018

What is the best proxy for computing LFPs based on LIF network simulations?

- NOT average firing rate or membrane potential, rather a weighted sum of synaptic currents

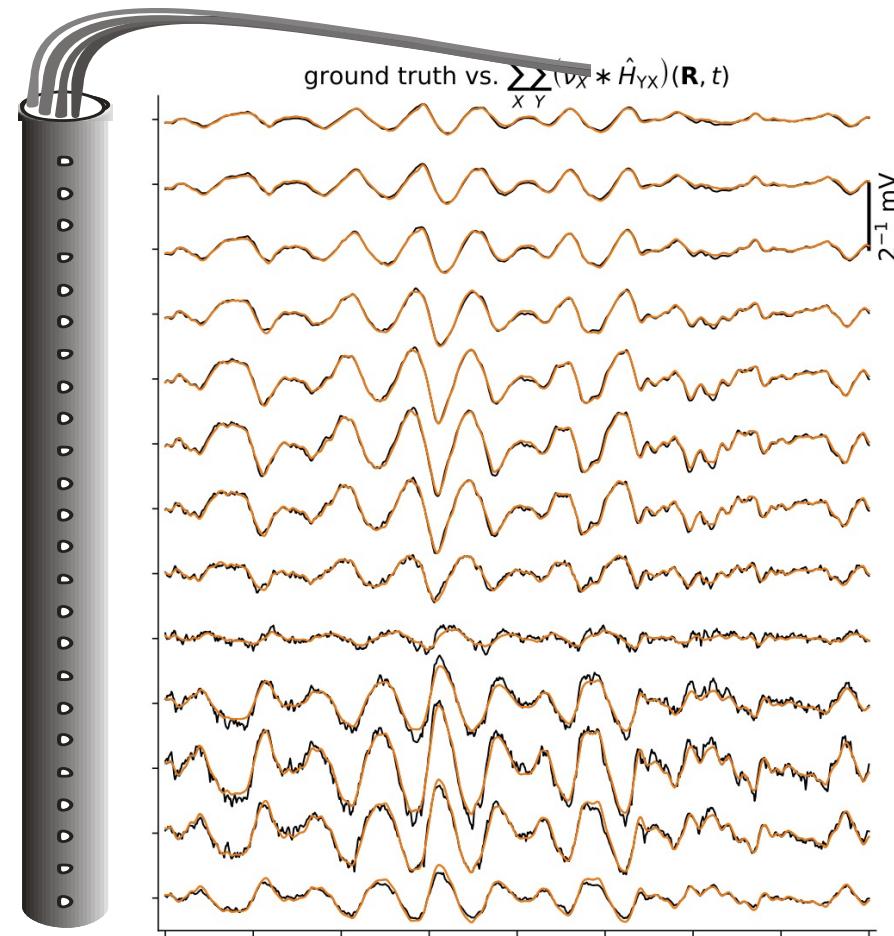


LFP, EEG and MEG from population firing-rate models

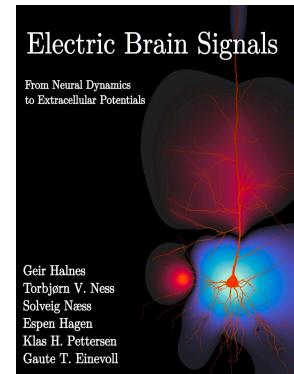


Kernel trick

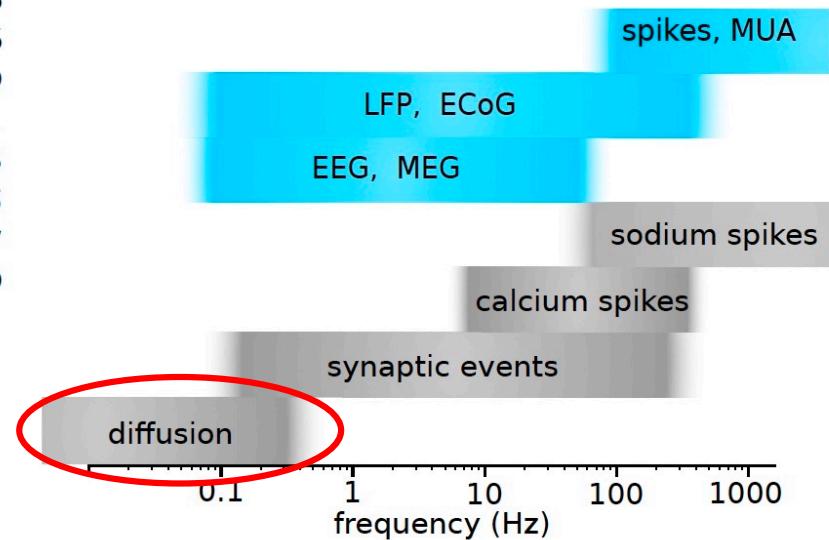
- Computer time grows with the number of **populations**, not the number of **neurons**



Diffusion potentials



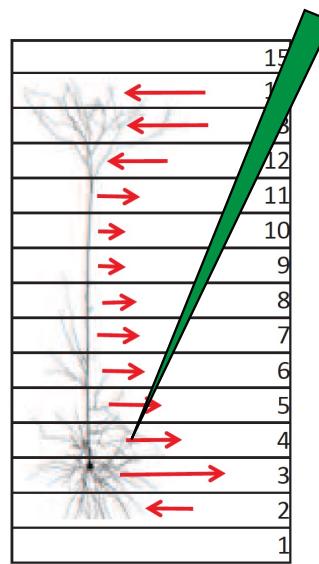
12	Diffusion potentials in brain tissue	292
12.1	What is a diffusion potential?	293
12.2	Theory for computing diffusion potentials	296
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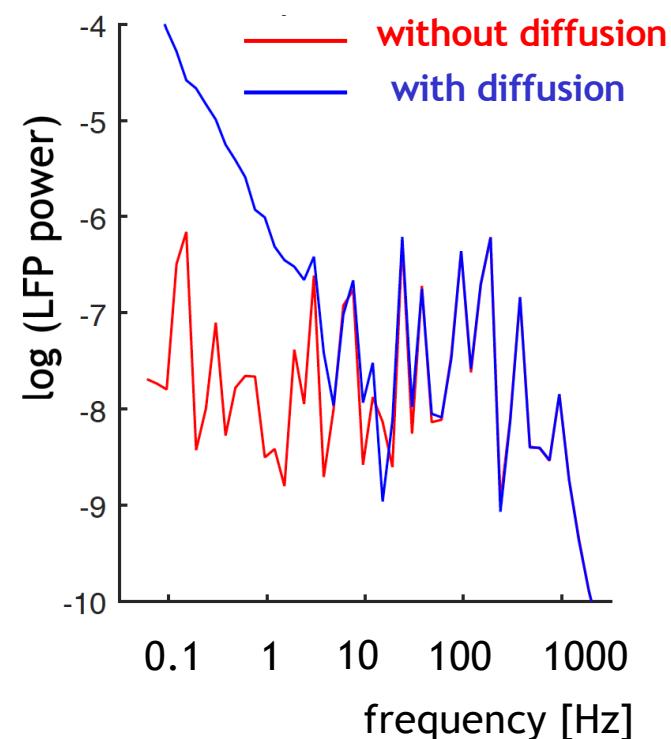
Effects of diffusion current?

