Neural fields: from single neurons to populations

Axel Hutt

Team NEUROSYS

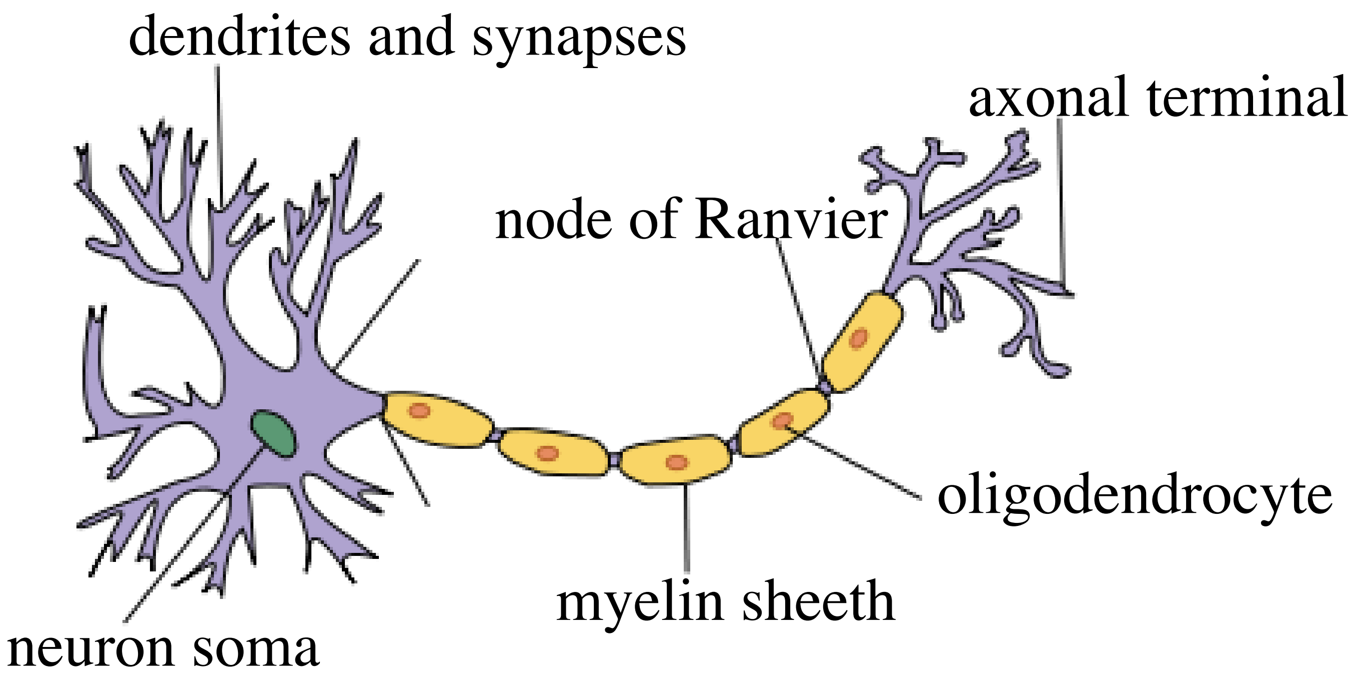
INRIA Nancy
France

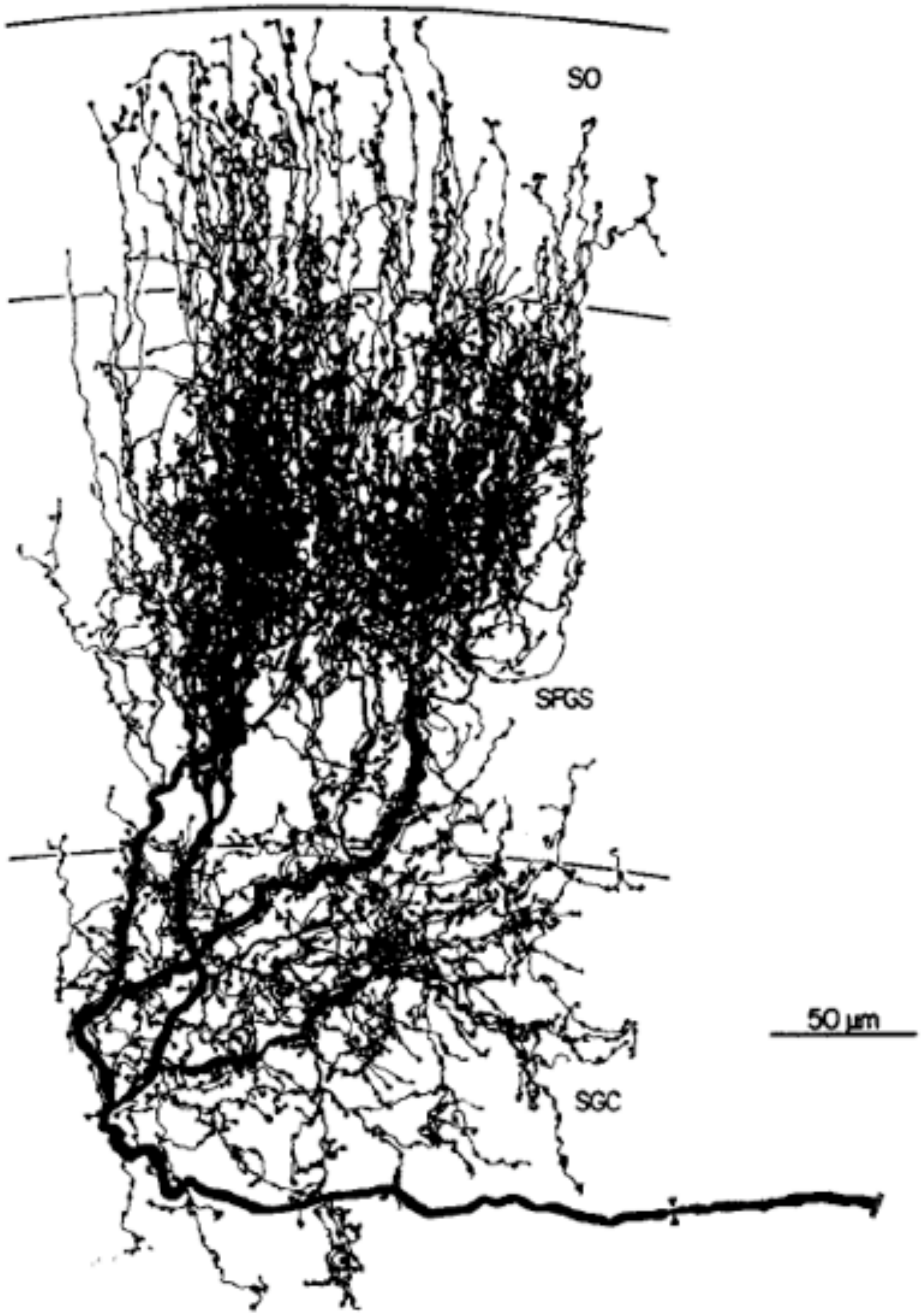
Structure

- traversing scales
- neural mass models
- neural field models
- perspectives

- traversing scales
- neural mass models
- neural field models
- perspectives

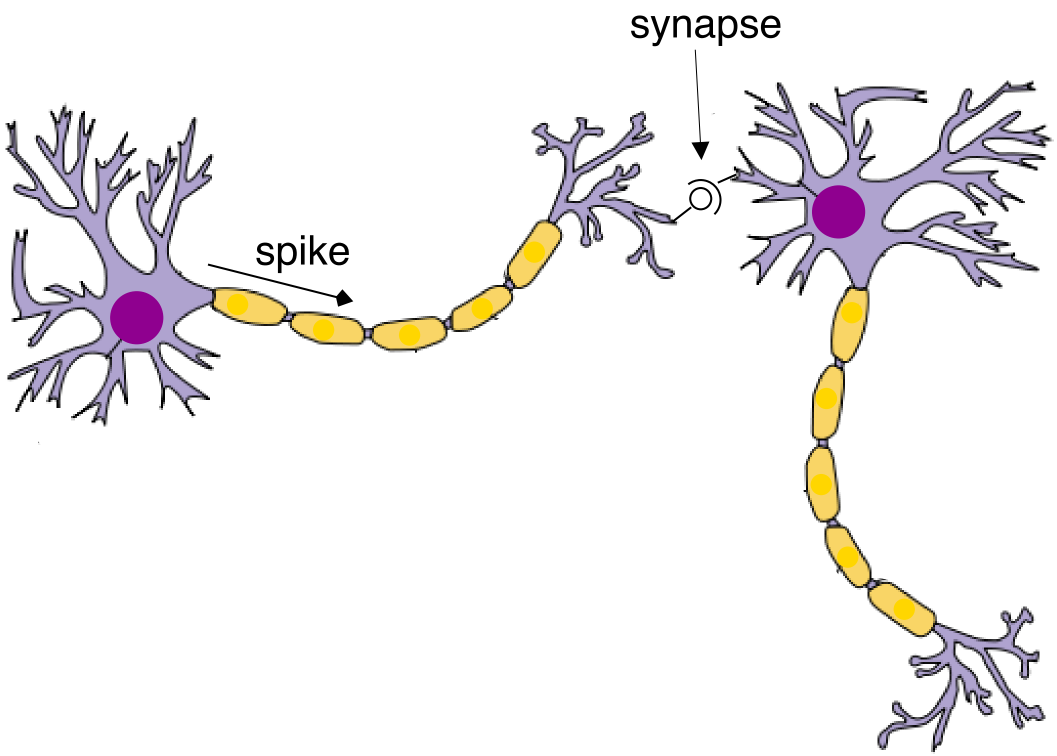
From single neurons to populations



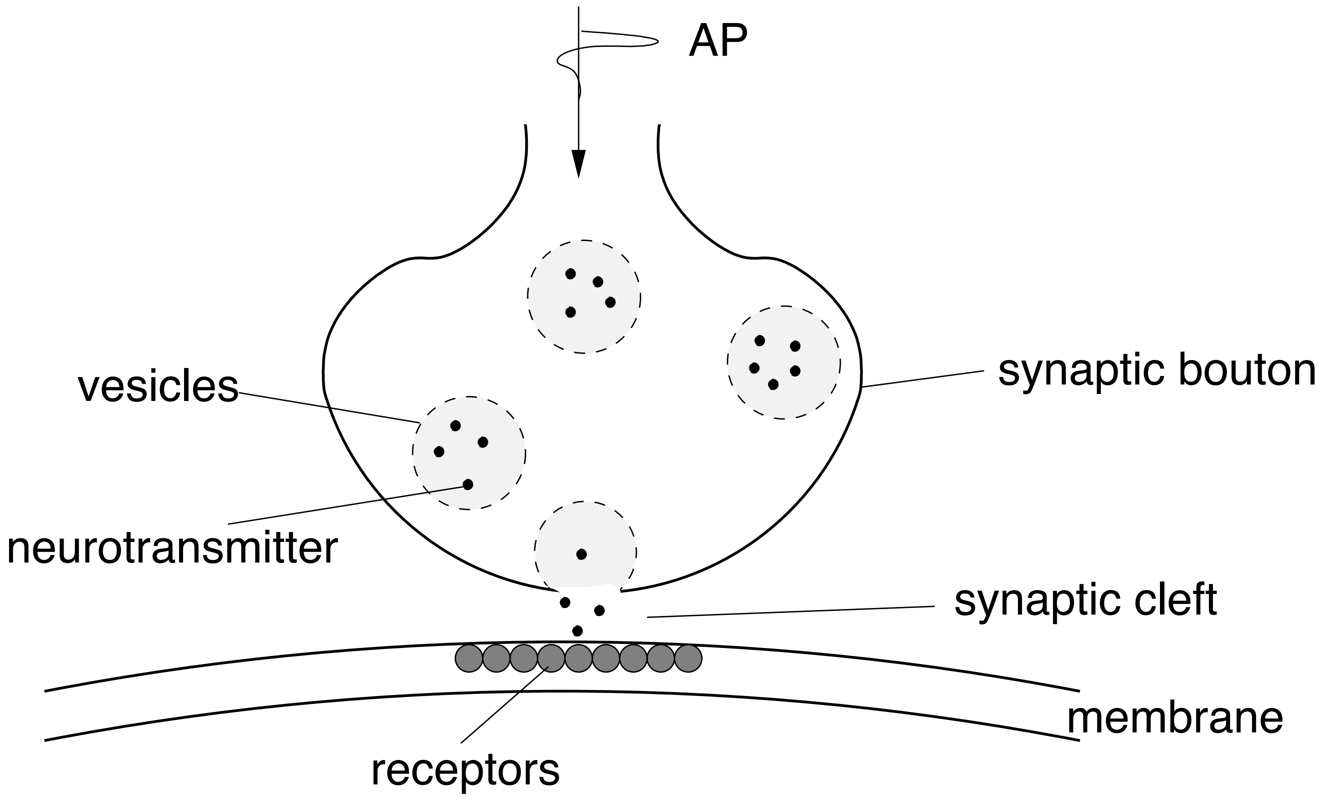


(adapted from Segev and Schneidmann (1999))

synaptic activity

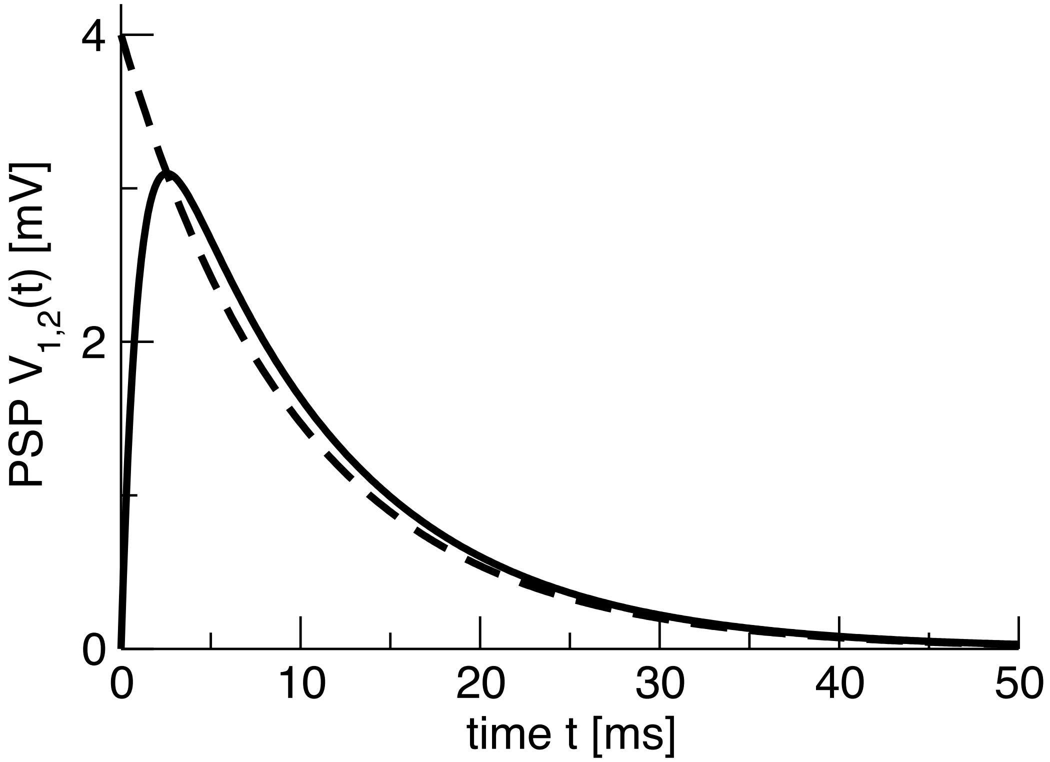


- about **6000-10000 chemical synapses** at each dendritic tree of a single neuron
- **excitatory and inhibitory synapses** depolarize and hyperpolarize the membrane potential on the dendrite



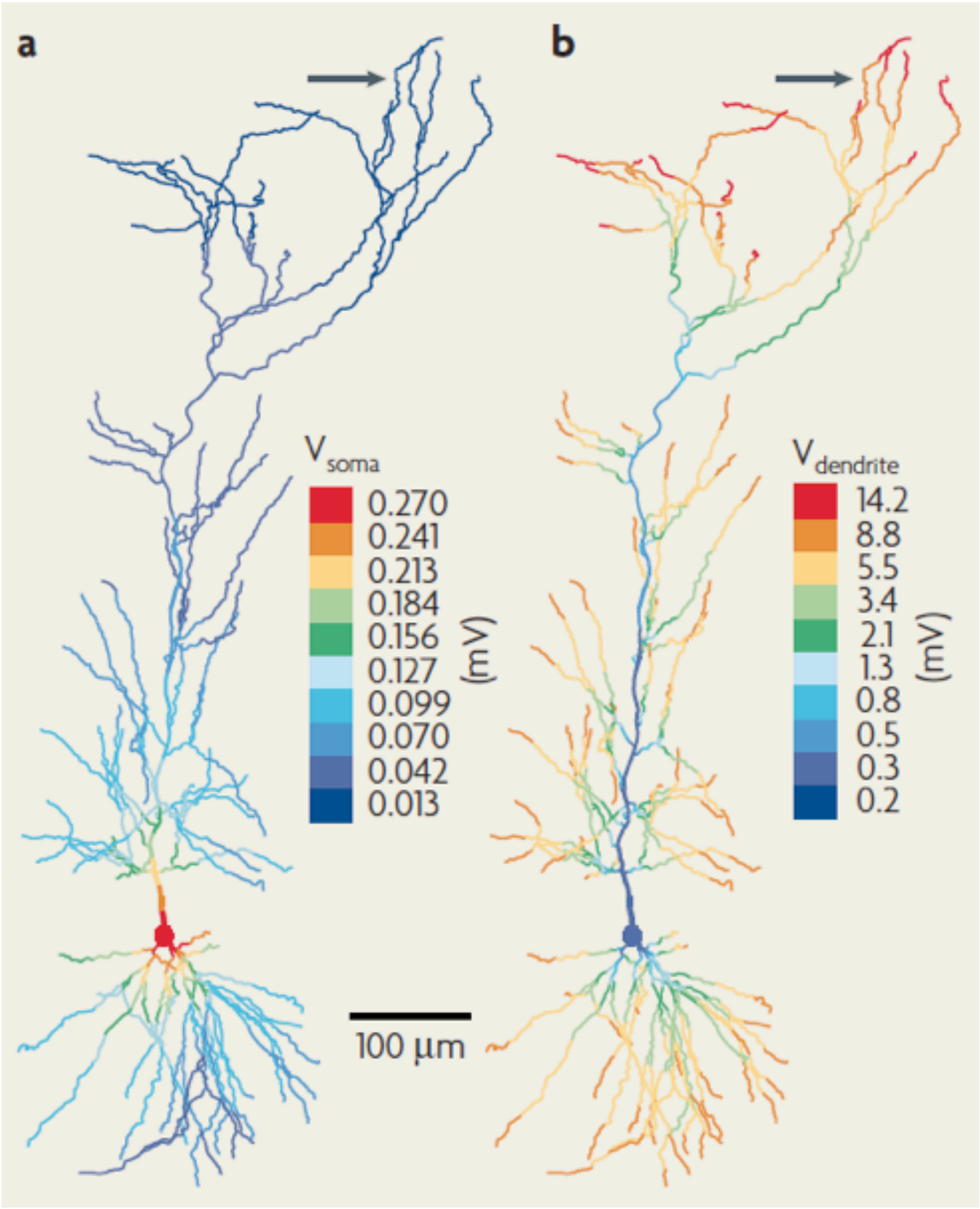
neurotransmitter	**receptor**	
glutamate	NMDA	*excitatory*
glutamate	non-NMDA	*excitatory*
GABA	GABA$_A$	*inhibitory*
GABA	GABA$_B$	*inhibitory*

synaptic response on the dendrite



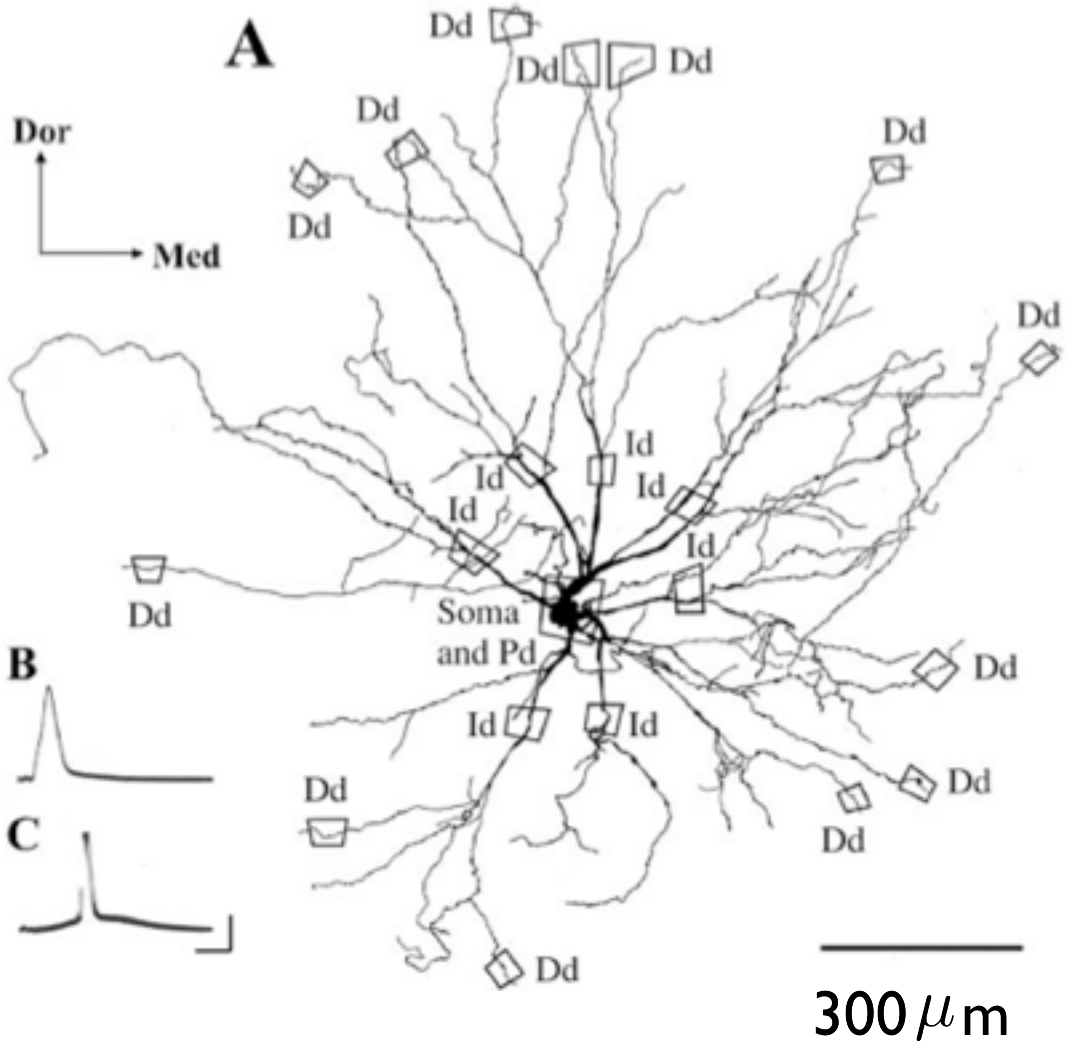
$$V_1(t) = \frac{\bar{u}}{\tau_s} e^{-t/\tau_s} H(t)$$

$$V_2(t) = \frac{\bar{u}}{\tau_2 - \tau_2} \left(e^{-t/\tau_1} - e^{t/\tau_2} \right) H(t)$$