- Ion concentration gradients in extracellular space (ECS) may give rise to **diffusion currents** - which in turn sets up an opposite **electrical current** - and thus also an **electrical potential**

- Model: Column of neurons firing action potentials - increased $[K^+]$ in ECS at soma level



- Here: Diffusion affects power spectrum for frequencies up to ~10 Hz at soma level



Halnes et al, Plos Comp Biol, 2016

Simulation of electric stimulation of neurons

- Pyramidal layer-5 neuron model from Hallermann, Nat Neurosci (2012)

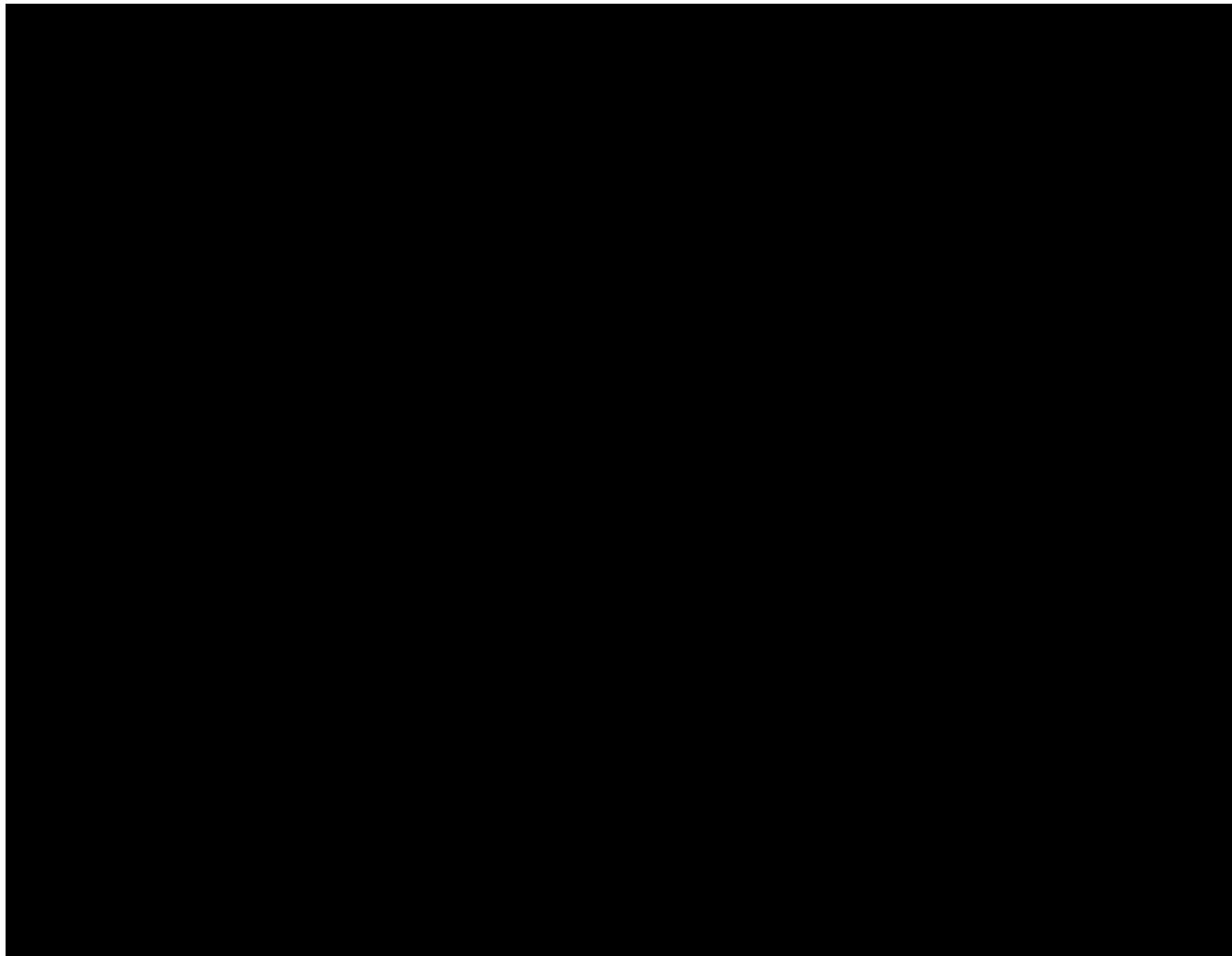
BISC: Bioelectronic Interfacing to Sensory Cortex



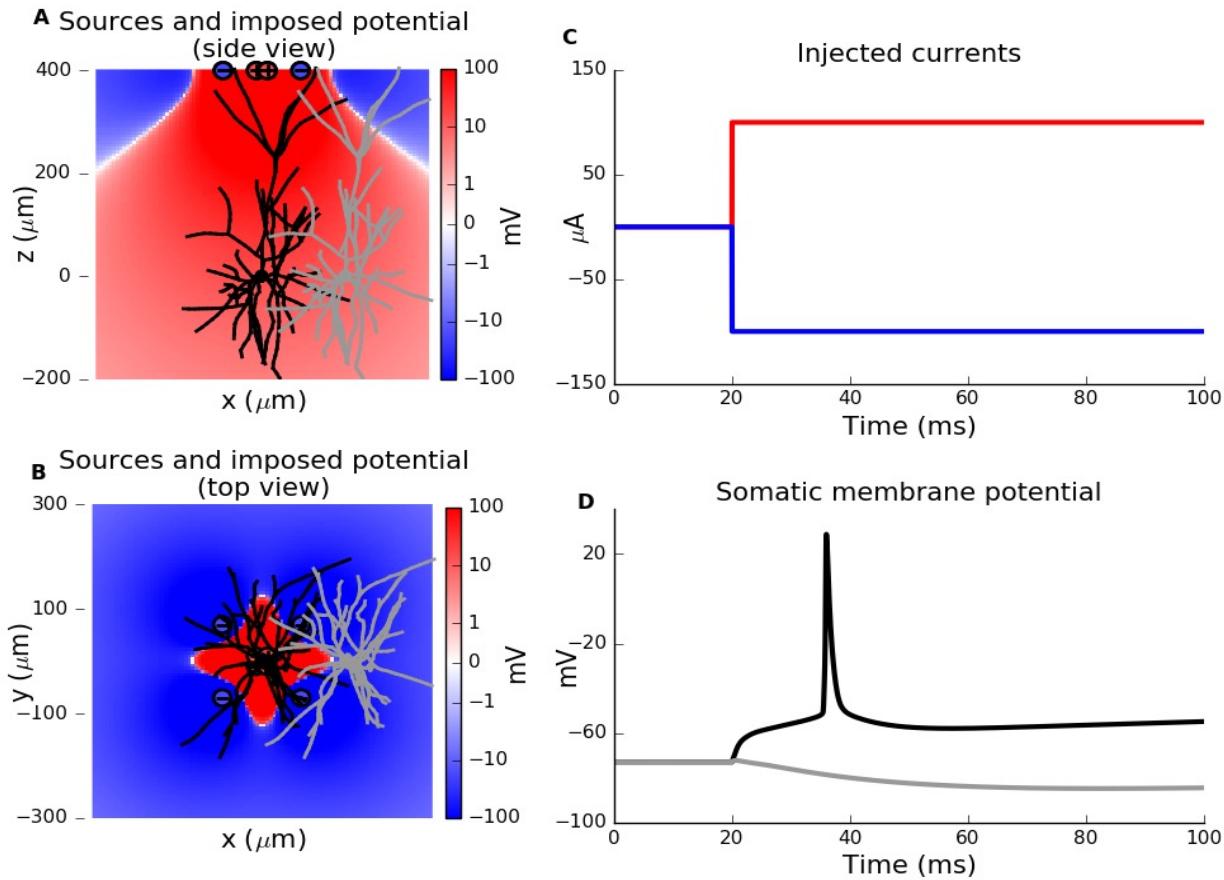
Ken Shepard,
Columbia Univ.



Animation by Torbjørn V. Ness

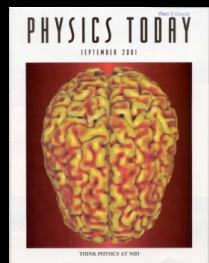


Selective electric activation of neurons



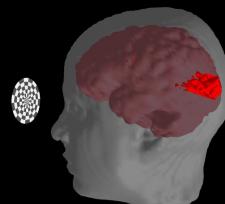
Brain imaging

- Structure:

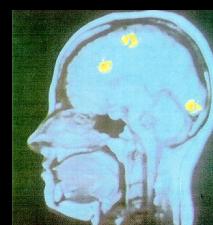


MRI → "tissue"

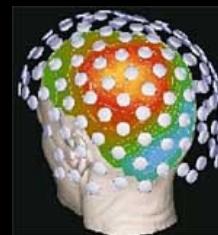
- Activity:



fMRI → "blood"



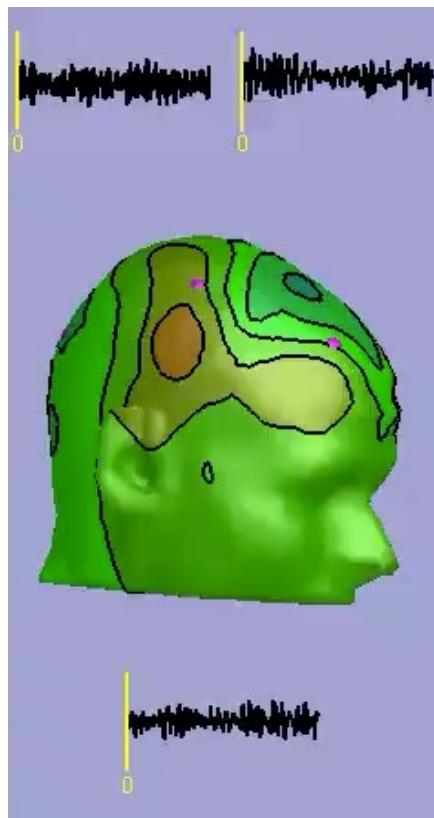
PET → "food"



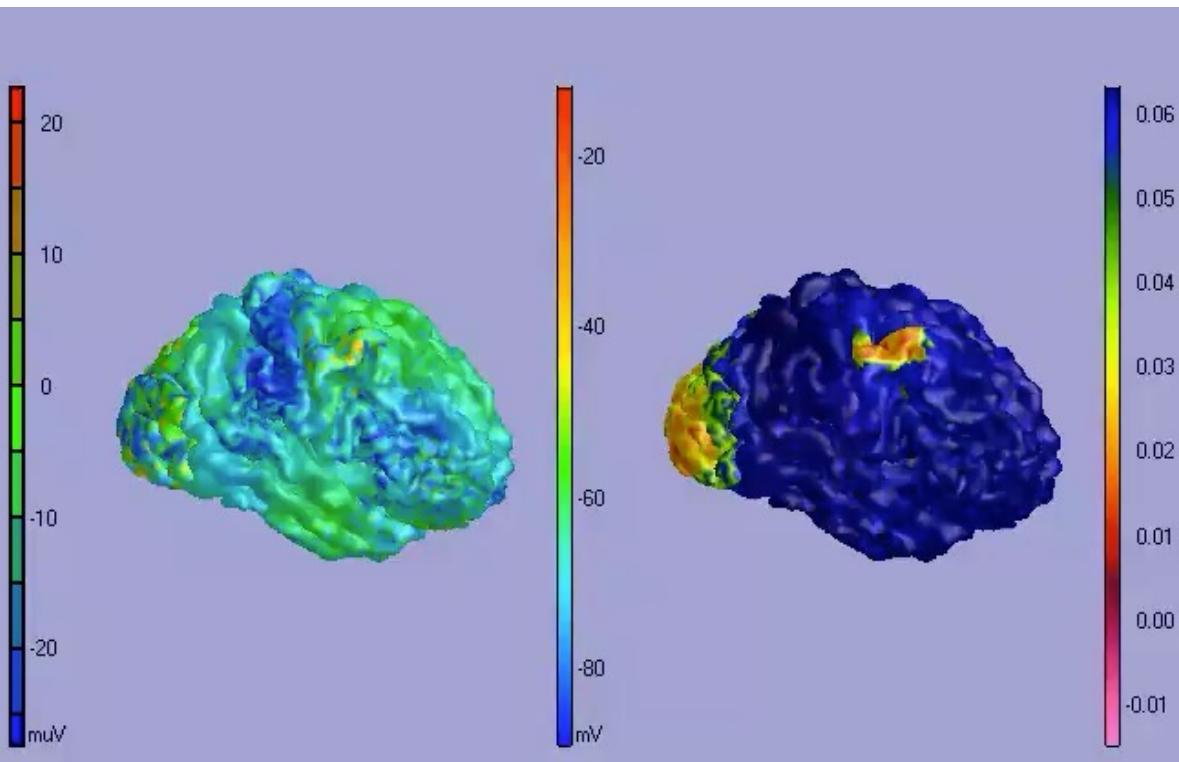
MEG/
EEG → "electricity"