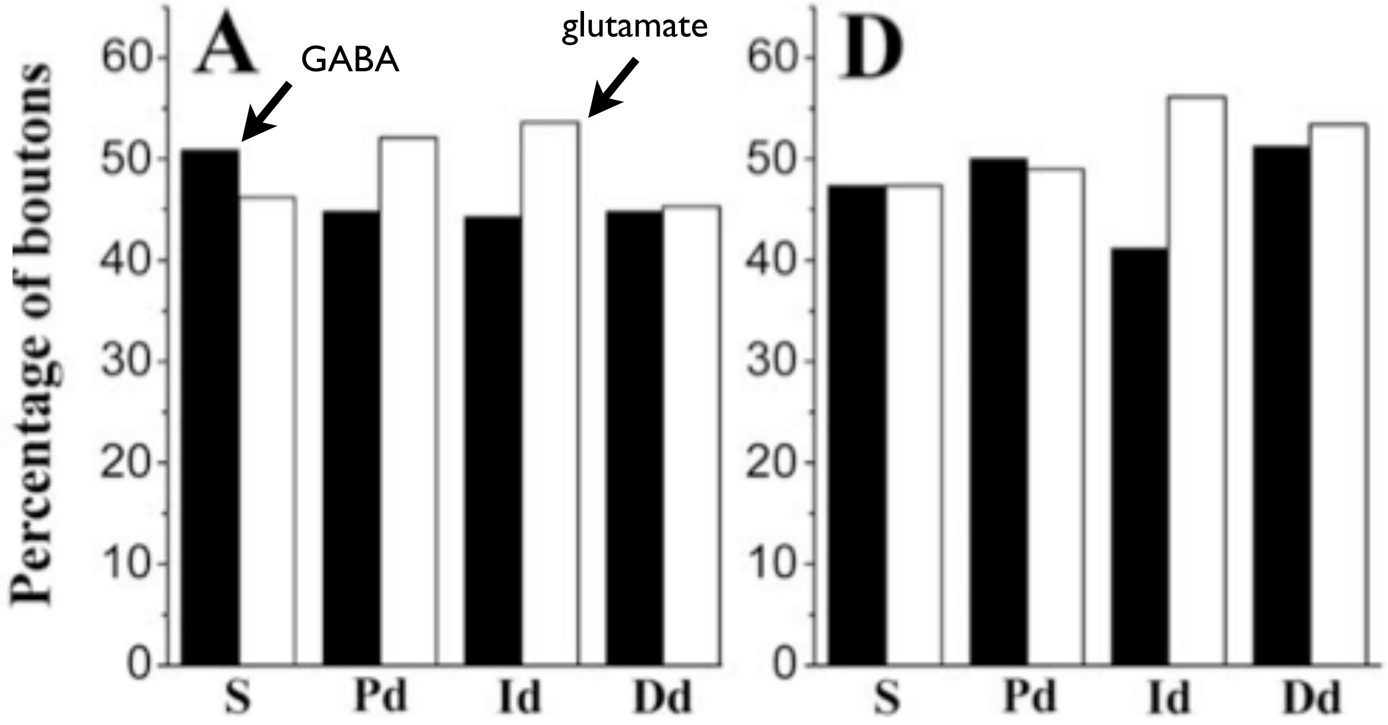


(taken from Spruston, Nature Rev. Neurosc. (2008))

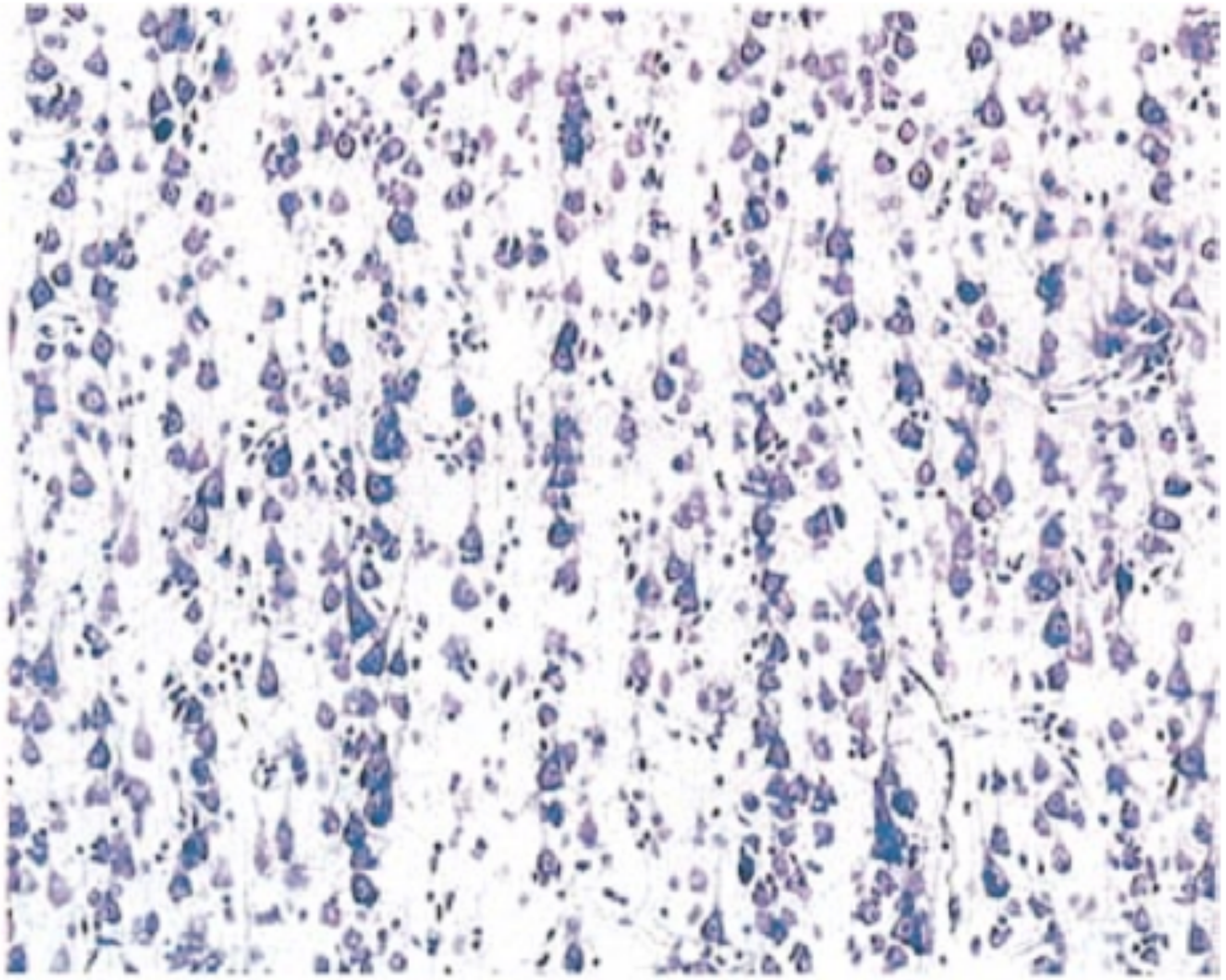
distribution of synapses

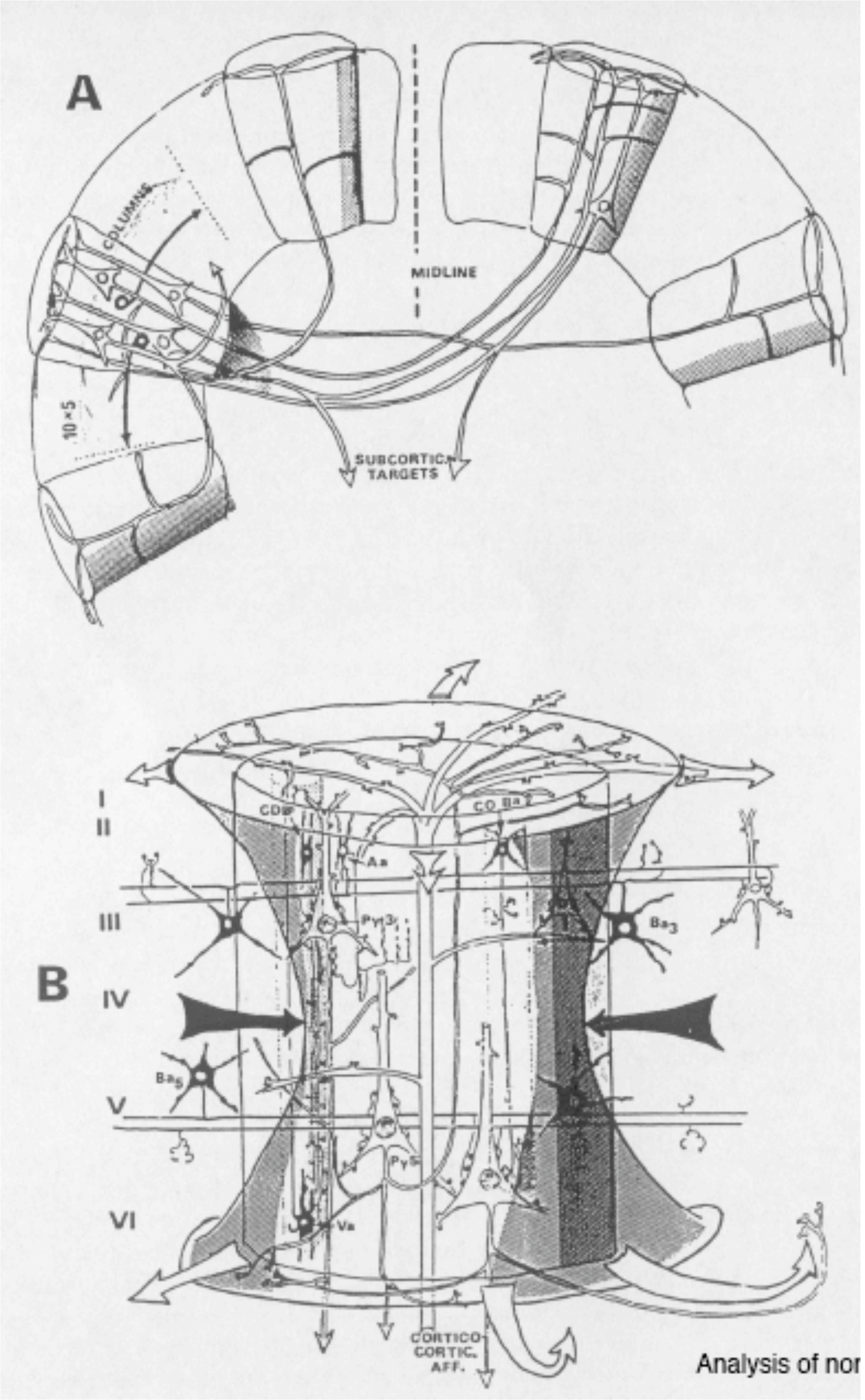


motor neurons in cat



(taken from Shigenaga et al, Neuroscience (2005))



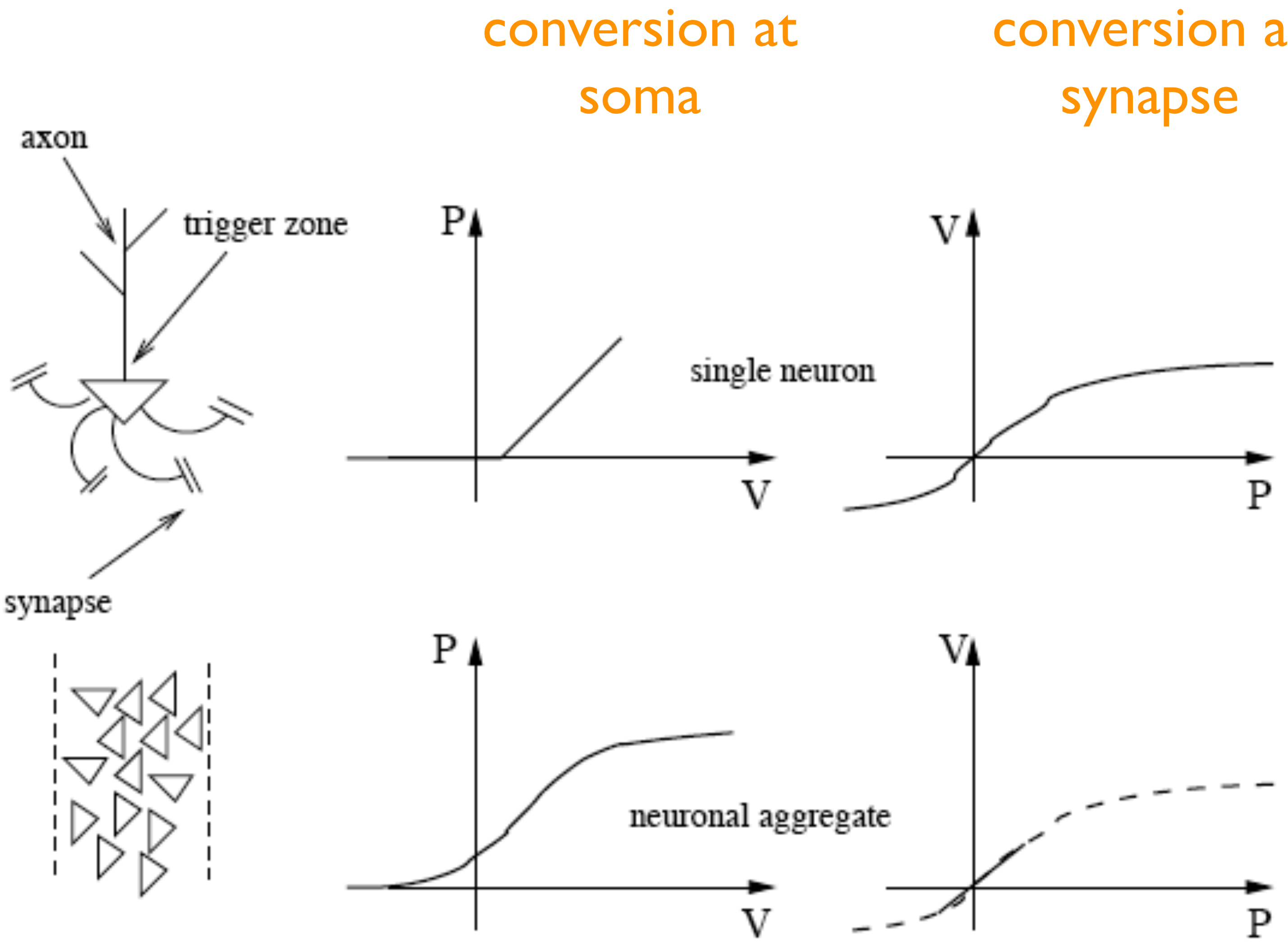


the cortex exhibits

columnar structures called

macrocolumns

neural populations



- spatial patches of 500μm to 1mm width $\rightarrow$ coarse graining in space
- patch contains from 1000 to 10^5 neurons
- observation: collective behavior (e.g. Wilson and Cowan 1972)
- mean impulse response response $\rightarrow$ coarse graining in time

- traversing scales

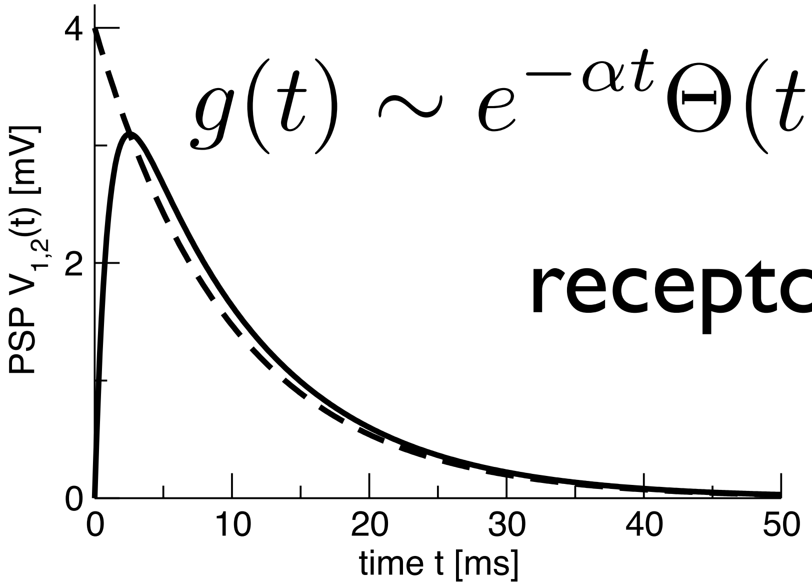
- neural mass models
  - basic assumptions
  - Local Field Potentials and EEG

- neural field models

- perspectives

single neuron

$$C\dot{V}(t) = -g_l(V(t) - E_l) - g(t)(V(t) - E)$$



$$g(t) \sim e^{-\alpha t}\Theta(t),\ (e^{-\alpha t} - e^{-\beta t})\Theta(t)$$

receptor response to incoming spike

If V decays fast to resting state and g(t) evolves slowly:

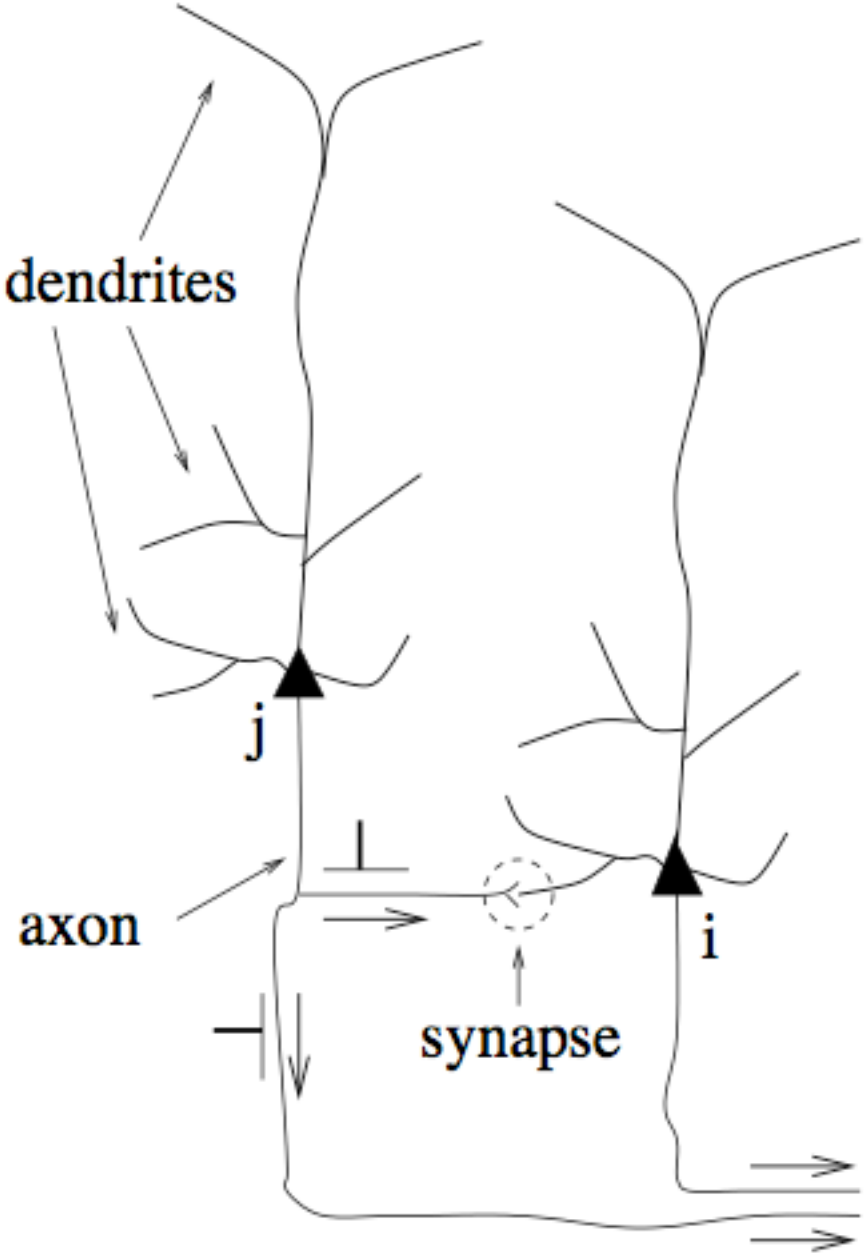
$$V(t) \approx V_{rest} = const$$

then $$I(t) \approx g(t)(V_{rest} - E) \ \rightarrow V_{extra} = RI(t) \sim g(t)$$

$$\uparrow$$

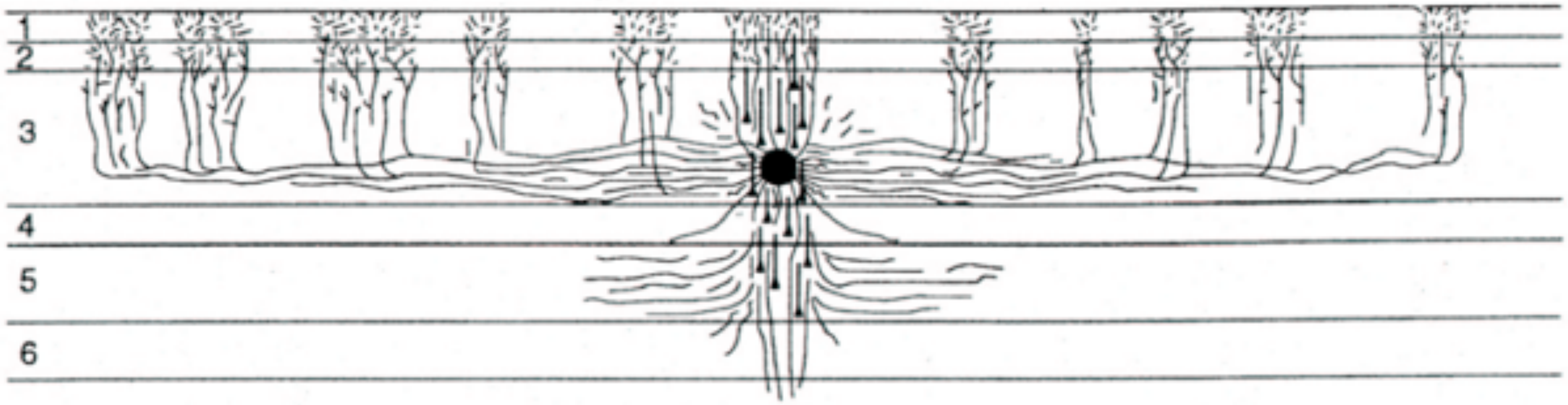
extra-cellular potential

consider a population
of neurons
with
population spike train s(t)

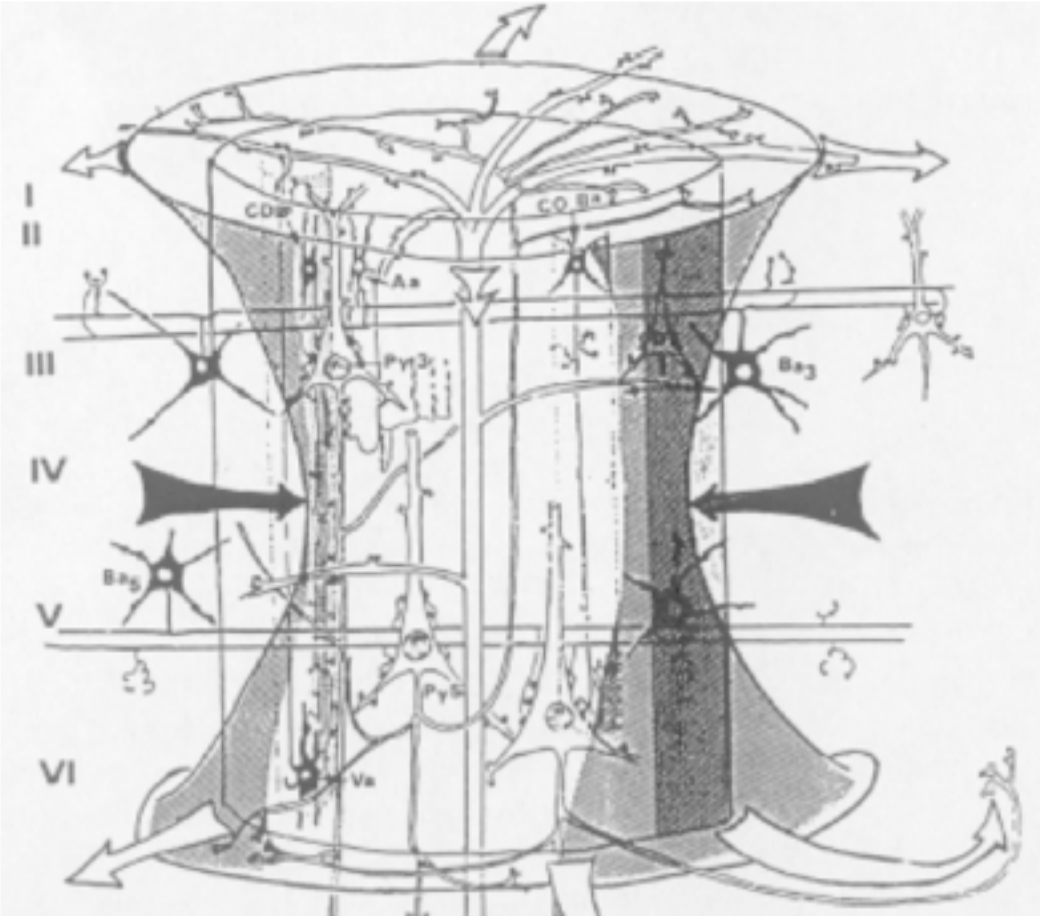


sum of post-synaptic currents in the population
generates extra-cellular electric field

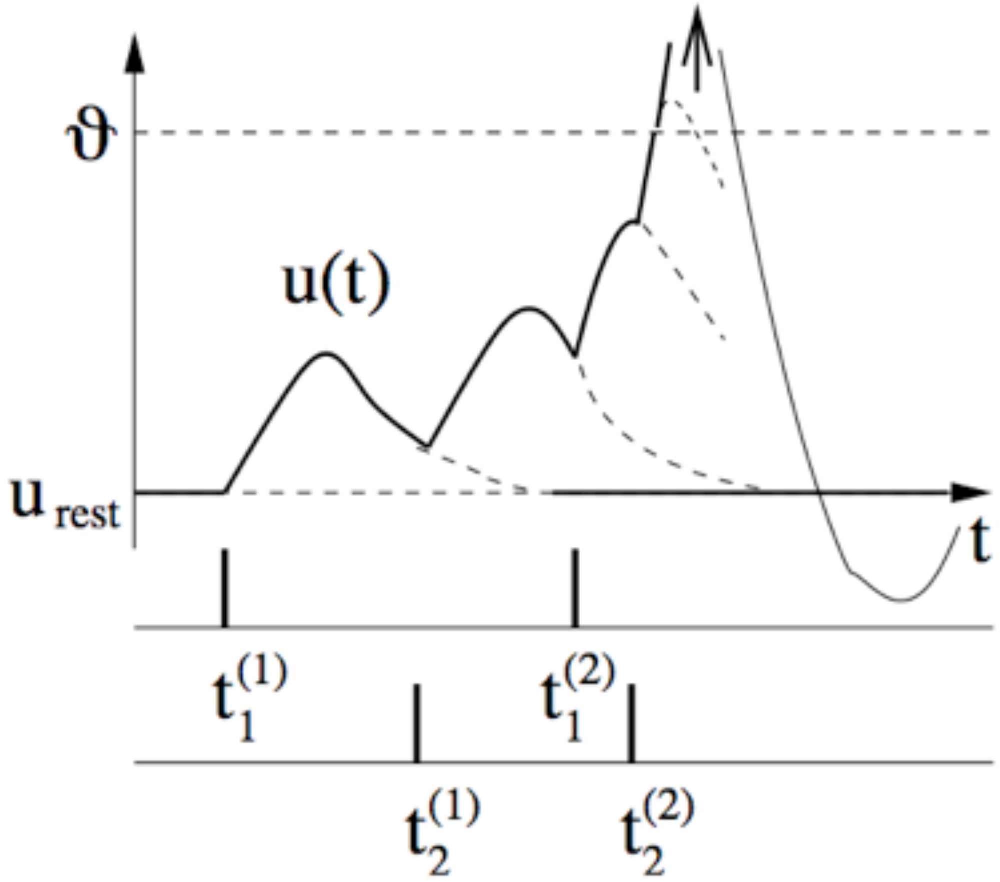
mesoscopic scale



network of neurons



neural mini-column



$$V_{extra}(t) = \sum_i \int_{-\infty}^{t} \underset{\substack{\big\uparrow \\ \text{synaptic response}}}{h(t-\tau)}\, s_i \underset{\substack{\big\uparrow \\ \text{spike train s(t)}}}{\delta(\tau-\tau_i)}\, d\tau$$

$$= \int_0^{\infty} h(t')s(t-t')dt'$$

$$\bar{V}_{extra}(t) = \frac{1}{\Delta t}\int_t^{t+\Delta t} V_{extra}(T)dT = \frac{1}{\Delta t}\int_0^{\infty} h(t')\int_t^{t+\Delta t} s(T-t')dTdt'$$

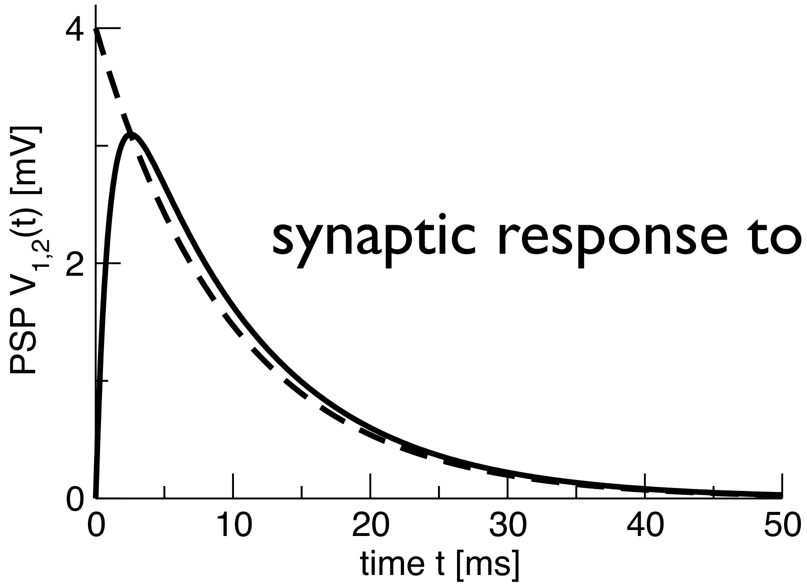
Δt : short time interval (~1ms)

$s(t)$: spike train of all neurons in a neuron population

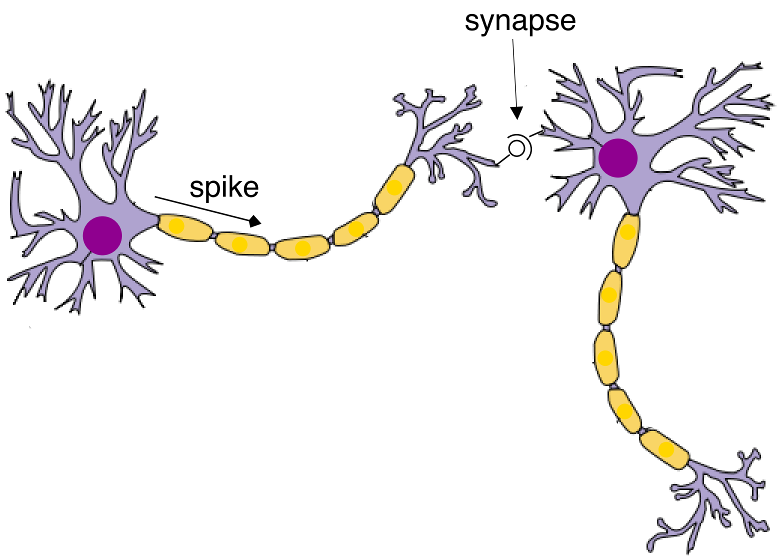
$$\bar{V}_{extra}(t) = \int_0^{\infty} h(t')P(t-t')dt'$$

$$P(t) = \int_t^{t+\Delta} \sum_i \frac{s_i}{\Delta t}\delta(t'-t_i)dt' = \frac{n(t)}{\Delta t}$$

$P(t)$: number of spikes in time interval Δt (**population firing rate**)



synaptic response to a single pulse $h_{e,i}(t)$



pulse train of all pulses in population at time t $\bar{P}_{e,i}(x,t)$:

$$\bar{V}^{\mathrm{e,i}}(x,t)=\int_{-\infty}^{t}\mathrm{d}\tau\, h_{\mathrm{e,i}}(t-\tau)\bar{P}_{\mathrm{e,i}}(x,\tau)$$

e,i: excitatory and inhibitory synapses

probability density finding membrane potential $V=V_e-V_i$ at the soma:

$$p_{\mathrm{S}}(V-\bar{V})=\frac{1}{2\pi}\int \mathrm{d}z\,\phi_{\mathrm{S}}^{\mathrm{e}}(z)\phi_{\mathrm{S}}^{\mathrm{i}}(-z)\,\mathrm{e}^{-\mathrm{i}zV}$$

$D_k(V_{th} - \bar{V}_{th}, t)$: number of neurons with firing threshold *V_{th}* that fire at time *t*

$N_k(t)$: number of neurons that fire at time *t*

$$
\begin{aligned}
N_k(t) &= \int_{V_\mathrm{min}}^{V_\mathrm{max}} \mathrm{d}V \; p_\mathrm{S}(V - \bar{V}(t)) \int_{V_\mathrm{l}}^{V_\mathrm{h}} \mathrm{d}V_\mathrm{th} \; \Theta(V - V_\mathrm{th}) \, D_k(V_\mathrm{th} - \bar{V}_\mathrm{th}, t) \\
&= \int_{V_\mathrm{min} - \bar{V}}^{V_\mathrm{max} - \bar{V}} \mathrm{d}w \int_{V_\mathrm{l} - \bar{V}_\mathrm{th}}^{V_\mathrm{h} - \bar{V}_\mathrm{th}} \mathrm{d}u \; \Theta(w + \bar{V}(t) - \bar{V}_\mathrm{th}) \, p_\mathrm{S}(w) D_k(u, t).
\end{aligned}
$$

$\bar{N}_k(t)$: number of neurons in time interval Δt that fire at time *t* (population firing rate)

$$
\begin{aligned}
\bar{N}_k(t) &= \frac{1}{\Delta t} \int_t^{t + \Delta t} N_k(\tau) \, \mathrm{d}\tau \\
&\approx \int_{V_\mathrm{min} - \bar{V}}^{V_\mathrm{max} - \bar{V}} \mathrm{d}w \; p_\mathrm{S}(w) \int_{V_\mathrm{l} - \bar{V}_\mathrm{th}}^{V_\mathrm{h} - \bar{V}_\mathrm{th}} \mathrm{d}u \; \Theta(w + \bar{V}(t) - \bar{V}_\mathrm{th} - u) \bar{D}_k(u, t)
\end{aligned}
$$

$$
\boxed{\bar{N}_k(x, t) = \int_{-\infty}^{\infty} \mathrm{d}w \int_{-\infty}^{w + \bar{V}(x,t) - \bar{V}_\mathrm{th}} \mathrm{d}u \; p_\mathrm{S}(w) D_k(u, t)}
$$

for infinite borders

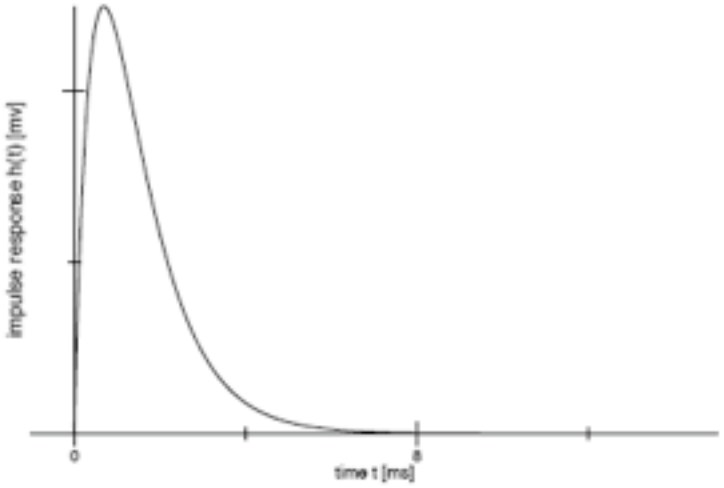
for Gaussian distributed PSPs and firing threshold distributions:

$$p_S \sim \mathcal{N}(0, \sigma_S^2) \qquad \bar{D}_k(u,t) = \frac{P_{\max}}{\sqrt{2\pi}\sigma_k} e^{-u^2/2\sigma_k^2}$$

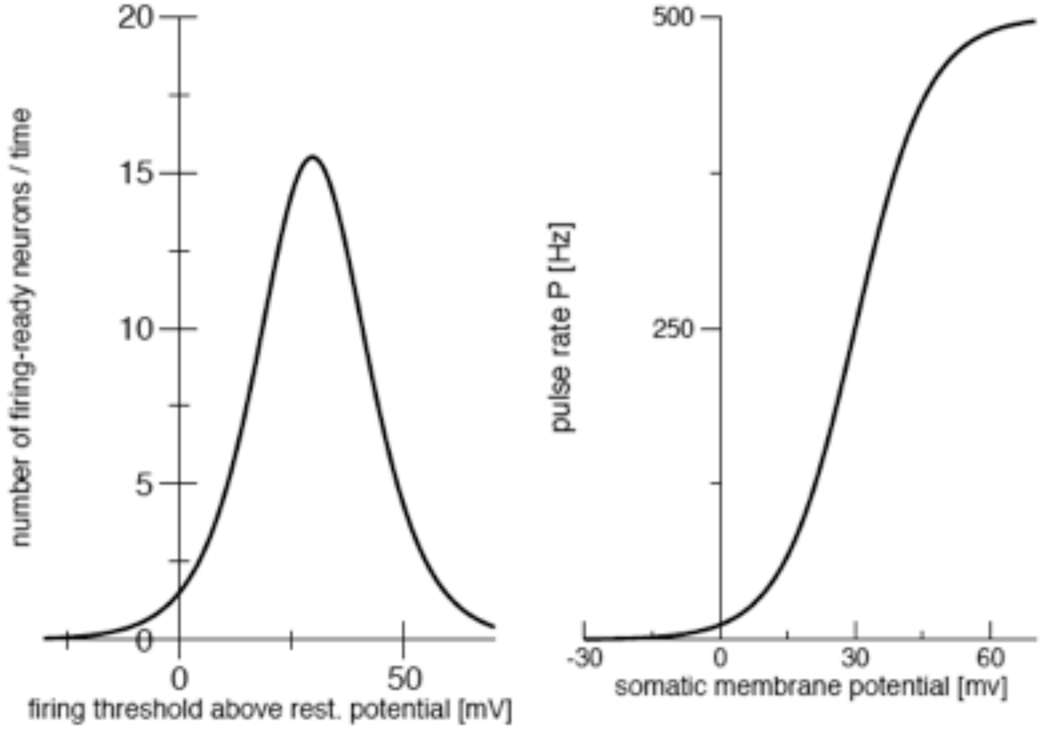
$$\bar{N}_k(x,t) = P_{\max} \underbrace{\frac{1}{2}\left(1 + \operatorname{erf}\left(\frac{\bar{V}(x,t) - \bar{V}_{\text{th}}}{\sqrt{2}\eta_k}\right)\right)}_{S_k(V(x,t)),}$$

sigmoidal firing rate function

mean impulse reponse function

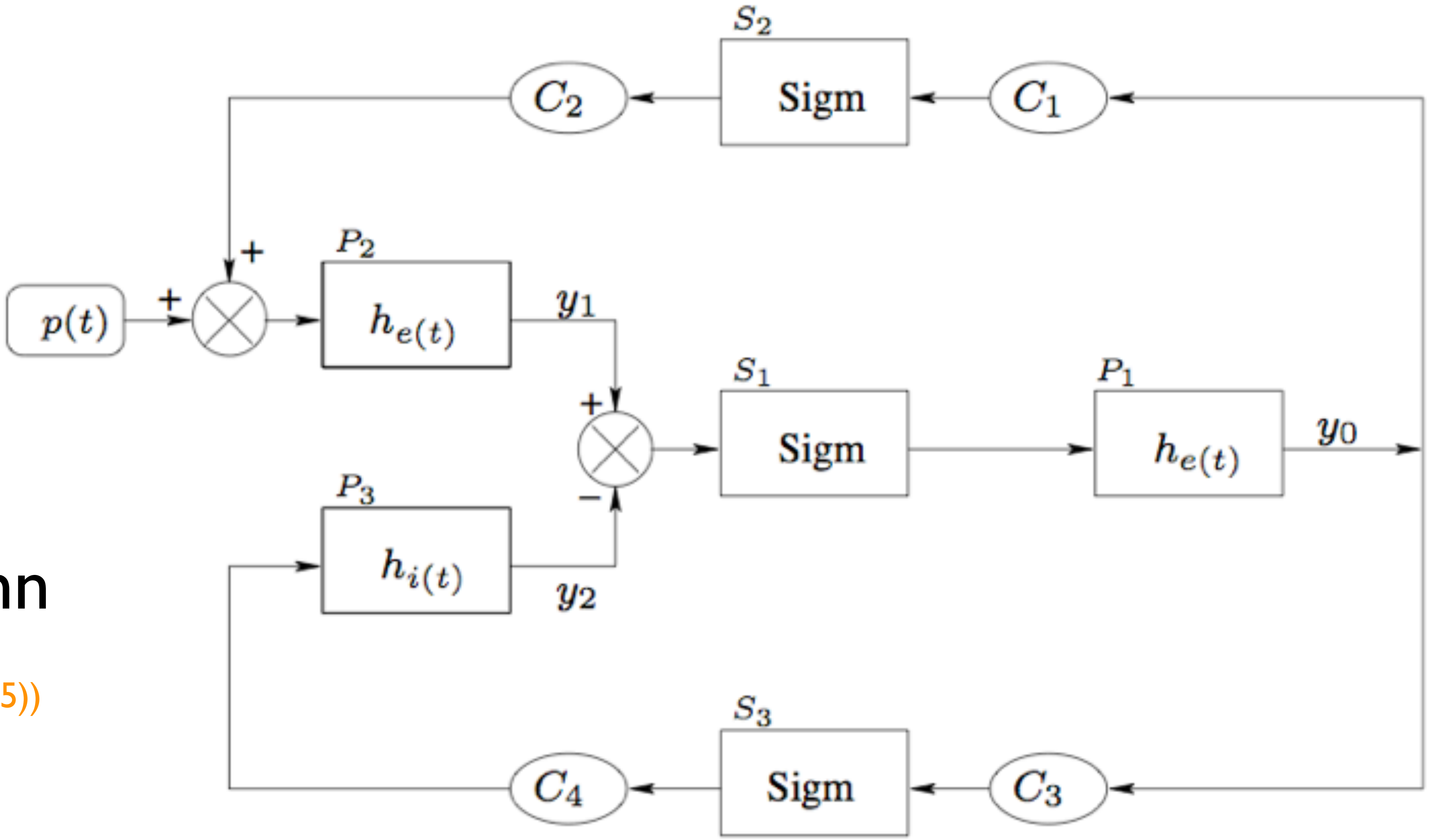


firing thresholds are Gauss-distributed → sigmoidal firing function



these are the major elements of neural mass models:

- mean synaptic response functions
- population firing rate - nonlinear transfer function



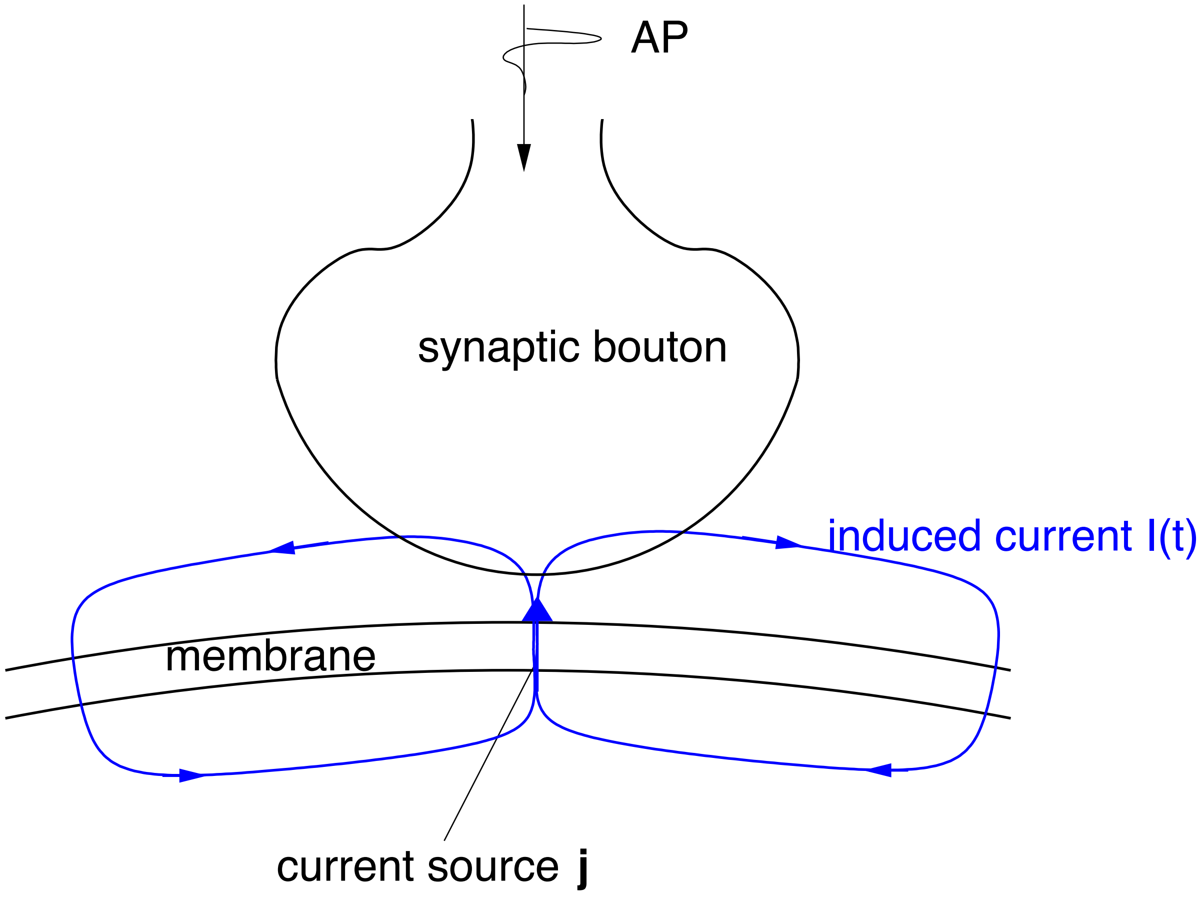
Example:
Jansen-Rit model
for cortical coloumn

(Jansen and Ritt, Biol. Cybern. (1995))

- traversing scales
- neural mass models
  - basic assumptions
  - Local Field Potentials and EEG
- neural field models
- perspectives

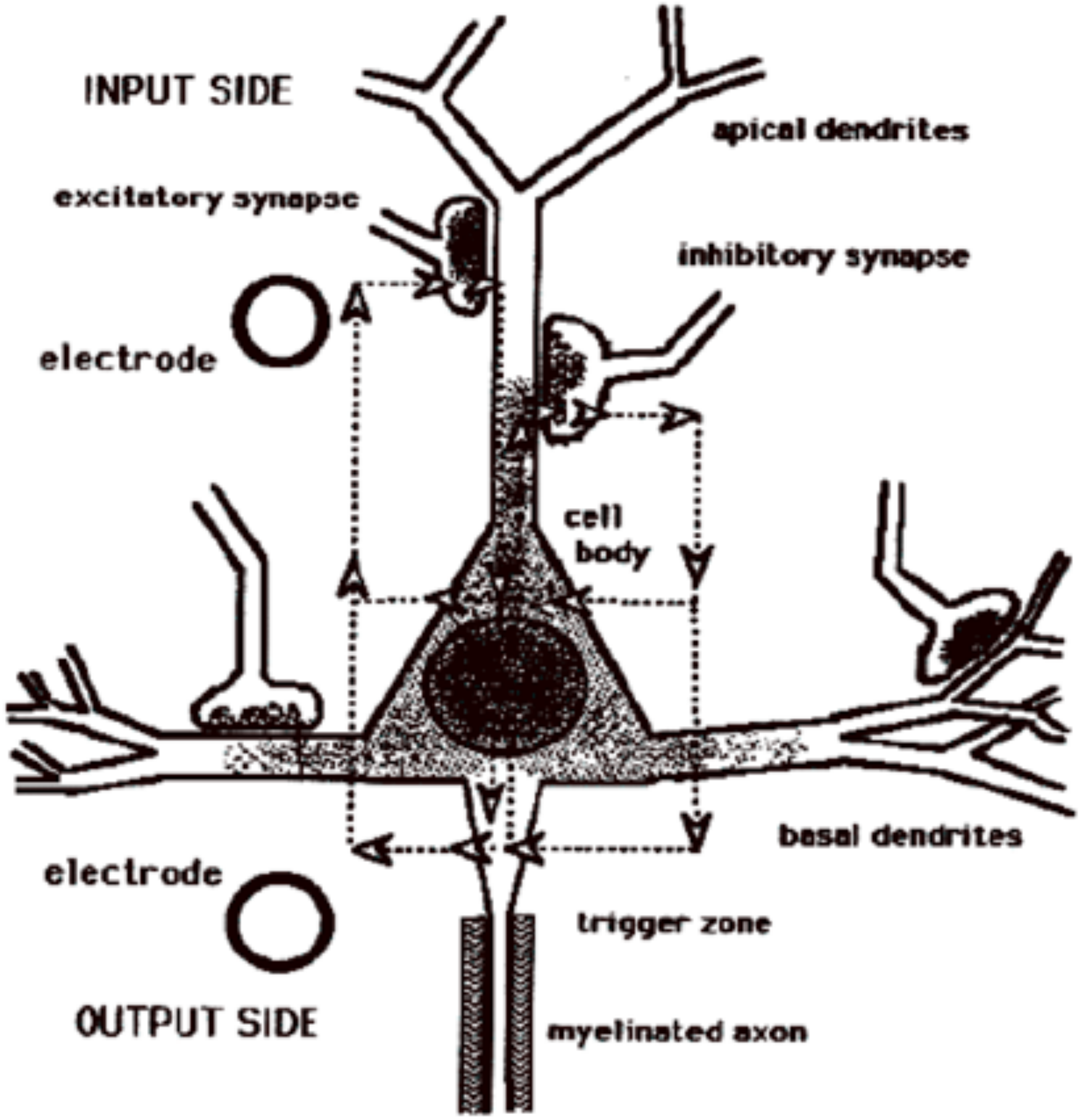
electroencephalographic activity (EEG)

single (inhibitory) synapse



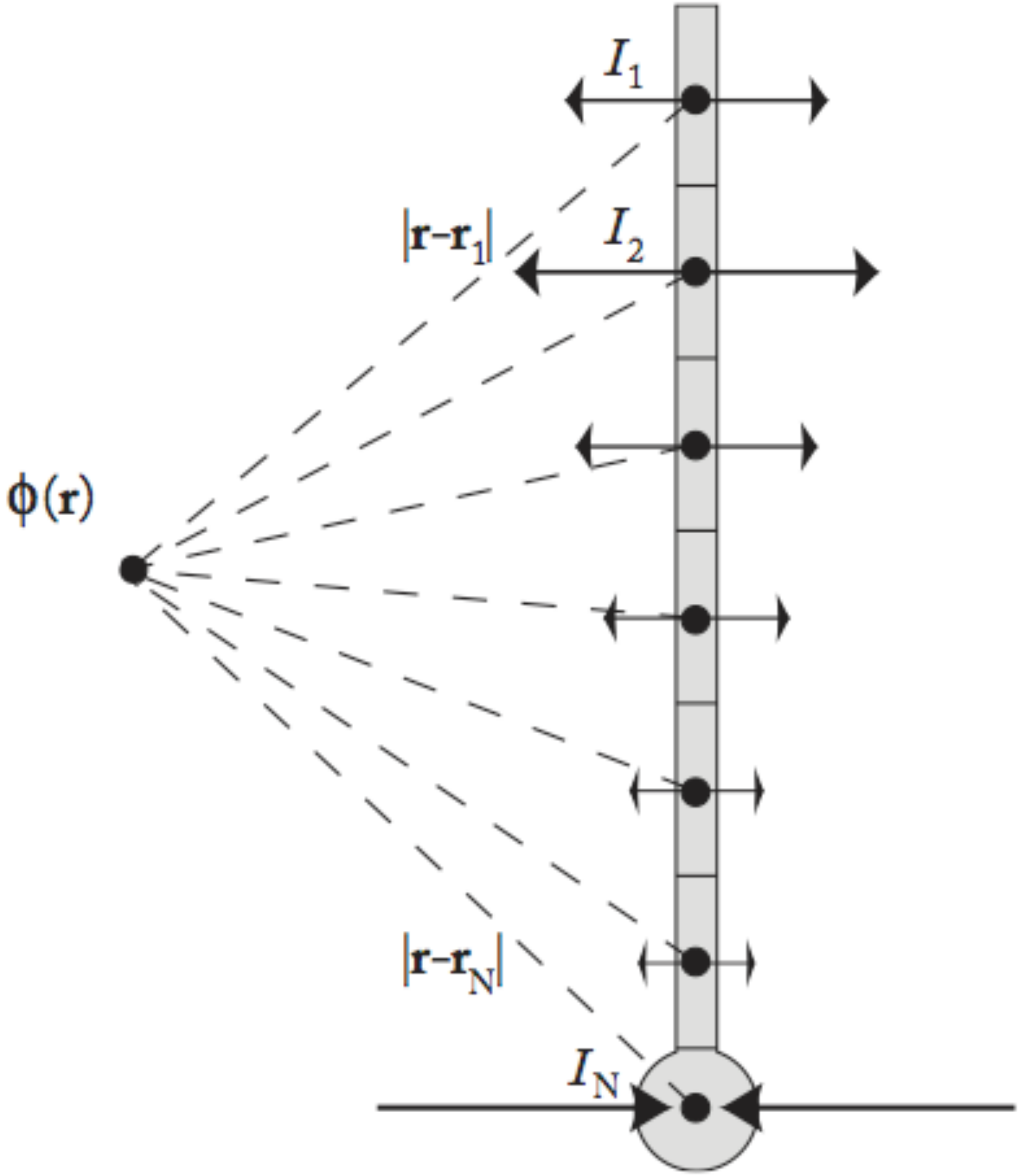
origin of
Local Field Potentials and EEG

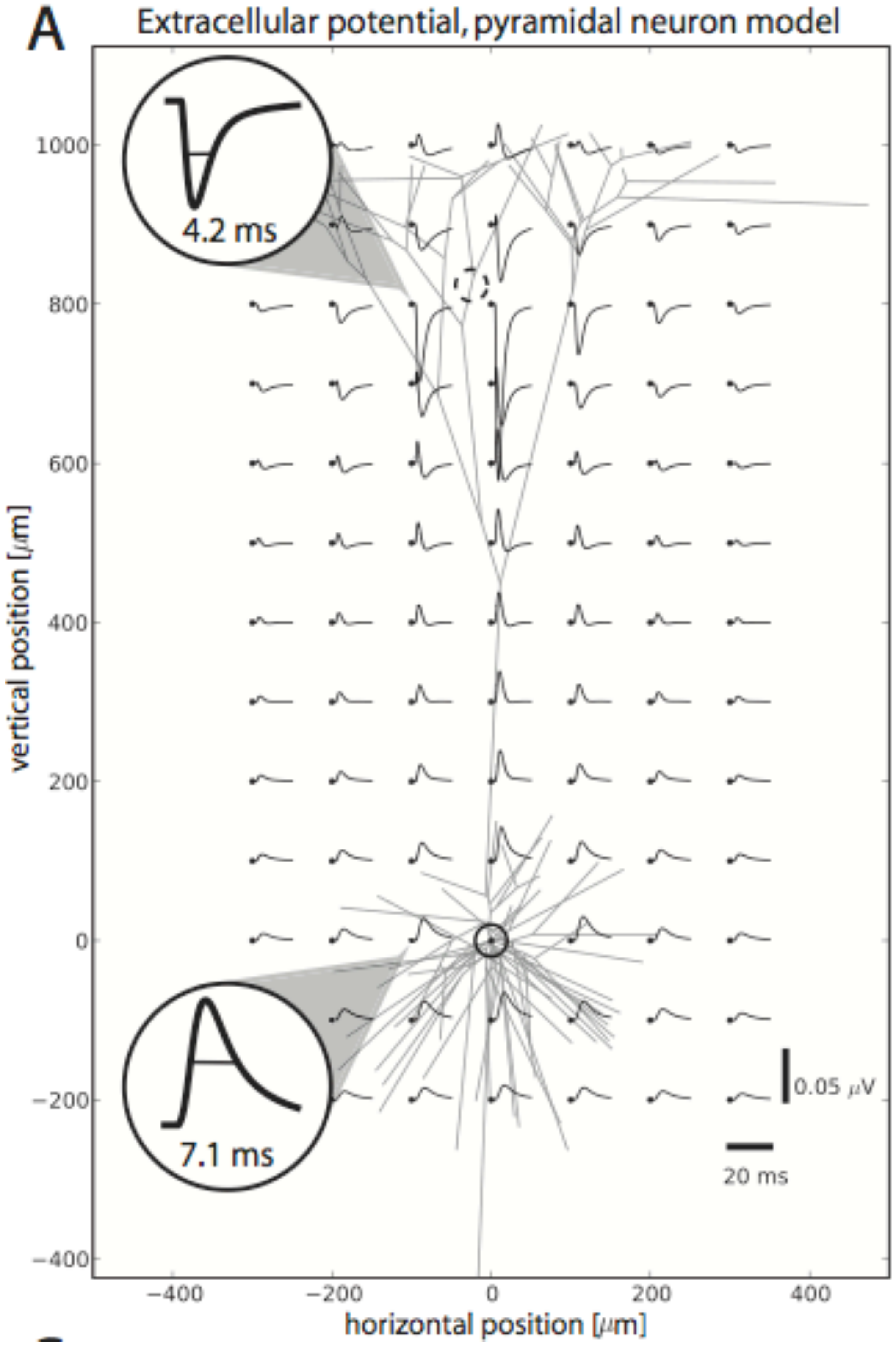
example: sum of synaptic currents



(taken from Freeman, Int. J. Bif. Chaos (1992))

Local Field Potentials



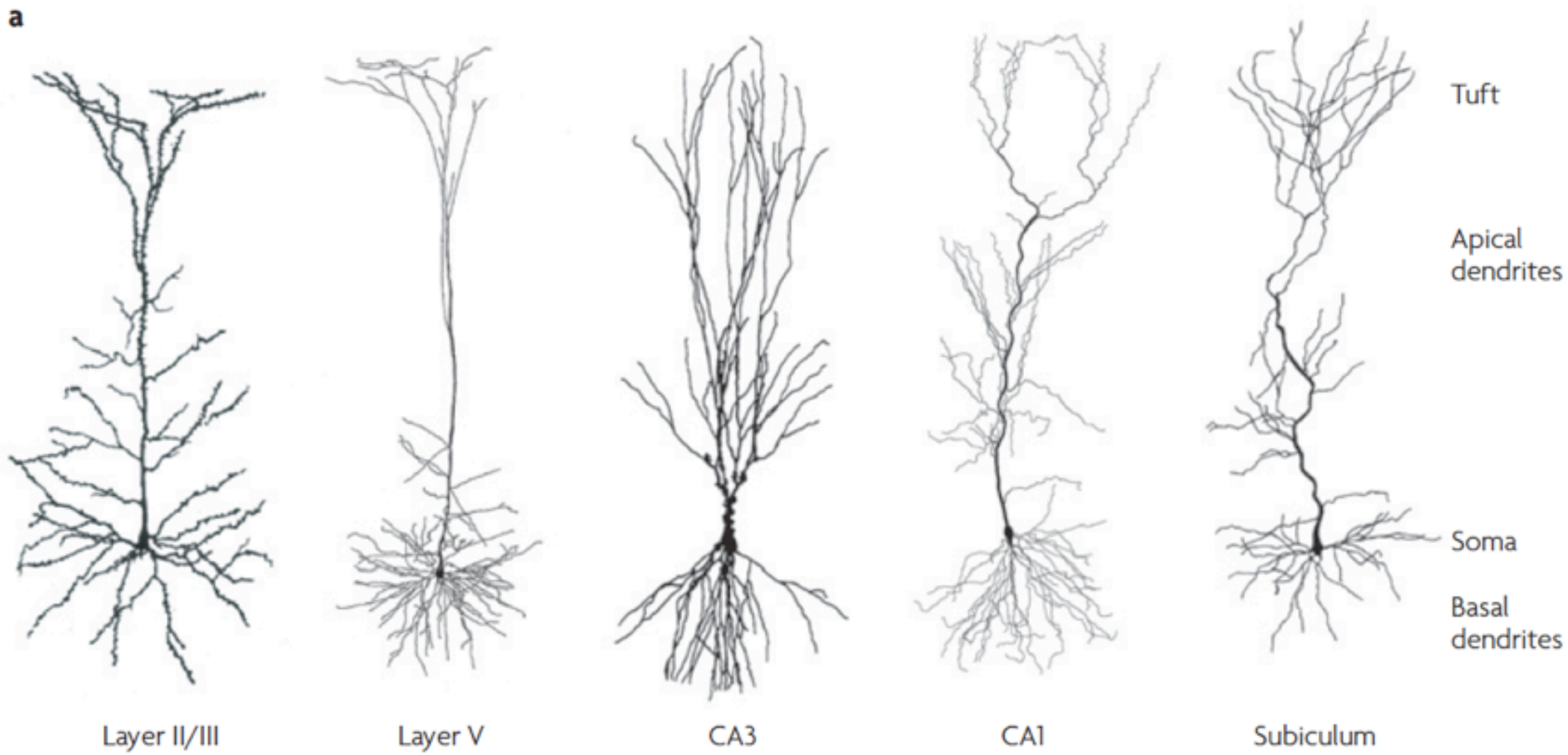


see also Tutorial 3:

Modeling and interpretation of extracellular potentials

Pettersen et al., In: Handbook of Neural Activity Measurement (2010)