Ultimate goal: Model prediction of EEG/MEG/PET/fMRI signals

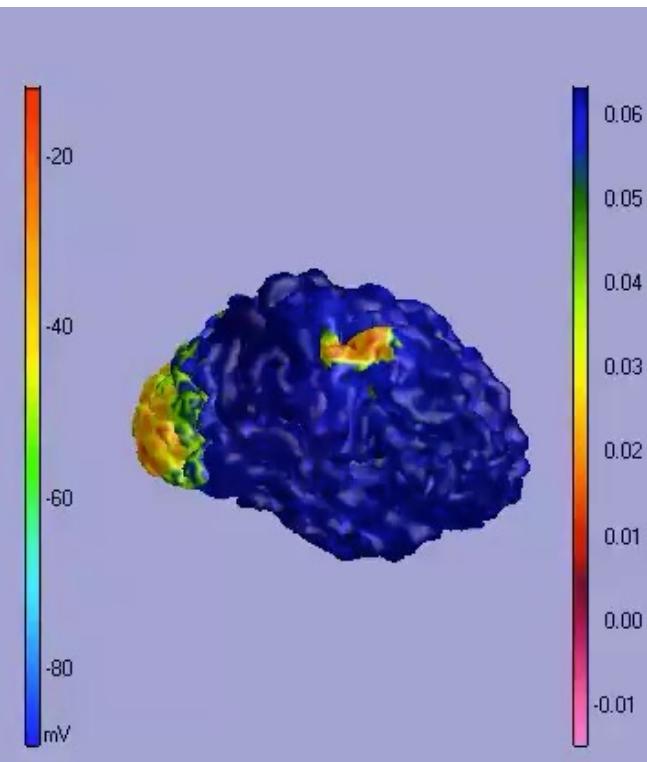
"VIRTUAL" EEG



"VIRTUAL" VSDI



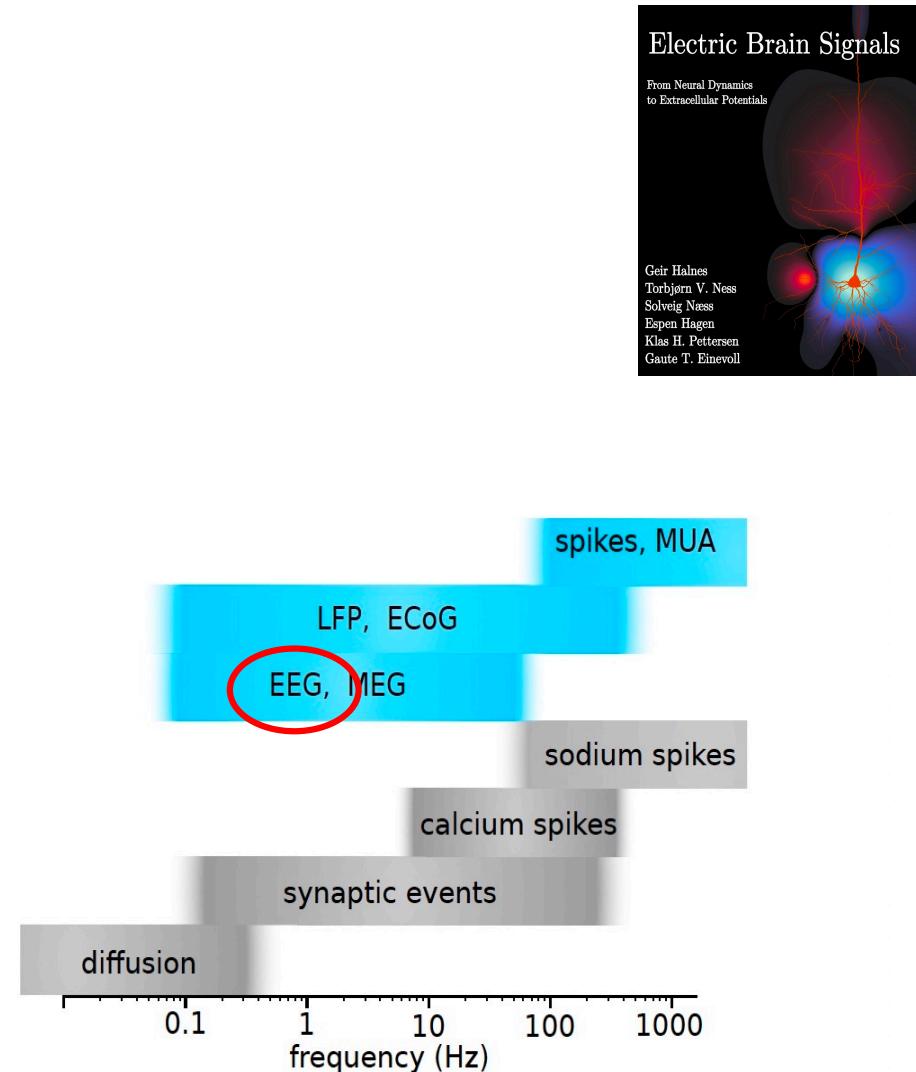
"VIRTUAL" fMRI



Animation by Ingo Bojak

EEG

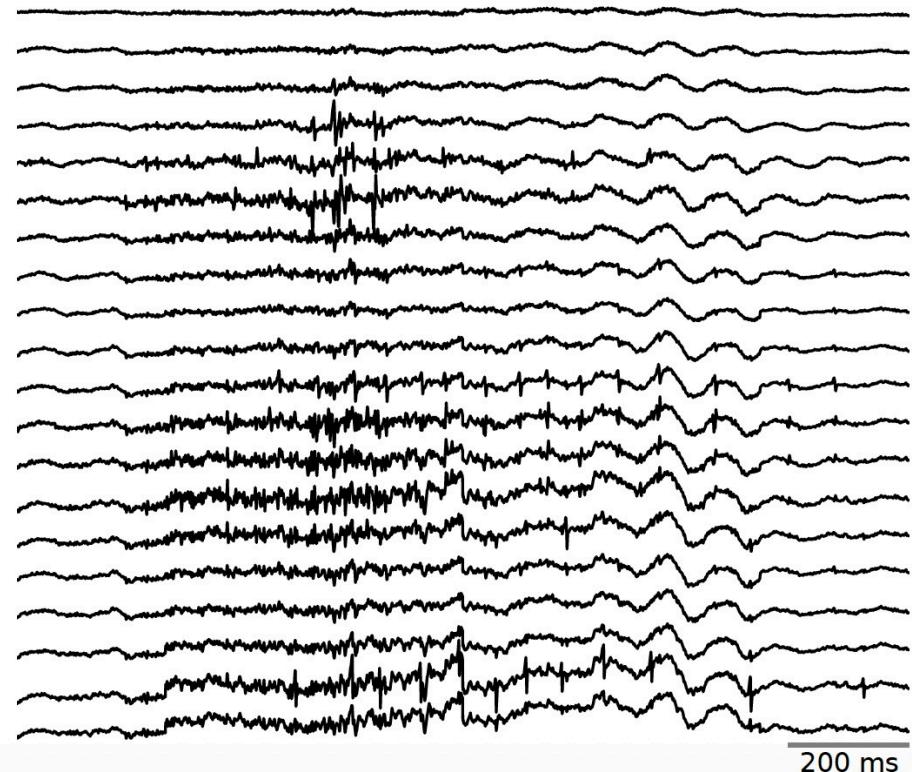
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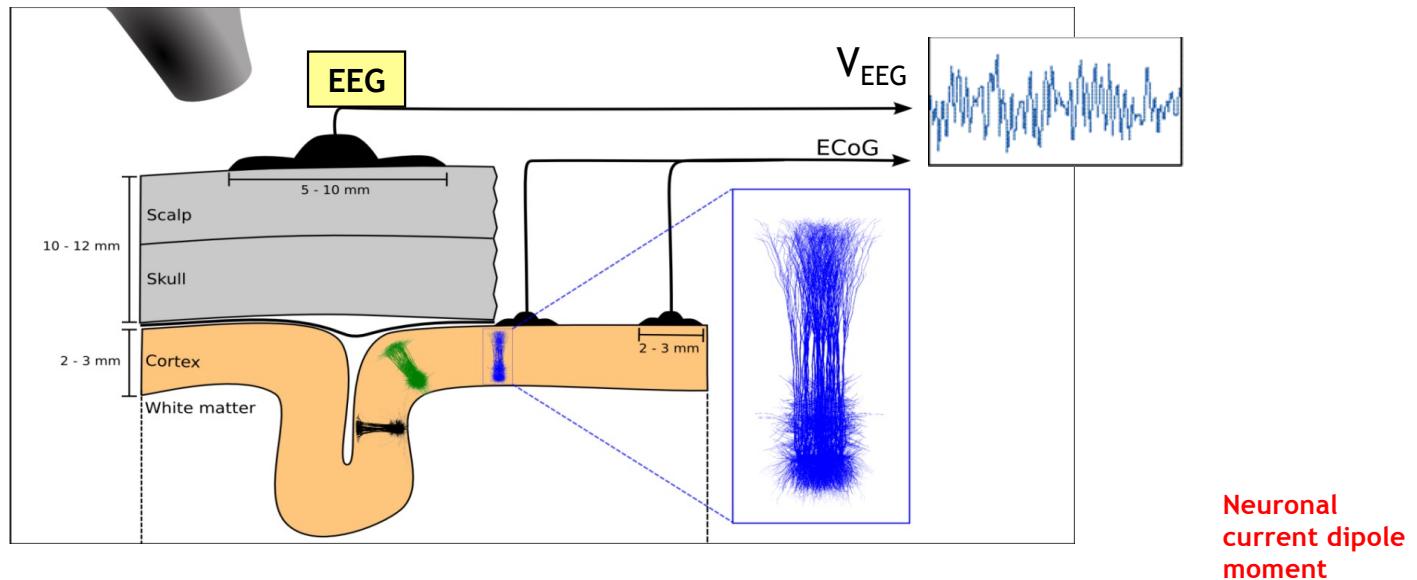
EEG



Torbjørn V. Ness



EEG signal sums contributions from millions of neurons

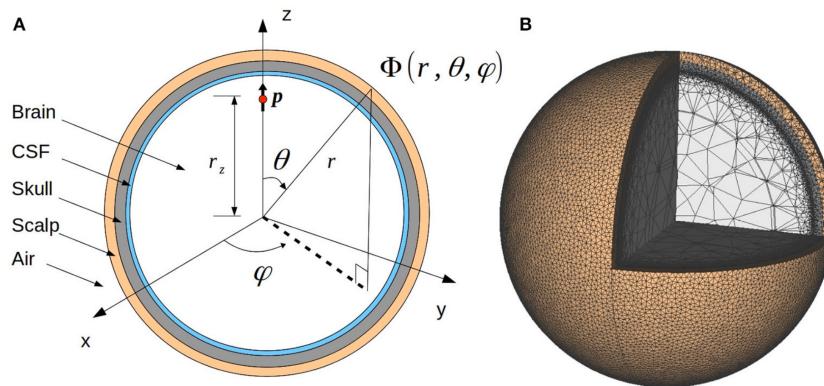


- Far-field dipole potential in an infinite volume conductor with conductivity σ :
- More complicated relationship ("forward model") for real heads, but EEG signal V_{EEG} can nevertheless be computed if we know all current dipole moments p_n

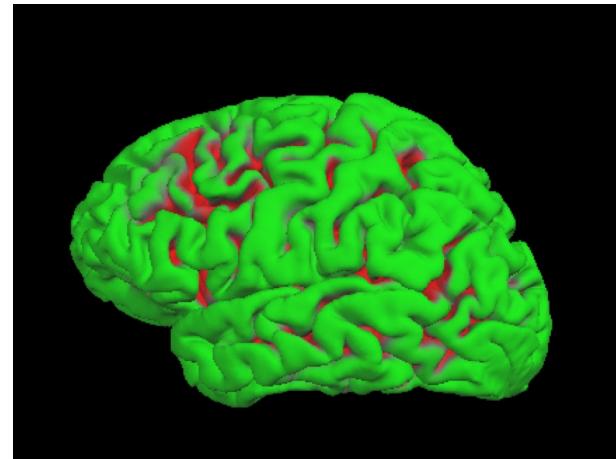
$$V_{\text{EEG}}(\mathbf{r}, t) = \frac{1}{4\pi\sigma} \sum_n \frac{p_n(t) \cos \theta_n}{|\mathbf{r} - \mathbf{r}_n|^2}$$

Electrical head models

Idealized
(spherical)



Detailed
(measured
by MRI)



4-sphere head model for EEG potential from current dipole

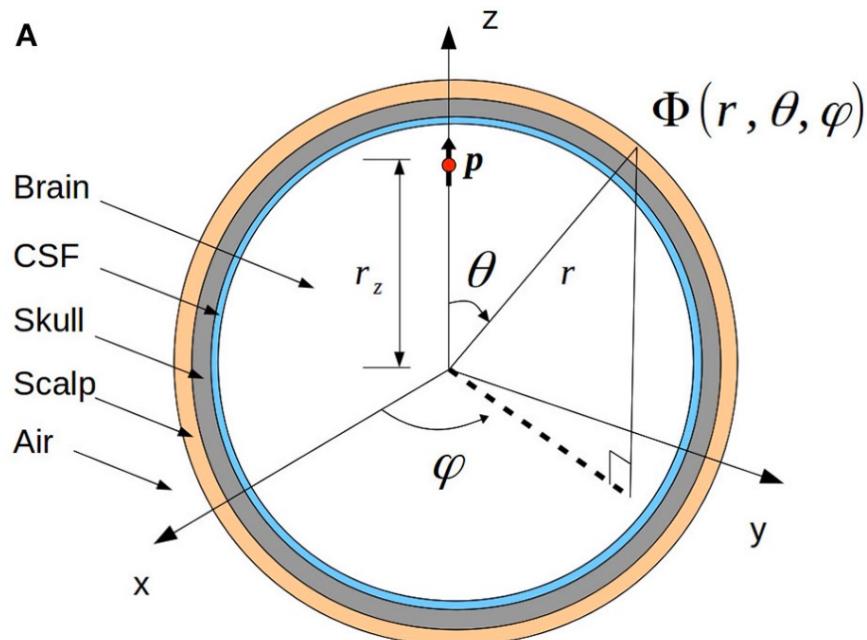
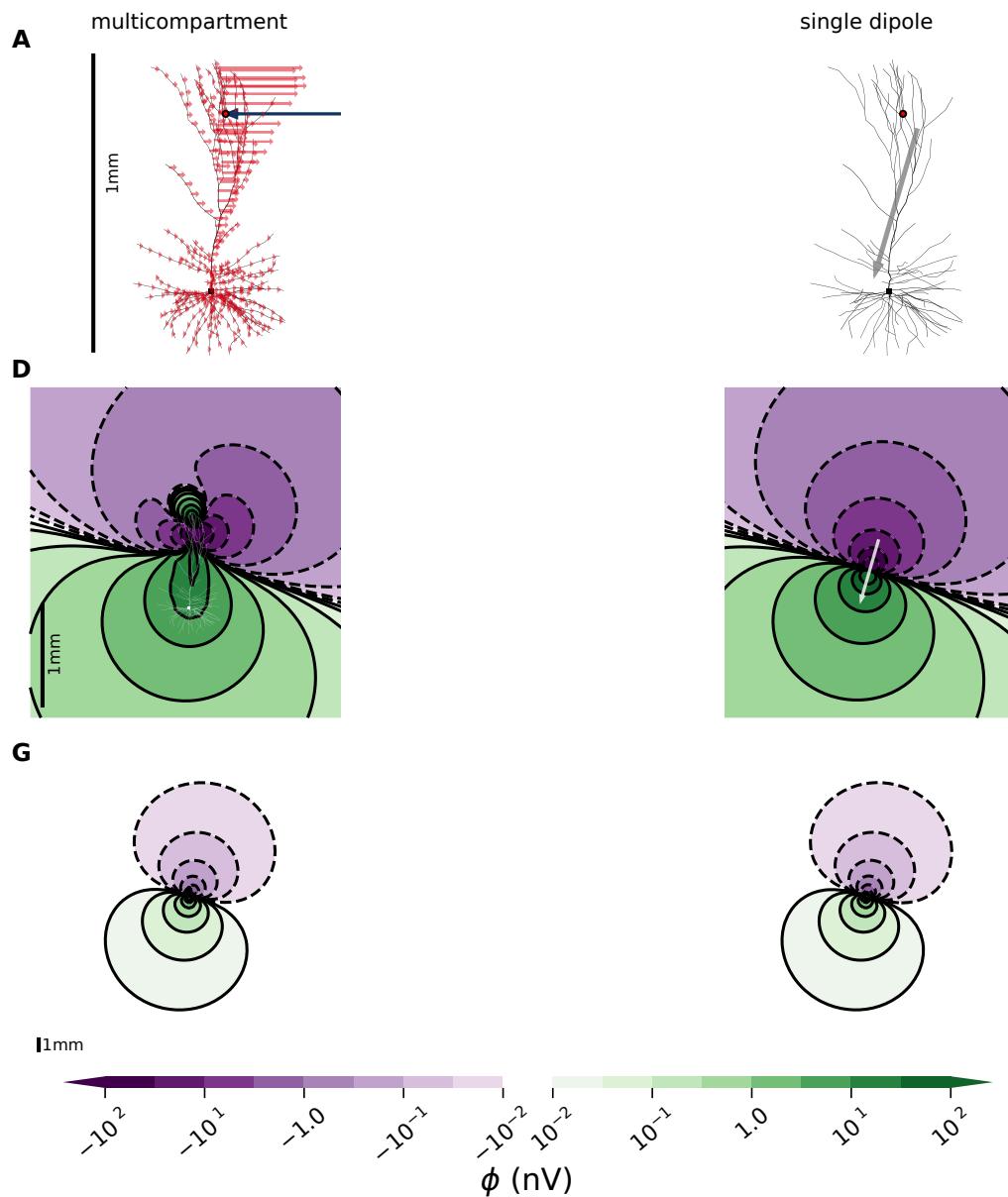