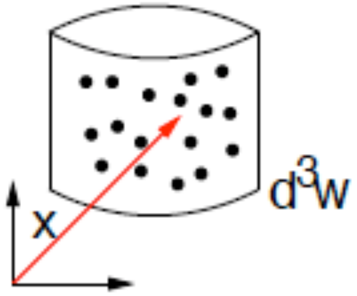
spatial structure of dendrites



(taken from Spruston, Nature Rev. Neurosc. (2008))

neocortical pyramidal cells have apical dendrites **orthogonal** to cortex surface

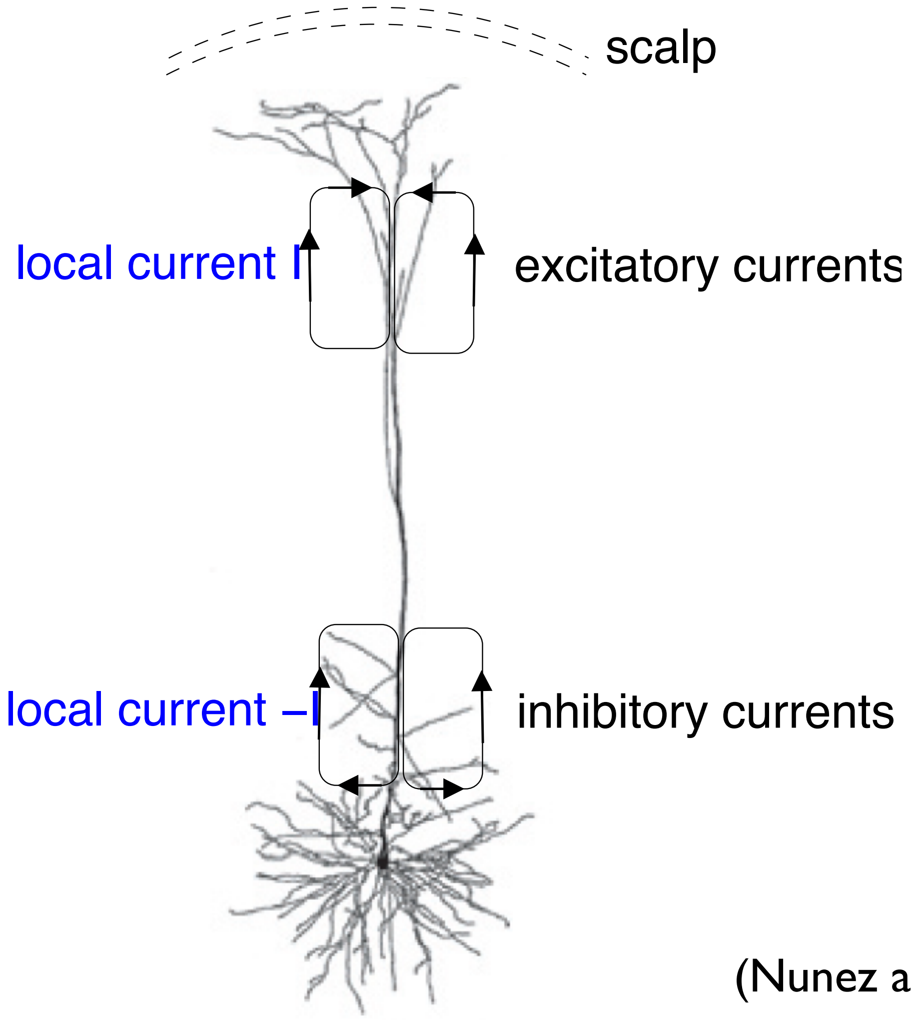
model example of simple neural population

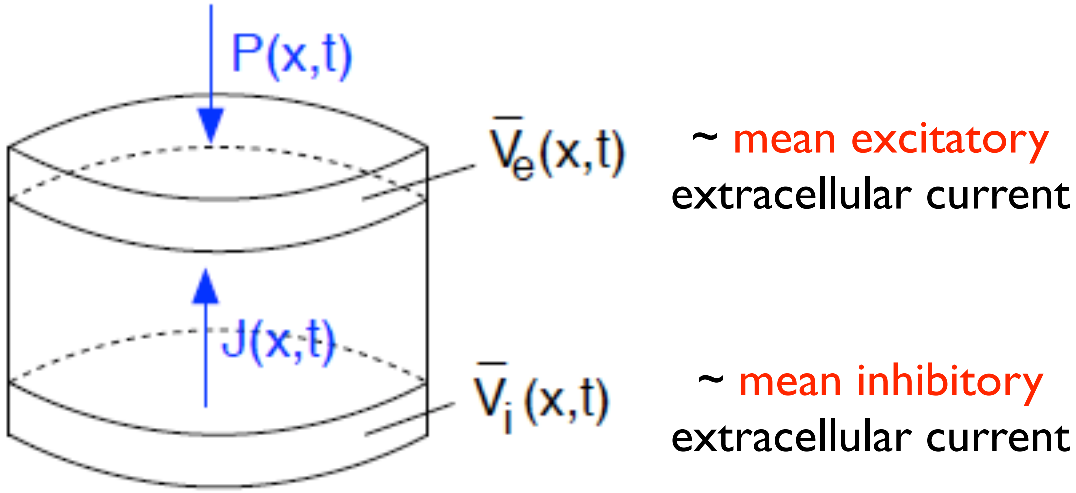


mesoscopic dipol moment $$P(\vec{x},t) = \frac{1}{W}\int_W \vec{w}\, s(\vec{x},\vec{w},t)\, d^3w$$

↑ volume current source density

→ $$\Phi_{scalp}(\vec{r},t) = \int_{neo-cortex} \vec{G}(\vec{r},\vec{x})\vec{P}(\vec{x},t)\; d^3x$$

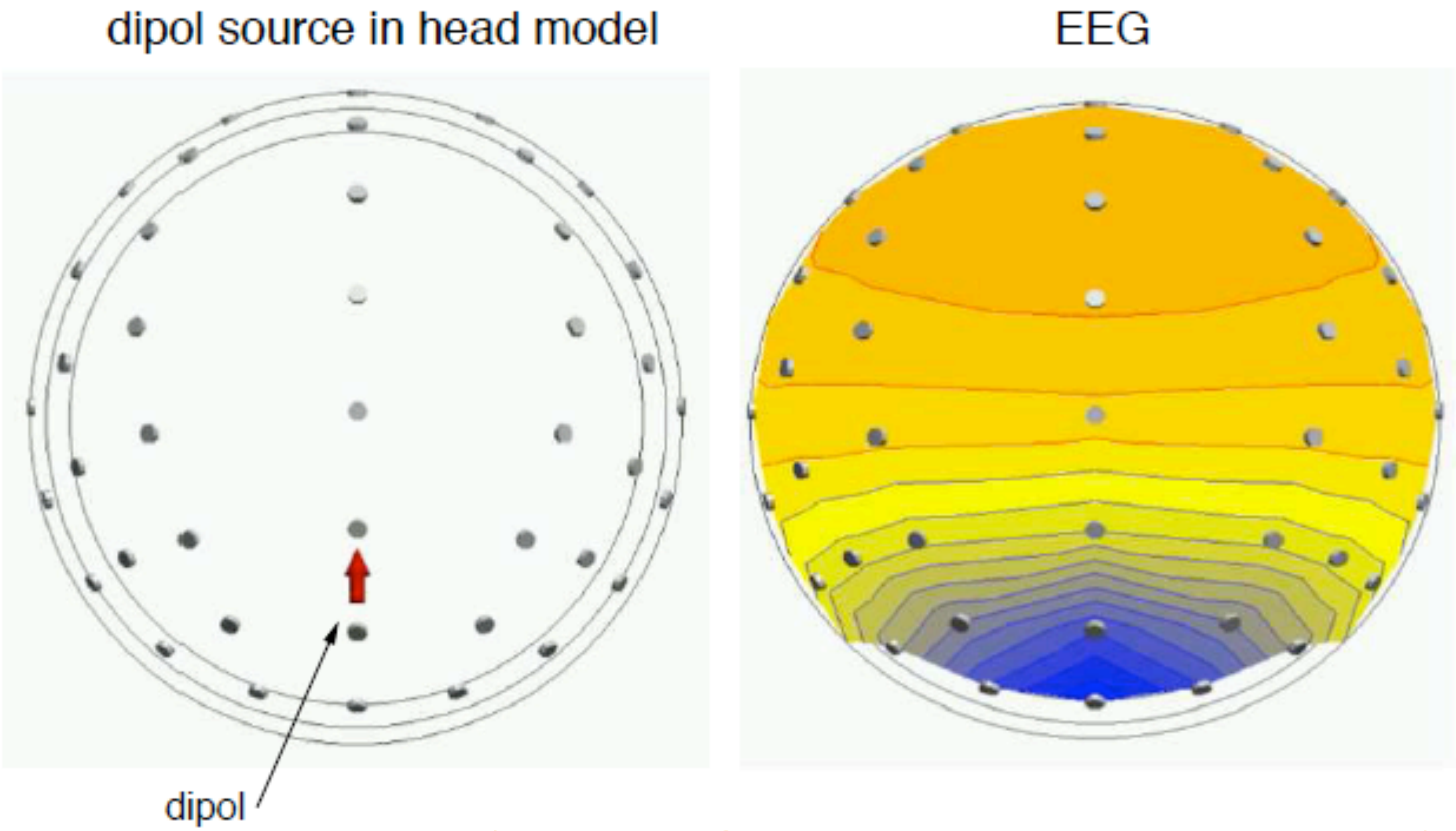




(Nunez and Srinivasan, Electric Fields of the Brain: The Neurophysics of EEG (2006))

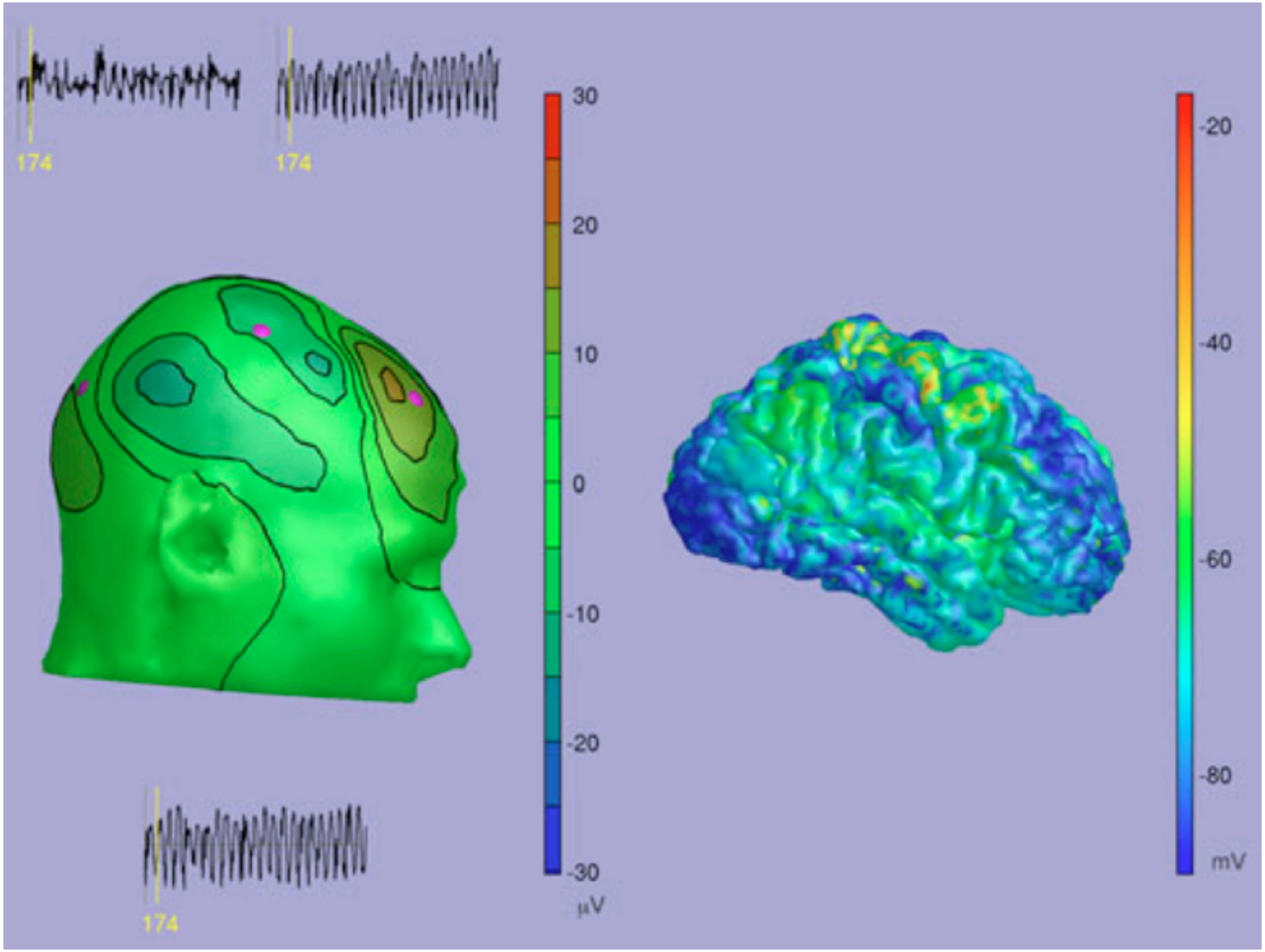
simulation of EEG activity

static dipol placed in a three-sphere head model:



(thanks to Christoph Herrmann, University of Oldenburg)

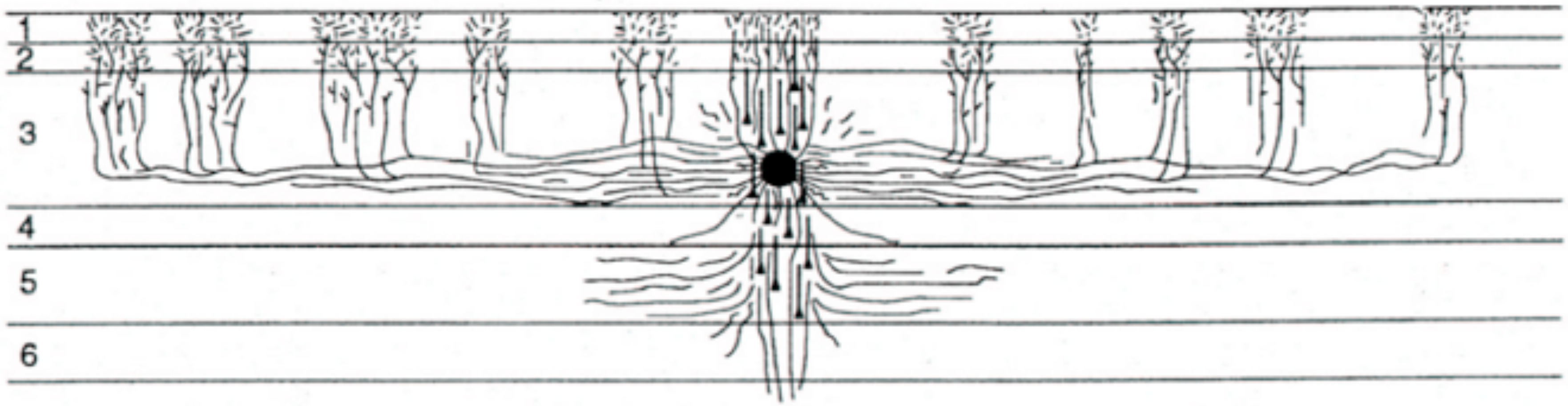
map on cortical surface



(taken from Bojak et al., Brain Top. (2010))

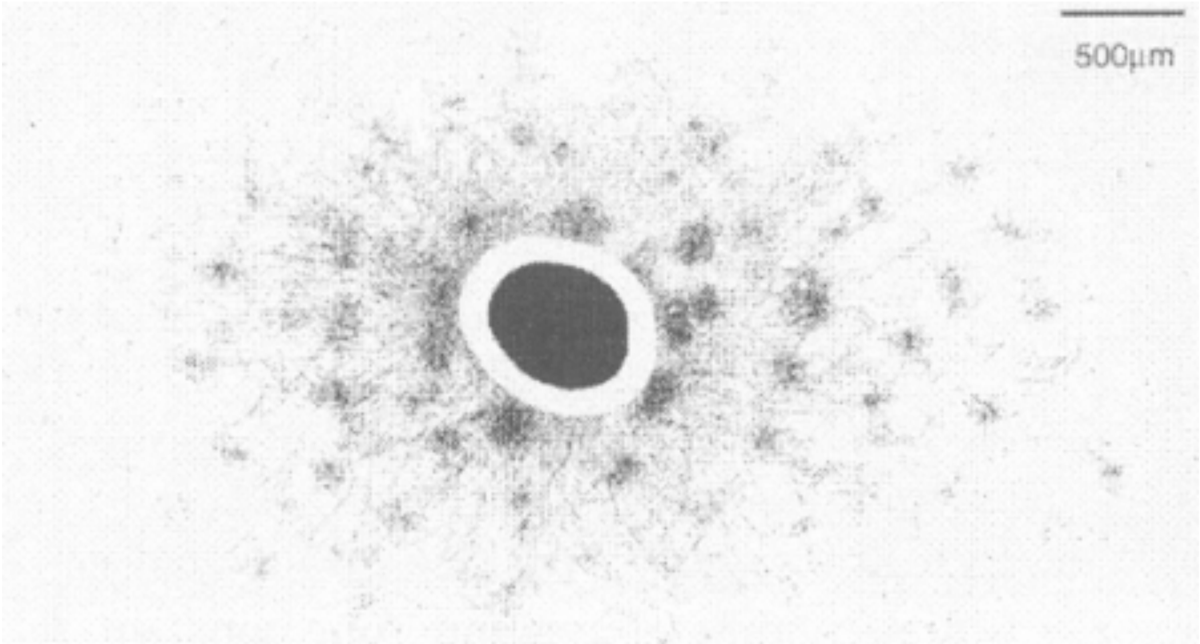
neuronal populations are spatially extended:

spatial interaction play an important role



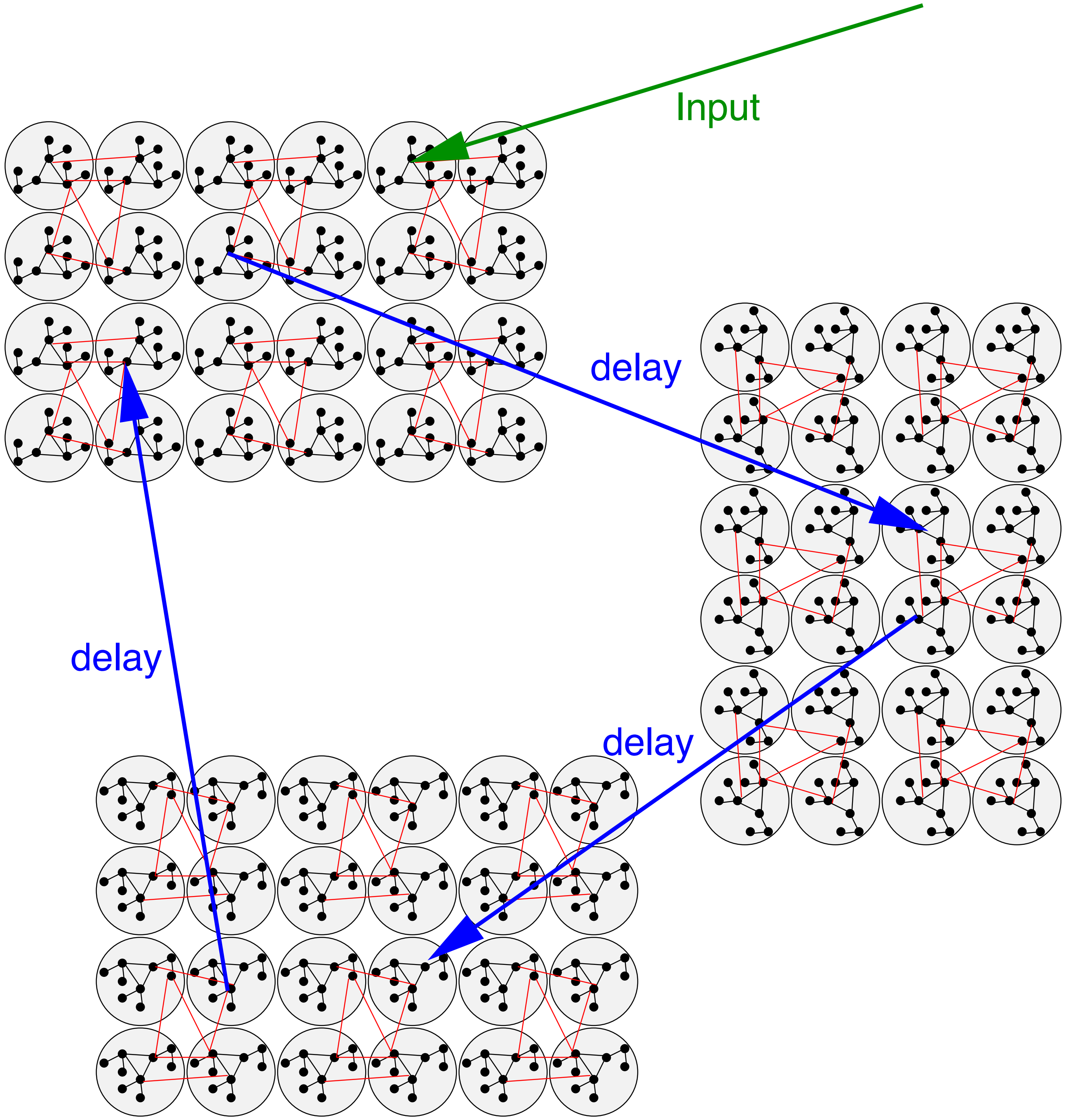
(prefrontal cortex)