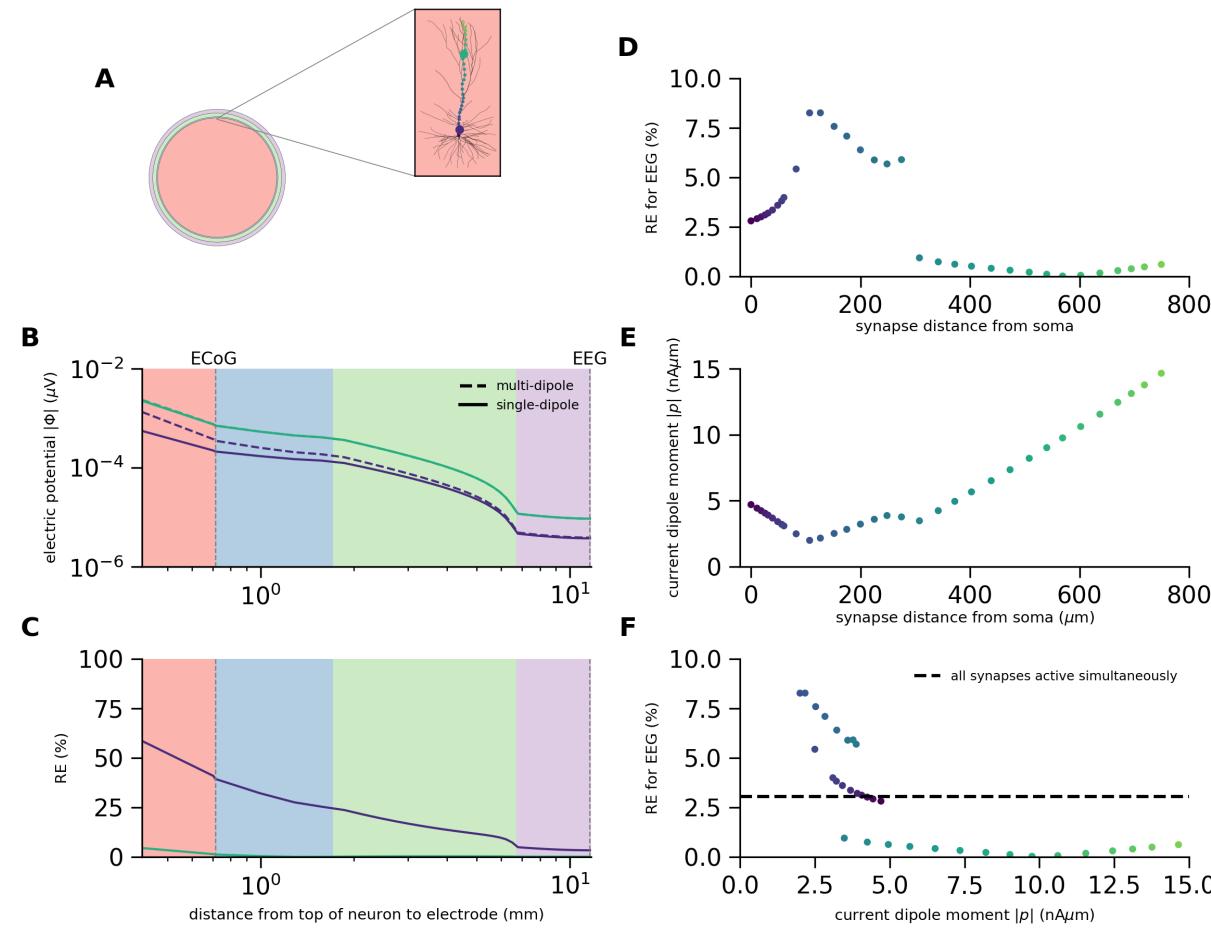
TABLE 1 | Radii and electrical conductivities of the present four-sphere model.

Labels	Name	Radius (cm)	σ (S/m)
1	Brain	7.9	$\sigma_{\text{brain}} = 0.33$
2	CSF	8.0	$5 \sigma_{\text{brain}}$
3	Skull	8.5	σ_{brain}/K
4	Scalp	9.0	σ_{brain}

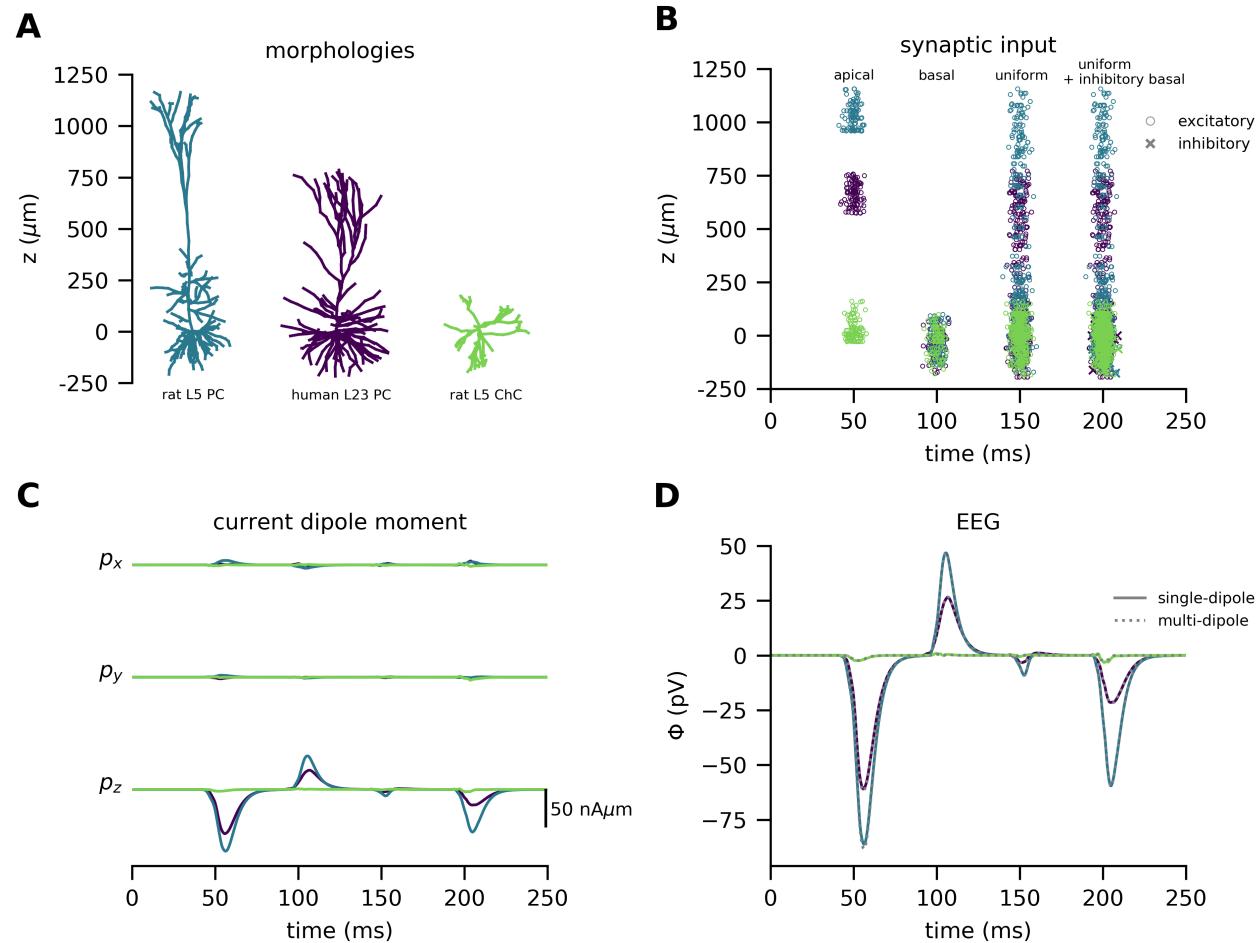
Test of dipole approximation



4-sphere head model for EEG potential from current dipole

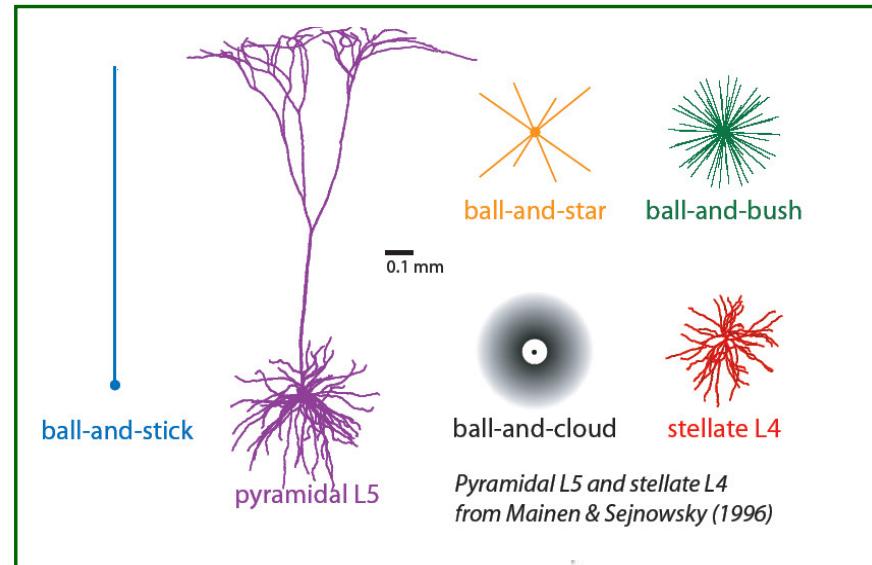


4-sphere head model: EEG potential from neurons

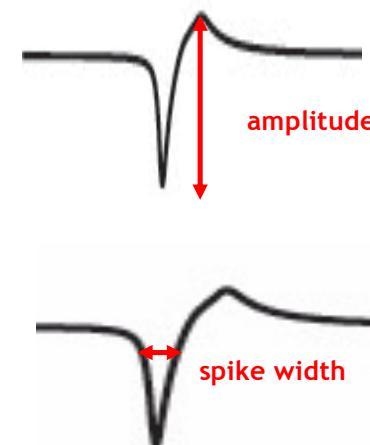


END - part 3

How do the extracellular spikes depend on neuronal morphology?



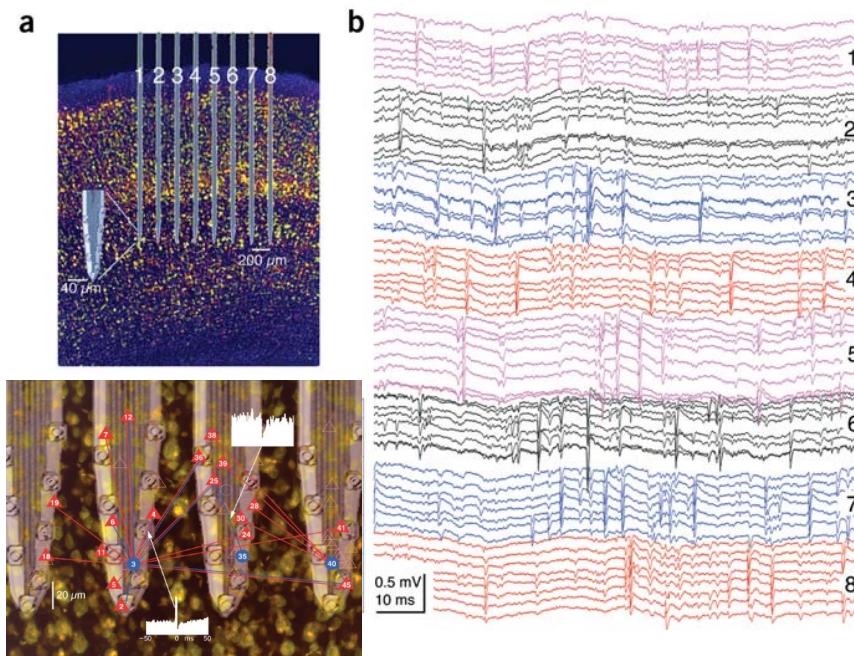
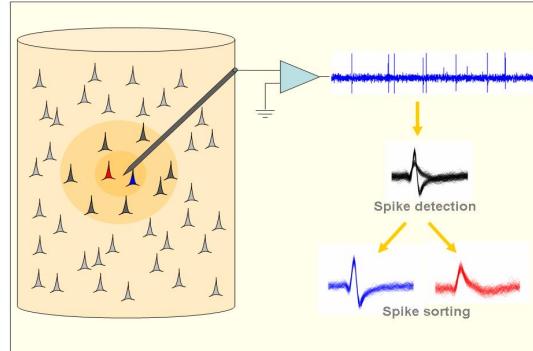
- Amplitude is (i) roughly proportional to *sum of cross-sectional areas* of dendrites connected to soma, (ii) independent of *membrane resistance* R_m , ...
- Spike width increases with distance from soma, i.e., high-frequency dampening also with simple ohmic extracellular medium