→ neural fields



(visual cortex)

Modell: mean-field approach → coarse-grained field



“each grain is a location x”

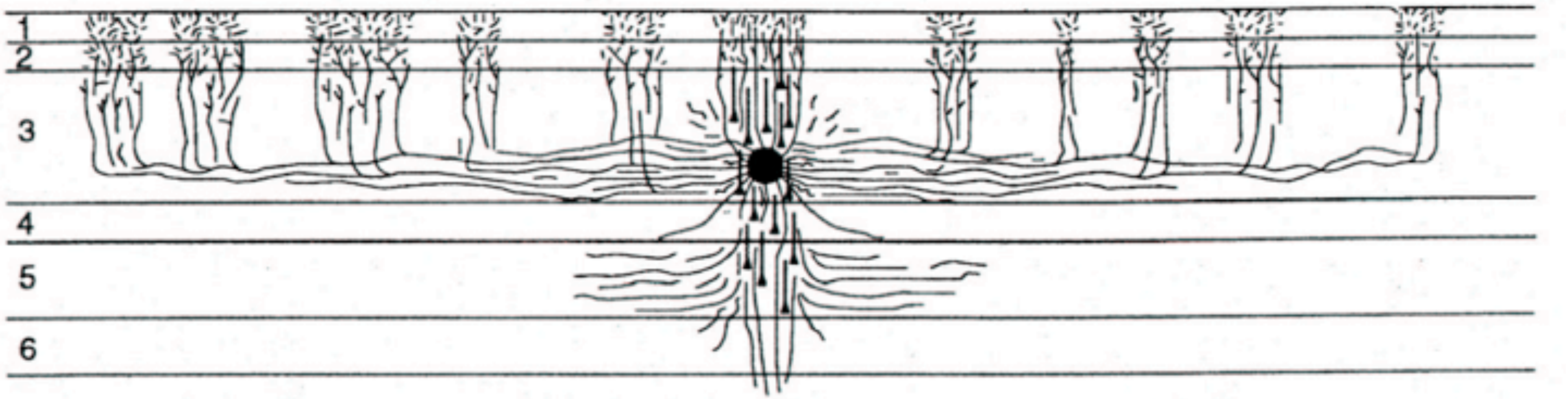
- traversing scales
- neural mass models
- neural field models
  - spatial connectivity
  - axonal transmission speed
  - various models
- perspectives

axonal connectivity

K(x,y): axonal connectivity function from neurons at spatial patch x to synapses in spatial patch y:

$$\bar{P}(x,t) = \int_\Omega K(x,y) S\left[V(y, t - \frac{|x-y|}{c})\right] dy$$

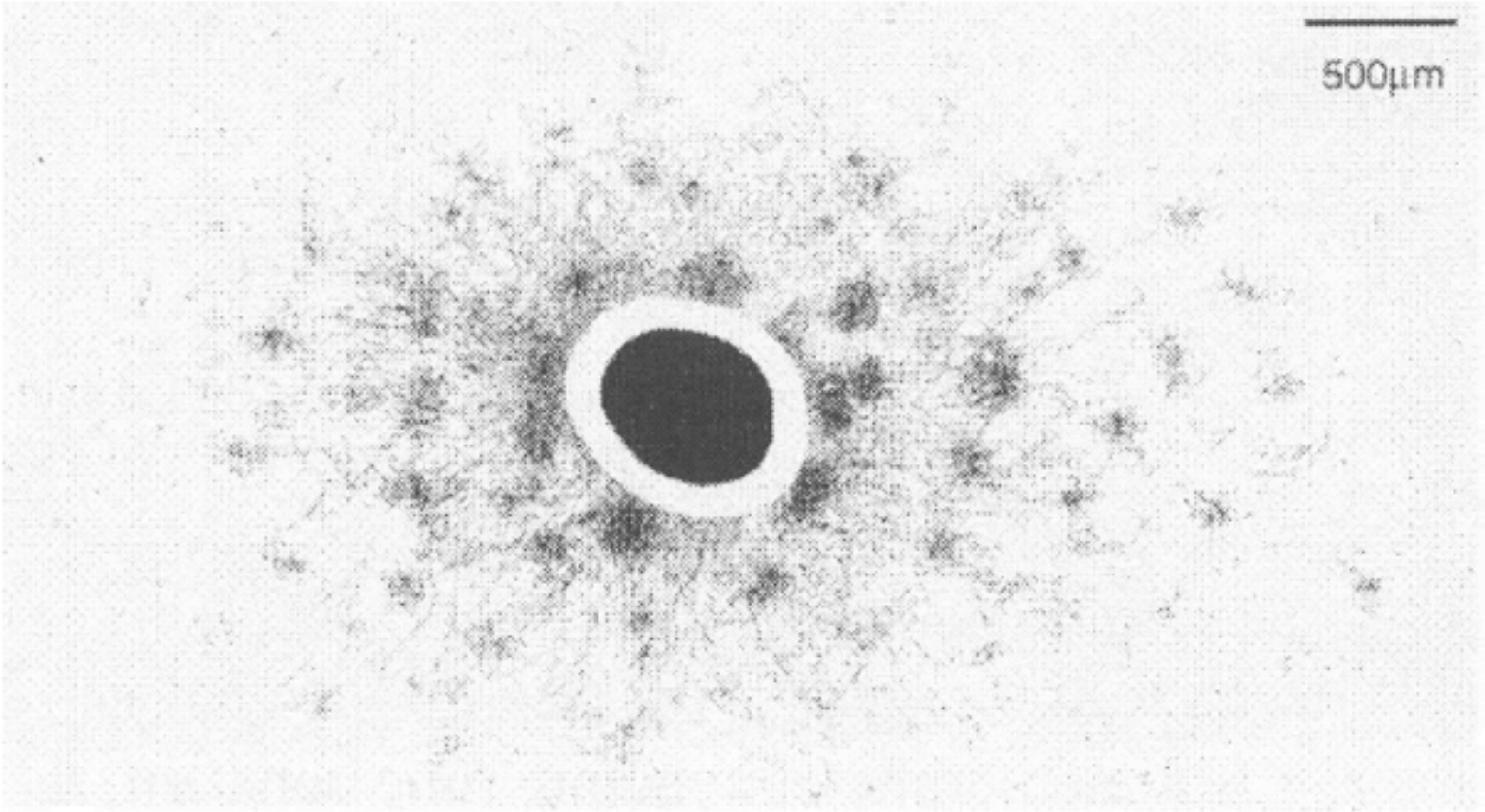
example for axonal connectivity: prefrontal cortex in monkeys



(taken from J.B.Levitt et al., J.Comp.Neur.338,360(1993))

- short-range lateral connections in layer 5
- periodic connectivity in layer 3
  $\rightarrow K_e(x,y) \sim K_h(x-y) + K_p(x,y)$
- $K_p(x,y)$: inhomogenous, anisotropic and periodic

visual cortex in monkeys

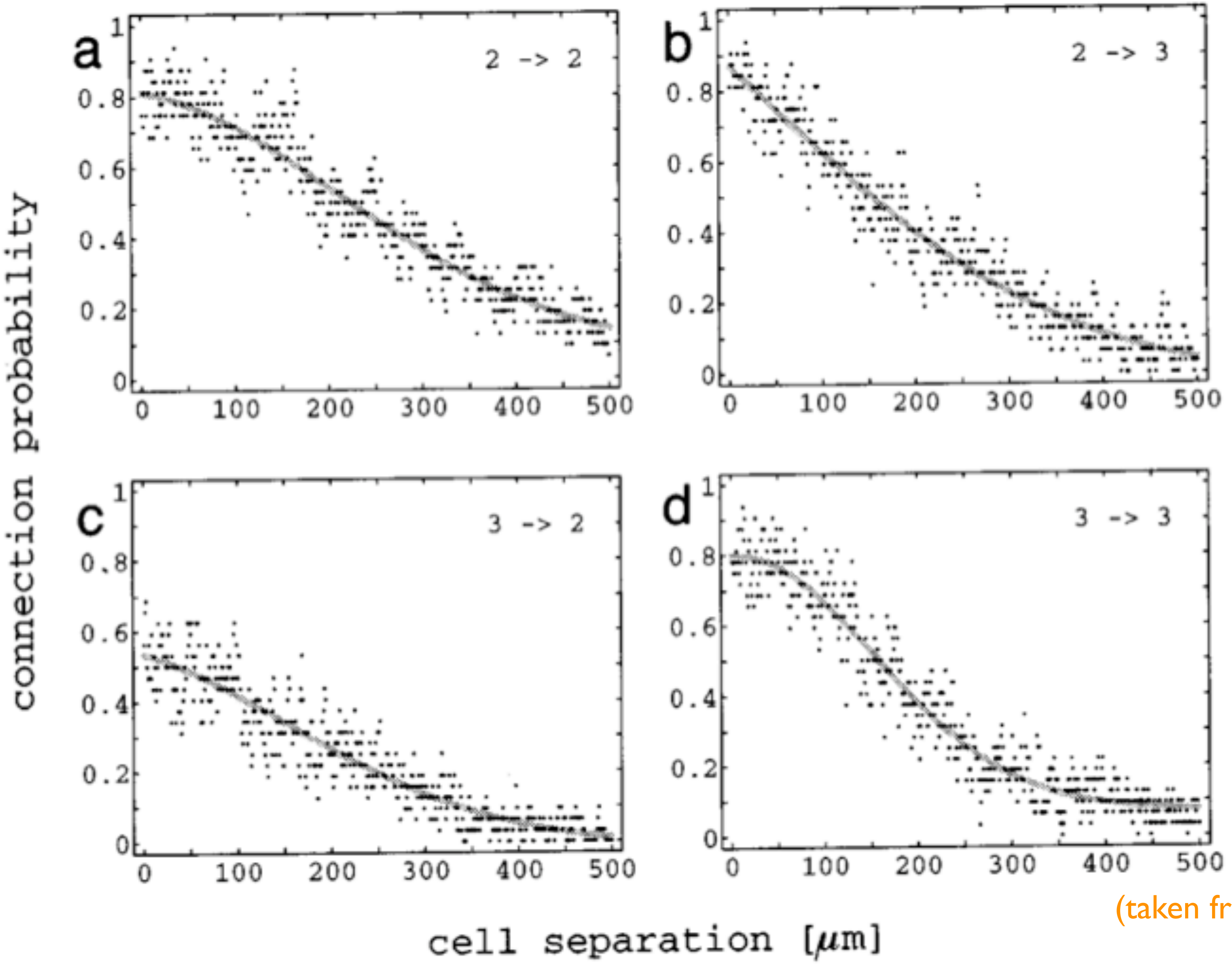


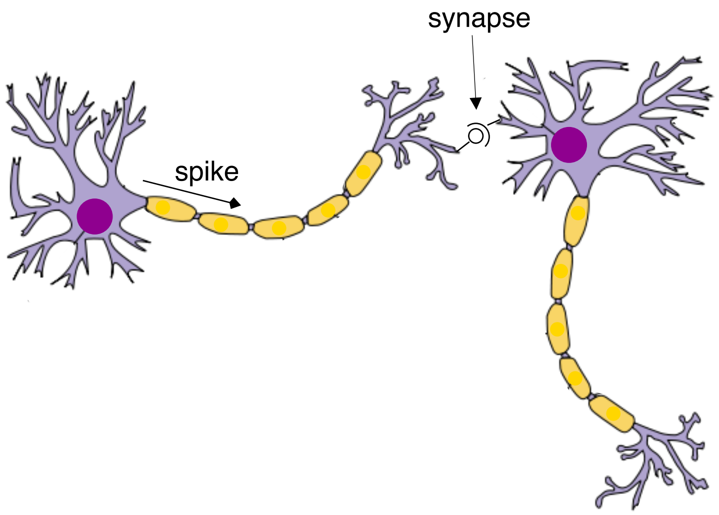
(taken from P.C.Bressloff, Physica D 185, 131(2003))

- tangential section through layer 2/3 showing lateral projections
- periodically spaced connection patches
  $\to K_e(x,y) \sim K_h(x-y) + K_p(x,y)$
- $K_p(x,y)$: inhomogenous, anisotropic and periodic

spatially homogeneous axonal connectivity

axon-dendrite connectivity in layer 2 and 3 in rat visual cortex





(taken from Hellwig, Biol. Cybern. (2000))

assumption of homogeneous distribution reasonable

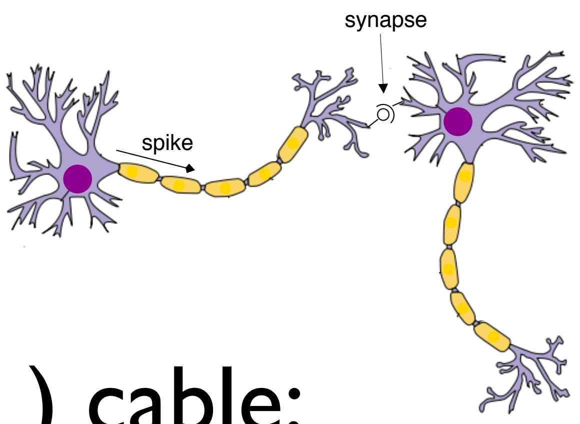
- traversing scales

- neural mass models

- neural field models
  - ✳ spatial connectivity
  - ✳ axonal transmission speed
  - ✳ various models

- perspectives

passive axonal propagation

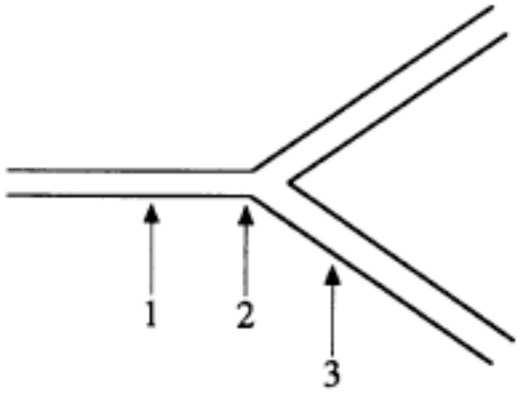


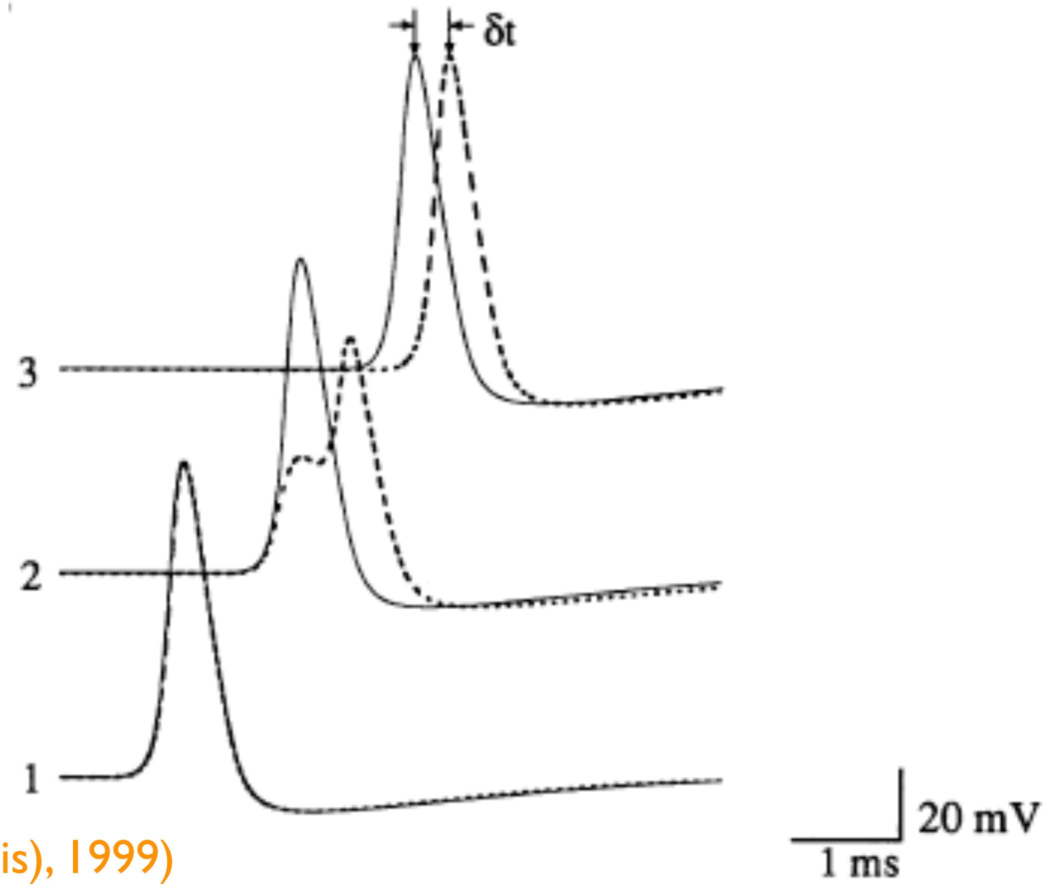
speed of action potential in a passive (un-myelinated) cable:

$$v_{passive} = \left(\frac{d}{R_m R_i C_m^2}\right)^{1/2}$$

d : diameter of the cable, R_i : intracellular resistivity, R_m : cross-membrane resistance, C_m :membrane capacitance

simulation of cable equation (GR=8):



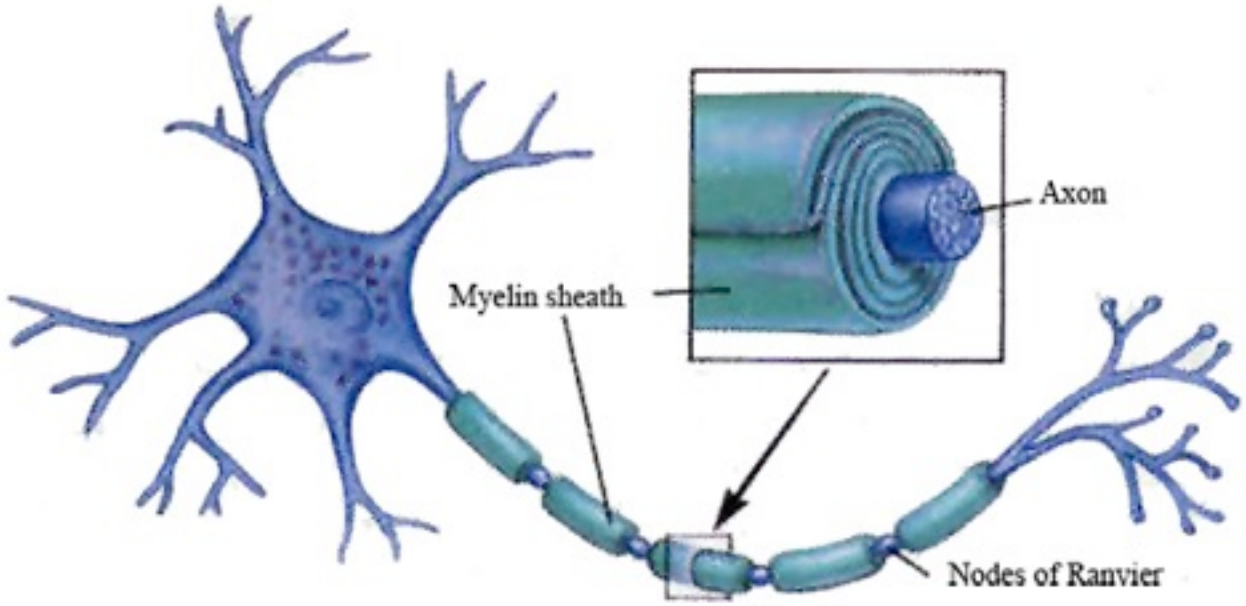


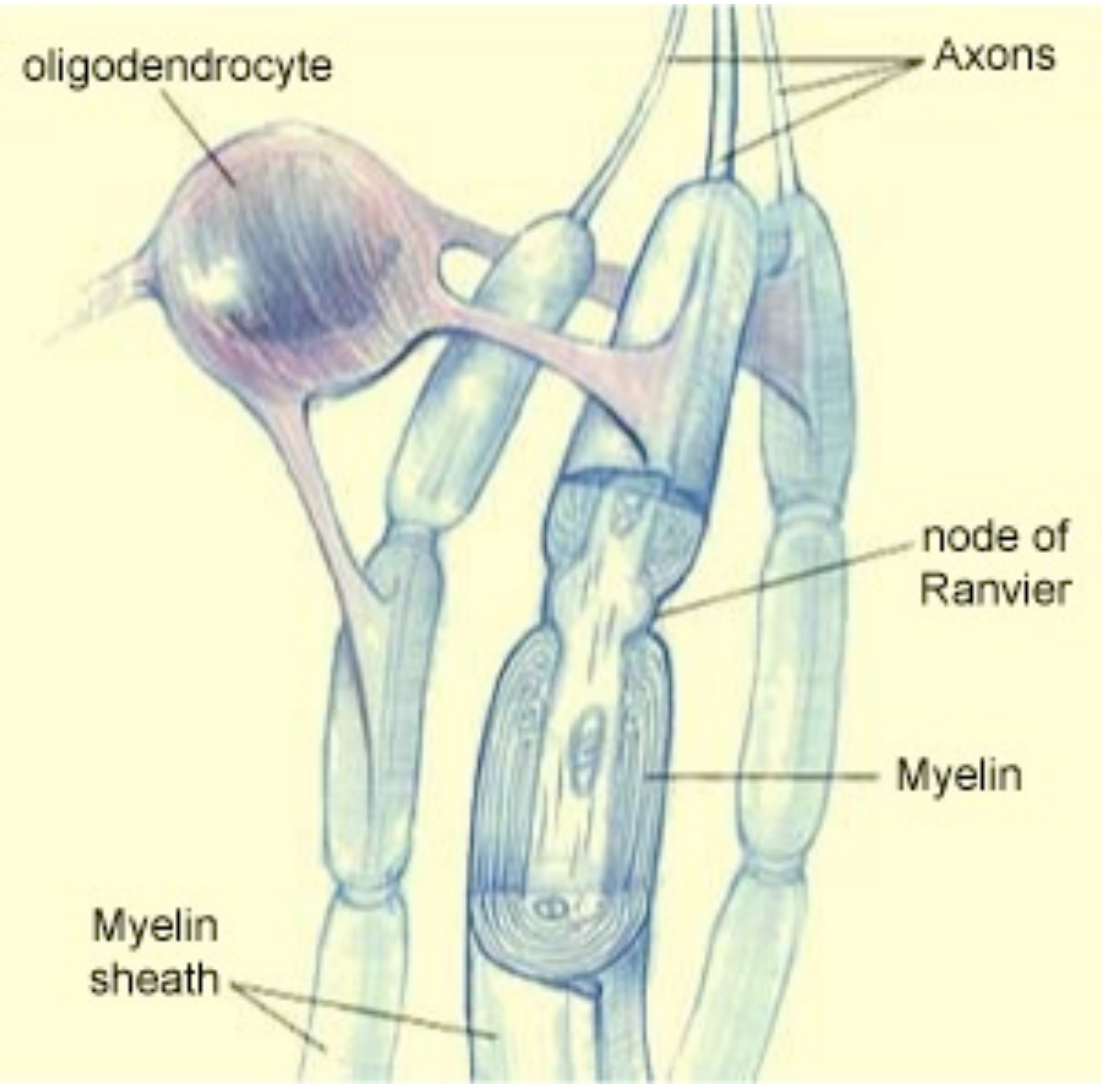
geometrical ratio

$$GR = \sum_{i=1}^{2} (d_i/d_p)^{3/2}$$

(taken from Segev and Schneidmann, J. Physiol. (Paris), 1999)

myelination



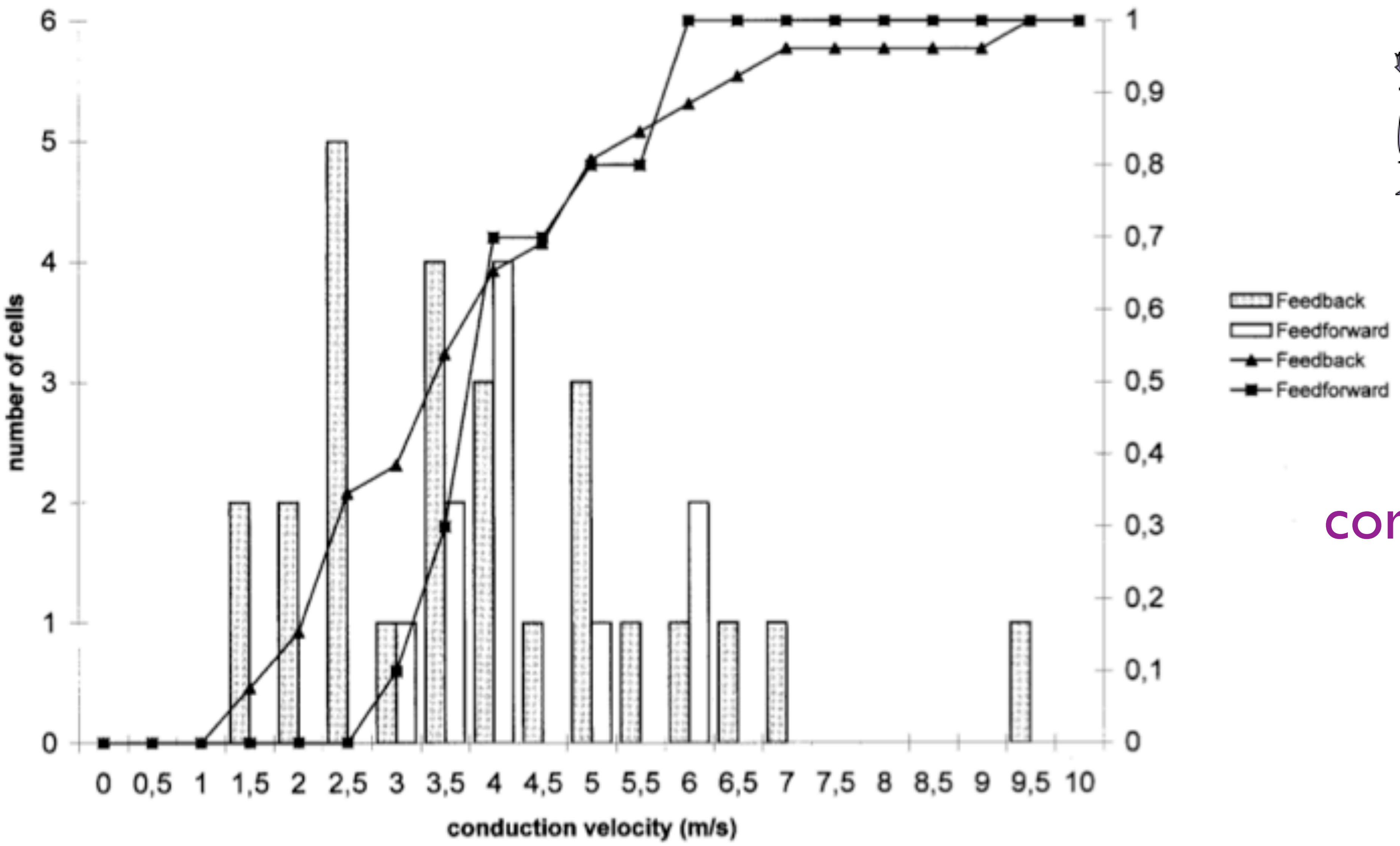


intra-cortical axons :
not myelinated

axons between cortical areas :
myelinated

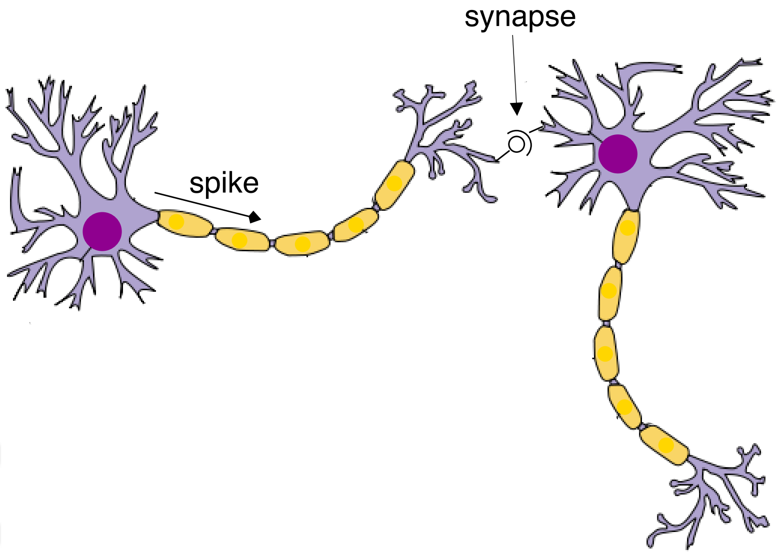
the myelination level may change on single axonal branch

finite axonal conduction speed

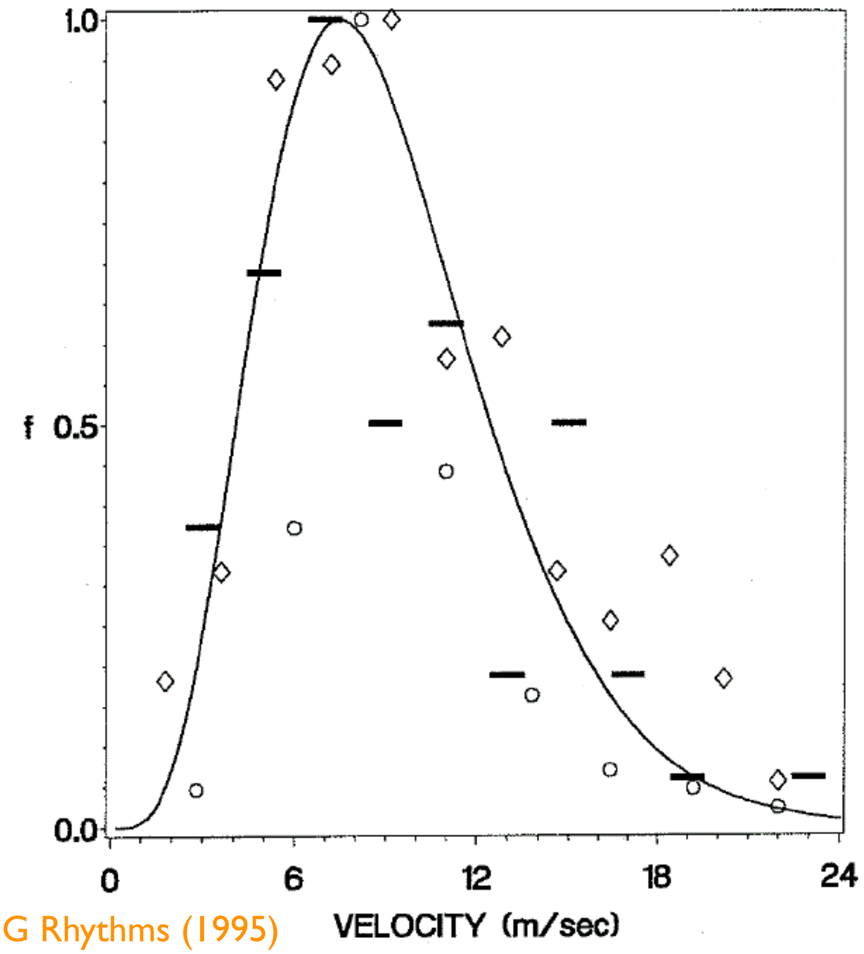


(taken from Girard_etal, J Neurophysiol 85: 1328–1331 (2001))

cortico-cortical connections between V1 and V2 in monkeys



cortico-cortical connections in mice



(taken from P. Nunez, Neocortical Dynamics and Human ECG Rhythms (1995))

assumption of homogeneous axonal connectivity:

$$\bar{P}_{e,i}(x,t) = \int_\Omega K(x-y) S_{e,i}\left[V(y, t - \tfrac{|x-y|}{c})\right] dy$$

→

$$\bar{V}^{e,i}(x,t) = \int_{-\infty}^{t} h_{e,i}(t-\tau) \int_\Omega K(x-y) S_{e,i}\left[V(y, t - \frac{|x-y|}{c})\right] dy$$

if only one synapse type: $h_e(t)=h_i(t)$:

$$\boxed{\hat{L}_t V(x,t) = \int_\Omega dy K(y) S[V(x-y, t - \frac{|y|}{c})] + E(x,t)}$$

neural field equation

$E(x,t)$: input

mathematical remark: what is the operator L ?

assume $$h(t) = \frac{\bar{h}_0}{\tau_1 - \tau_2}\left(e^{-t/\tau_1} - e^{t/\tau_2}\right)$$

$$V(t) = \int_{-\infty}^{t} h(t-\tau)P(\tau)d\tau$$

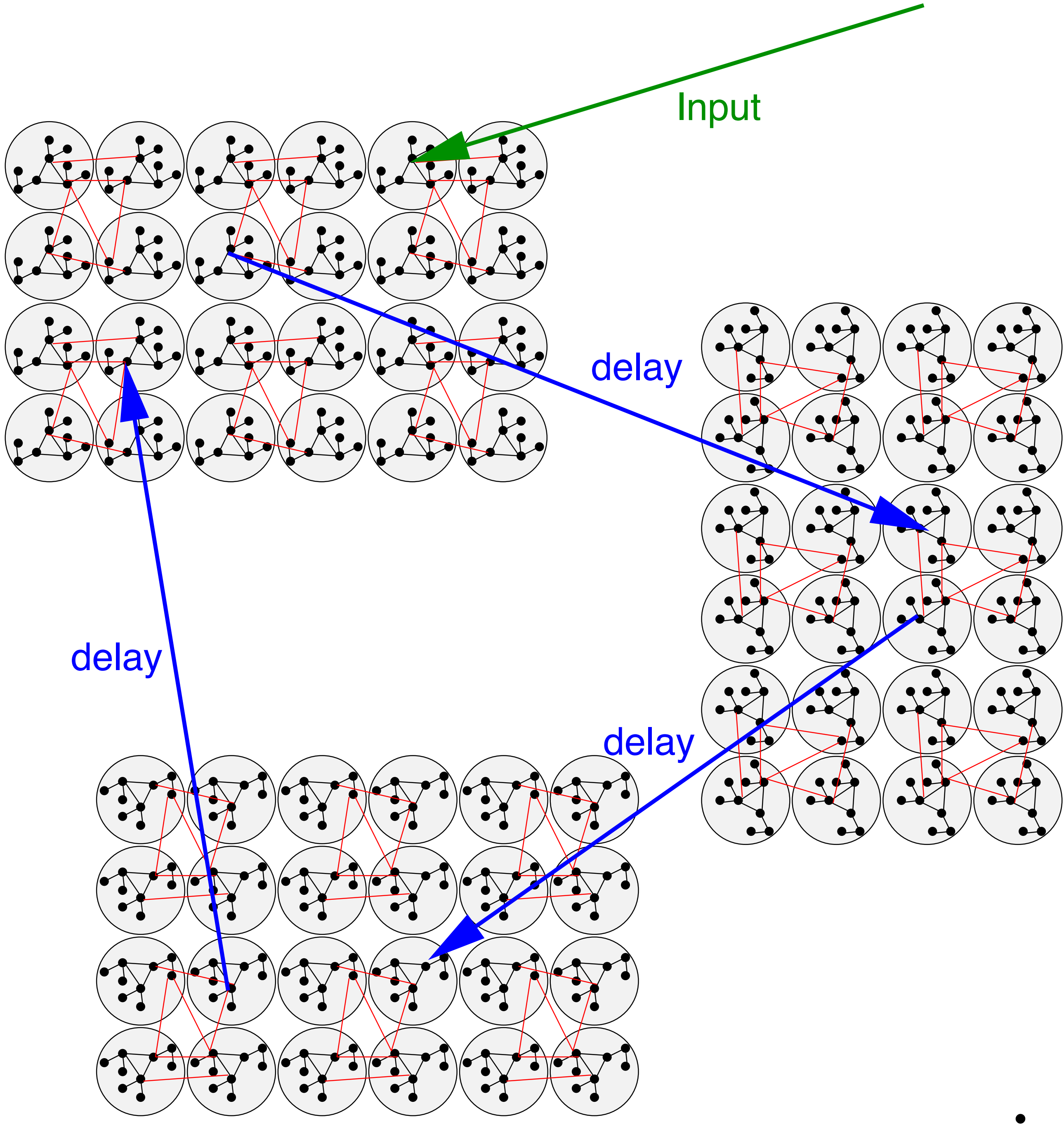
$$\frac{d^2}{dt^2}V(t) = \frac{\bar{h}_0}{\tau_1\tau_2}P(t) + \frac{\bar{h}_0}{\tau_1 - \tau_2}\int_{-\infty}^{t}\left(\frac{1}{\tau_1^2}e^{-t/\tau_1} - \frac{1}{\tau_2^2}e^{-t/\tau_2}\right)P(\tau)d\tau$$

$$= \frac{\bar{h}_0}{\tau_1\tau_2}P(t) - \left(\frac{1}{\tau_1} + \frac{1}{\tau_2}\right)\frac{d}{dt}V(t) - \frac{1}{\tau_1\tau_2}V(t)$$

⇒ $\boxed{\hat{L}V(t) = \bar{h}_0 P(t)}$ **with** $\boxed{\hat{L}\left(\frac{d}{dt}\right) = \tau_1\tau_2\frac{d^2}{dt^2} + (\tau_1 + \tau_2)\frac{d}{dt} + 1}$

- traversing scales
- neural mass models
- neural field models
  - ✳ spatial connectivity
  - ✳ axonal transmission speed
  - ✳ various models
- perspectives

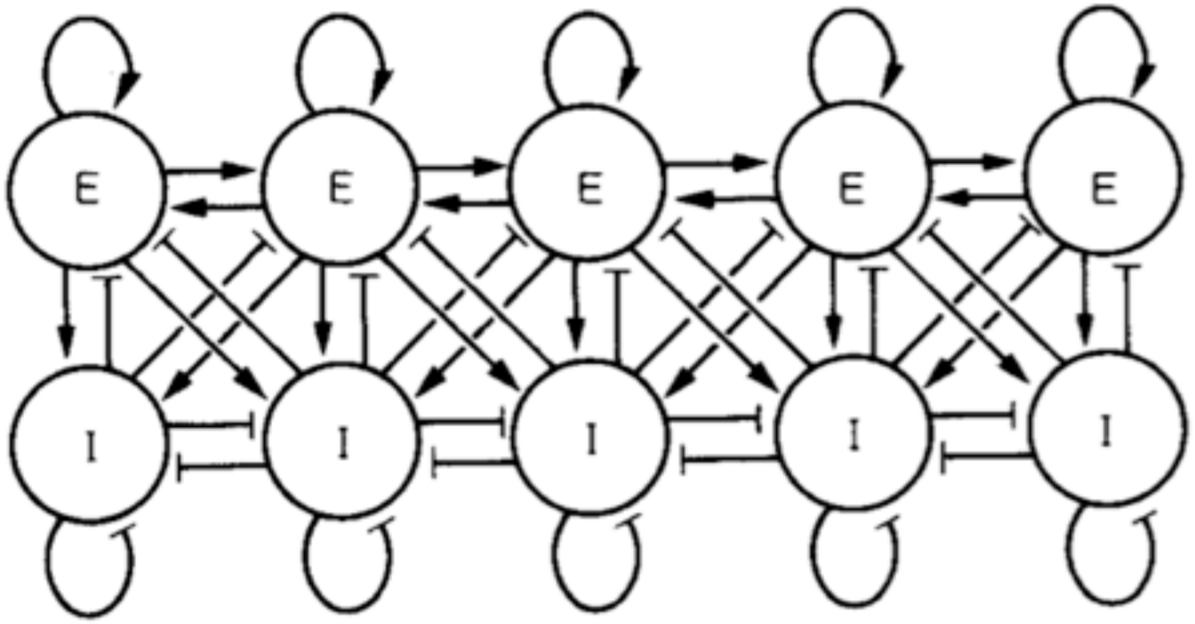
Integral-differential equations



considers probability that
two neural grains are connected

Integral-differential equations

spatio-temporal dynamics of population firing rates



Wilson and Cowan,
Kybernetik (1973)

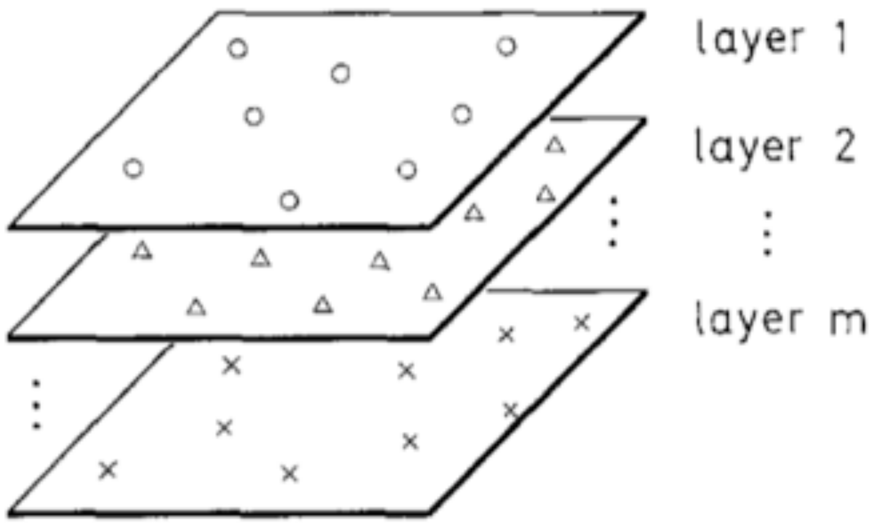
$$\tau \frac{\partial E(x,t)}{\partial t} = -E(x,t) + [1 - r_e E(x,t)] S_e \left[\alpha K_{ee} \otimes E - \beta K_{ie} \otimes I + P(x,t) \right]$$

$$\tau \frac{\partial I(x,t)}{\partial t} = -I(x,t) + [1 - r_i I(x,t)] S_i \left[\alpha K_{ei} \otimes E - \beta K_{ii} \otimes I + Q(x,t) \right]$$

$$K \otimes V = \int_{-\infty}^{\infty} K(|x-y|) V(y) dy$$

Integral-differential equations

spatio-temporal dynamics of mean membrane potential



Amari (1977)

$$\tau_i \frac{\partial u_i(x,t)}{\partial t} = -u_i(x,t) + \sum_{j=1}^{m} K_{ij} \otimes S_j[u_j] + h_i + s_i(x,t)$$

link to **partial**-differential equations

$$\left(1+\frac{1}{\alpha}\frac{\partial}{\partial t}\right)u=\psi$$

$$\psi(x,t)=\int_{-\infty}^{\infty}K(x-y)S\left[u(y,t-\frac{|x-y|}{v})\right]dy$$

$$=\int_{-\infty}^{\infty}\int_{-\infty}^{\infty}G(x-y,t-s)\rho(y,s)dyds$$

$$G(x,t)=K(x)\delta\left(t-\frac{|x|}{v}\right) \qquad \rho=S[u]$$

$$\left(1+i\frac{w}{\alpha}\right)\tilde{u}(k,w)=\tilde{G}(k,w)\tilde{\rho}(k,w)$$

$$K(x) = e^{-|x|/2} : \tilde{G}(k,w) = \frac{1+i\frac{w}{v}}{(1+i\frac{w}{v})^2+k^2}$$

$$\left(1+i\frac{w}{\alpha}\right)\left(\left(1+i\frac{w}{v}\right)^2+k^2\right)\tilde{u}(k,w) = \left(1+i\frac{w}{v}\right)\tilde{\rho}(k,w)$$

$$k^2 \to -\partial^2/\partial x^2 \ , \ iw \to \partial/\partial t$$

$$\boxed{\left(1+\frac{1}{\alpha}\frac{\partial}{\partial t}\right)\left(v^2+v\frac{\partial}{\partial t}-v^2\frac{\partial^2}{\partial x^2}\right)u(x,t) = \left(v^2+v\frac{\partial}{\partial t}\right)S[u(x,t)]}$$

nonlinear damped wave equation

Jirsa and Haken, Phys. Rev. Lett. (1997); Coombes et al., Phys. Rev. E (2007)

for more general spatial kernels:

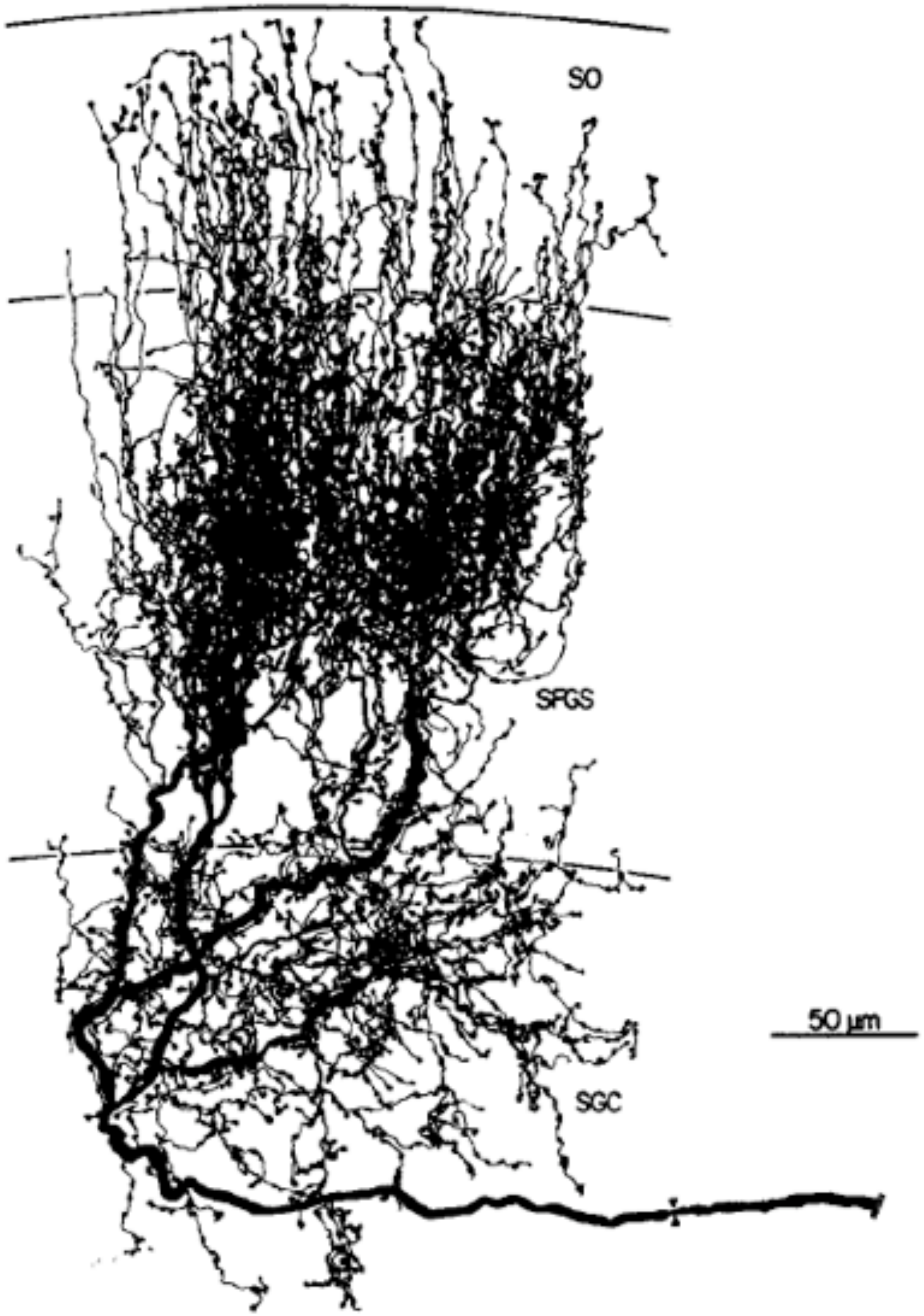
$$\int_{-\infty}^{\infty} K(x-y)V(y)dy = \sum_{n=0}^{\infty} K_n \frac{\partial^n V(x)}{\partial x^n}$$

$$K_n = \frac{(-1)^n}{n!} \int_{-\infty}^{\infty} x^n K(x)dx$$

partial differential equations
are specific cases of
integral-differential equations

(A. Hutt, Phys. Rev. E (2007))

Partial differential equations



(adapted from Segev and Schneidmann (1999))

consider wave propagation of pulse activity between neurons

Partial differential equations

$$\left(v^2\frac{\partial^2}{\partial t^2}+v\frac{\partial}{\partial t}-v^2\frac{\partial^2}{\partial x^2}\right)\underset{\substack{\uparrow\\ \text{pulse activity}}}{\phi(x,t)}=\left(v^2+v\frac{\partial}{\partial t}\right)S[\underset{\substack{\uparrow\\ \text{dendritic potential}}}{h_e(x,t)}]$$

$$B\frac{\partial h_{e,i}(t)}{\partial t}=h_r-h_{e,i}+CI_{e,i}(t)+DJ_{e,i}(t)$$

exc. postsyn. potential

$$\left(\gamma_e+\frac{\partial}{\partial t}\right)^2 I_{e,i}=E\left(S_e[h_e(x,t)]+F\phi(x,t)+p(x,t)\right)$$

A,B,..,H: constants

inh. postsyn. potential

$$\left(\gamma_i+\frac{\partial}{\partial t}\right)^2 J_{e,i}=G\left(S_i[h_i(x,t)]+H\phi(x,t)\right)$$

(Liley et al., Neurocomputing (1999))

applications:

EEG during epileptic seizures, general anaesthesia and sleep

Partial differential equations

includes spatial range

axonal transmission speed

$$\underbrace{\left(\frac{\partial^2}{\partial t^2} + 2\gamma_{e,i}\frac{\partial}{\partial t} + \gamma_{e,i}^2 - v^2\frac{\partial^2}{\partial x^2}\right)}_{\text{axonal propagation}}\phi_{e,i}(x,t) = \gamma_{e,i}^2 S[V_{e,i}(x,t)]$$

pulse activity

dendritic potential

$$\underbrace{\left(\frac{\partial^2}{\partial t^2} + 2\alpha\frac{\partial}{\partial t} + \alpha^2\right)}_{\text{synaptic response}} V_{e,i}(x,t) = g\alpha^2 Q[V_{e,i}(x,t), \phi_{e,i}(x,t), x, t]$$

input to synapses: external stimulation, pulse activity

(Robinson et al., Phys. Rev. E (1997))

applications:

EEG during epileptic seizures, general anaesthesia and sleep

new field models

- single neurons are subjected to random fluctuations from e.g.
  - ✳ ion channel fluctuations
  - ✳ spontaneous synaptic activity

- how do fluctuations on single neuron level translate into population fluctuations ?

- to answer question, re-derivation of model equations necessary by considering mean-field theory

new models - 2 -

Bressloff, SIAM J. Appl. Math. (2009):

- assuming two-state neurons (no firing/firing)
- a jump process between neurons (Master equation)

old: Wilson-Cowan model

$$\tau \frac{\partial f(x,t)}{\partial t} = -f(x,t) + S\left[\int_\Omega K(x,y) f(y,t) dy\right]$$

new: extended Wilson-Cowan model

$$\tau\frac{\partial f(x,t)}{\partial t} = -f(x,t) + S\left[\int_\Omega K(x,y)f(y,t)dy\right]$$

$$\underline{+\frac{\alpha}{2N}S''\left[\int_\Omega K(x,y)f(y,t)dy\right]\int_\Omega\int_\Omega K(x,y)K(x,z)C(y,z,t)dydz}$$

new

$$\underline{\tau\frac{\partial C(x,y,t)}{\partial t} = -2C(x,y,t)+\beta\left(f(x,t)+S\left[\int_\Omega K(x,y)f(y,t)dy\right]\right)\delta(x-y)}$$

$$\underline{+\gamma S'\left[\int_\Omega K(x,z)f(z,t)dz\right]\int_\Omega K(x,z)C(z,y,t)dz}$$

$$\underline{+\gamma S'\left[\int_\Omega K(y,z)f(z,t)dz\right]\int_\Omega K(y,z)C(z,y,t)dz}$$

- *f(x,t)* is mean firing rate, *C(x,y,t)* is covariance
- neglecting covariance yields original mean field equation

a **more realistic mean-field equation**

implies the spatial **covariance** of the activity !

new models - 2 -

Faugeras, Toboul and Cessac, Front. Comp. Neuroscience (2009):

- coupling of different populations, no spatial extension
- connections between single neurons are randomly distributed

old: Amari-type model

$$\frac{d\bar{V}_\alpha(t)}{dt} = -\frac{1}{\tau}\bar{V}_\alpha(t) + \sum_\beta \bar{J}_{\alpha\beta} S\left[\bar{V}_\beta(t)\right]$$

new: extended Amari-type model

$$\frac{d\bar{V}_\alpha(t)}{dt} = -\frac{1}{\tau}\bar{V}_\alpha(t) + \sum_\beta \bar{J}_{\alpha\beta} \int_{\mathcal{R}} S\left[x\sqrt{C_{\beta\beta}(t,t)} + \bar{V}_\beta(t)\right] N_x(0,1)dx$$

$$C_{\beta\beta}(t,t) = C_{\beta\beta}\left(t, \sum_\beta \sigma^2_{\alpha\beta} \int_{t_0}^{t}\int_{t_0}^{t} e^{(u+w)/\tau}\Delta_\beta(u,v)dudv\right)$$

$$\Delta_\beta(t,s) = \int_{\mathcal{R}^2} S_\beta\left[\frac{\sqrt{C_{\beta\beta}(t,t)C_{\beta\beta}(s,s) - C^2_{\beta\beta}(t,s)}}{\sqrt{C_{\beta\beta}(t,t)}}x + \frac{C_{\beta\beta}(t,s)}{\sqrt{C_{\beta\beta}(t,t)}}y + \bar{V}_\beta(s)\right]$$

$$\times S_\beta\left[\sqrt{C_{\beta\beta}(t,t)}y + \bar{V}_\beta(t)\right] N_x(0,1)N_y(0,1)dxdy$$

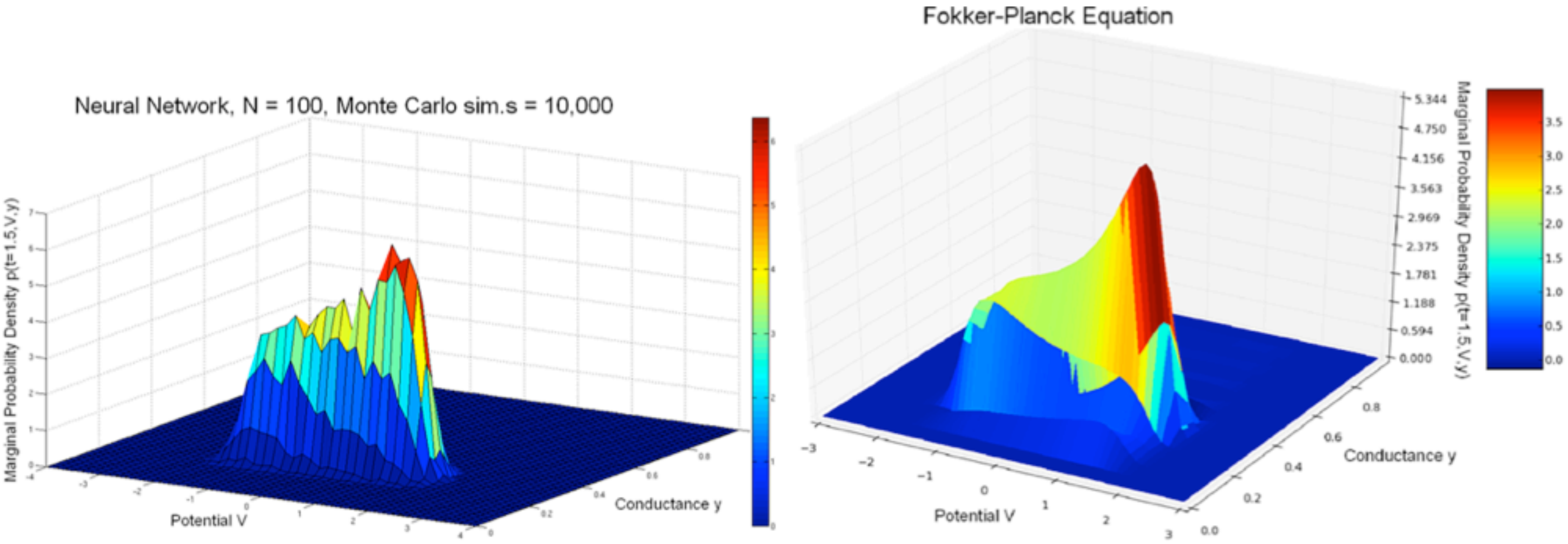
- $\bar{V}$ is the mean membrane potential,
  $C(t,s)$ is the temporal correlation function
- $C(t,s) = 0$ yields standard Amari model

a **more realistic mean-field equation**
implies the temporal **covariance** of the activity !

new models - 3 -

<u>Baladron et al., J. Math. Neuroscience (2012):</u>

- mean field equation for spiking neural networks
- network exhibits all-to-all coupling
- leads to McKean-Vlasov Fokker-Planck equation



- traversing scales

- neural mass models

- neural field models

- perspectives

neural fields

- do
  - consider mean synaptic and dendritic currents in population
  - involve threshold properties of neurons
  - consider axonal structures
  - assume rate coding
  - describe LFP+EEG

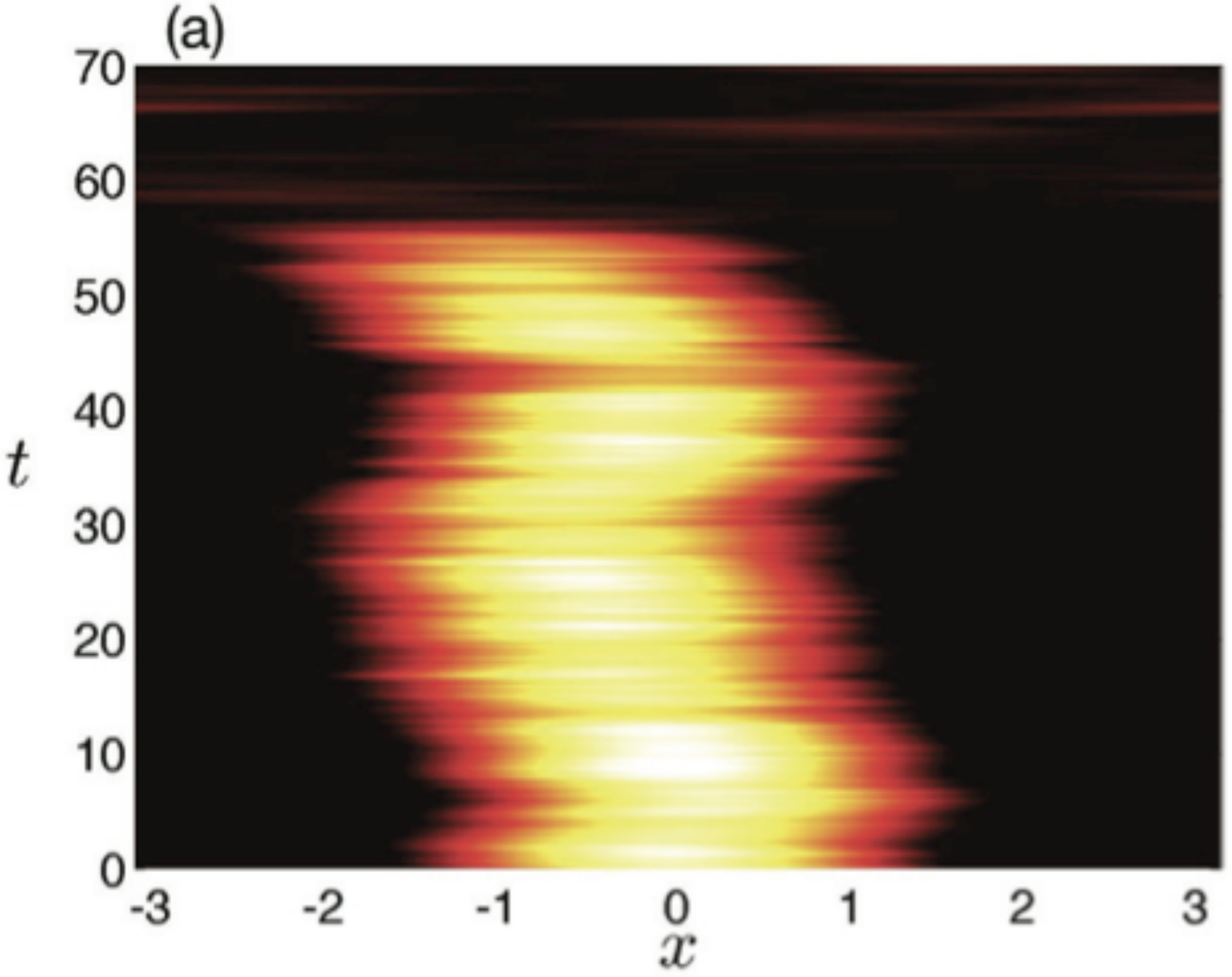
- do not
  - consider single neuron activity
  - consider single dendritic branches

recent extensions:

Effects of additive noise

Kilpatrick and Ermentrout, SIAM J. Appl. Dyn. Systems (2013):

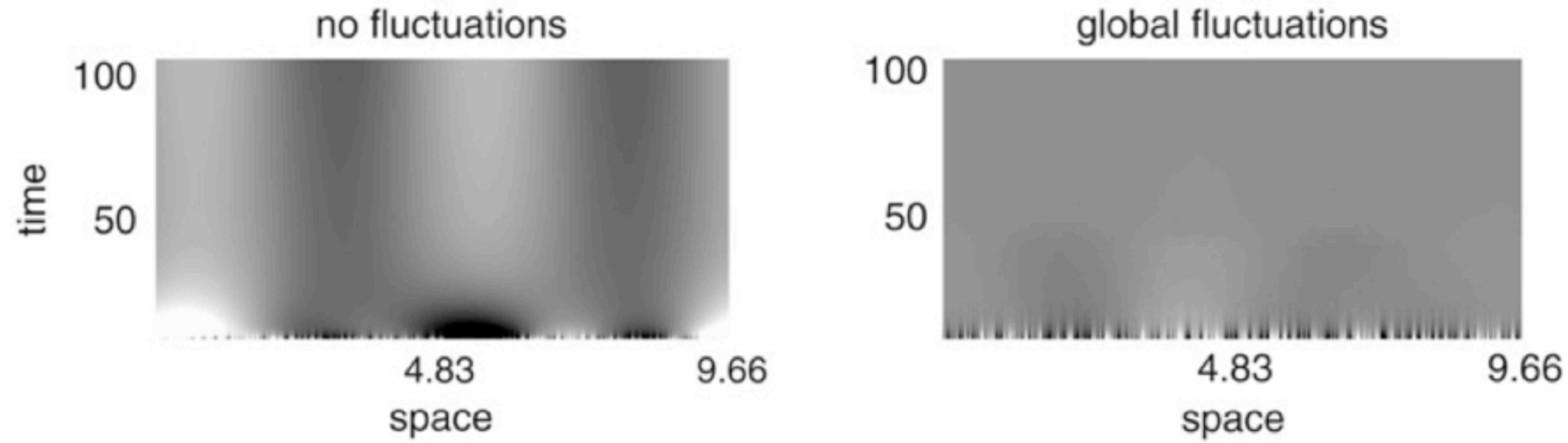
$$dV(x,t) = \left(-V(x,t) + \int_{-\pi}^{\pi} K(x-y) S\left[V(y,t)\right] dy + I(x) \right) dt + \sqrt{\epsilon} dW(x,t)$$



extinction of bump by noise

Hutt et al., Physica D (2008):

$$dV(x,t) = \left(-V(x,t) + \int_{-\infty}^{\infty} K(x-y) S\left[V(y,t)\right] dy + I_0 \right) dt + \kappa dW(t)$$



extinction of spatial pattern by noise

related workshops at CNS:

Wednesday:

Network and Neuroscience: structure and dynamics

Metastable dynamics of neural ensembles

Advances in neural mass modeling

Thursday:

Network and Neuroscience: structure and dynamics

Recent advances in experimental and computational characterization of neural assemblies

Modeling general anaesthesia: from theory to experiment

Validating neuro-computational models of neurological and psychiatric disorders

Full brain network dynamics