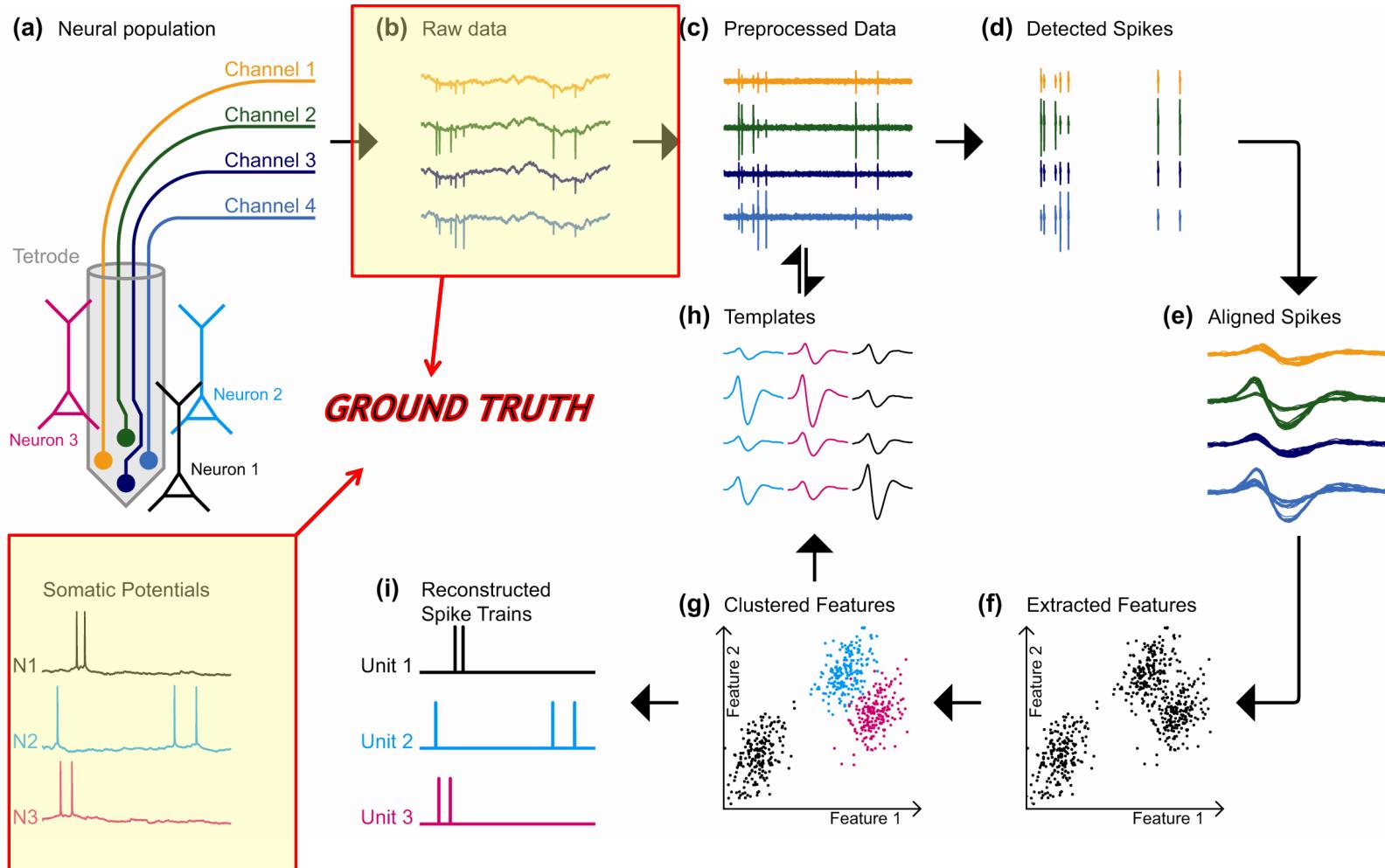
Spike sorting problem

- Electrodes pick up signals from many spiking neurons; must be sorted
- At present spike sorting is:
 - labor intensive
 - unreliable
- Need automated spike-sorting methods which are
 - accurate
 - reproducible
 - reliable
 - validated
 - fast

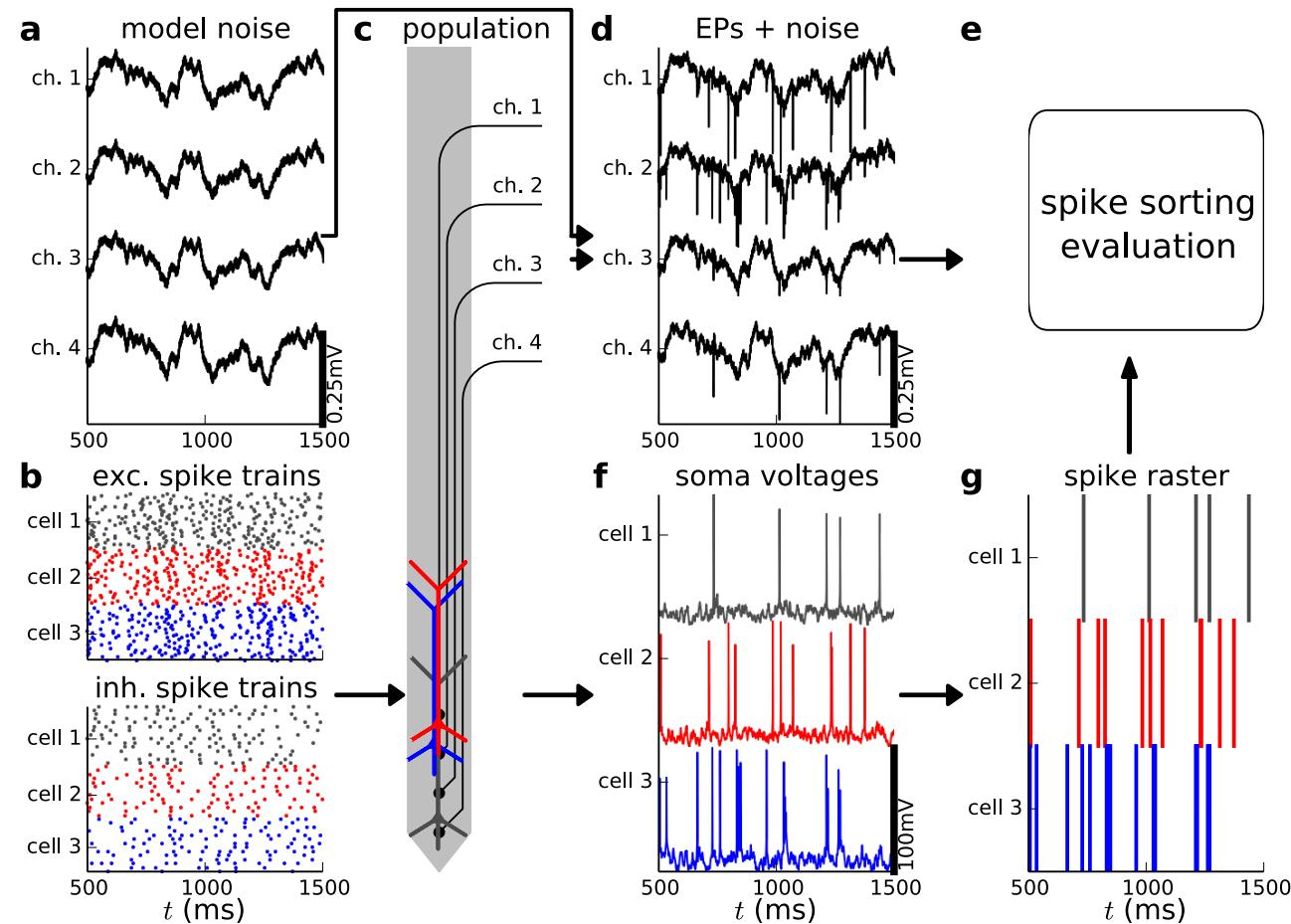
to take advantage of new generation of multielectrodes



Steps in spike sorting



Benchmarking of spike-sorting methods





Computational Neuroscience

ViSAPy: A Python tool for biophysics-based generation of virtual spiking activity for evaluation of spike-sorting algorithms



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HIGHLIGHTS

- Efficient, accurate and validated automatic spike-sorting methods needed.
- Introduces ViSAPy, a Python tool for generating model-based benchmarking data sets.
- ViSAPy allows arbitrary electrode geometries, neuron models and realistic noise.
- Tetrode, polytrode (in vivo cortex) and MEA (in vitro retina) benchmark sets provided.



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END - tutorial 3