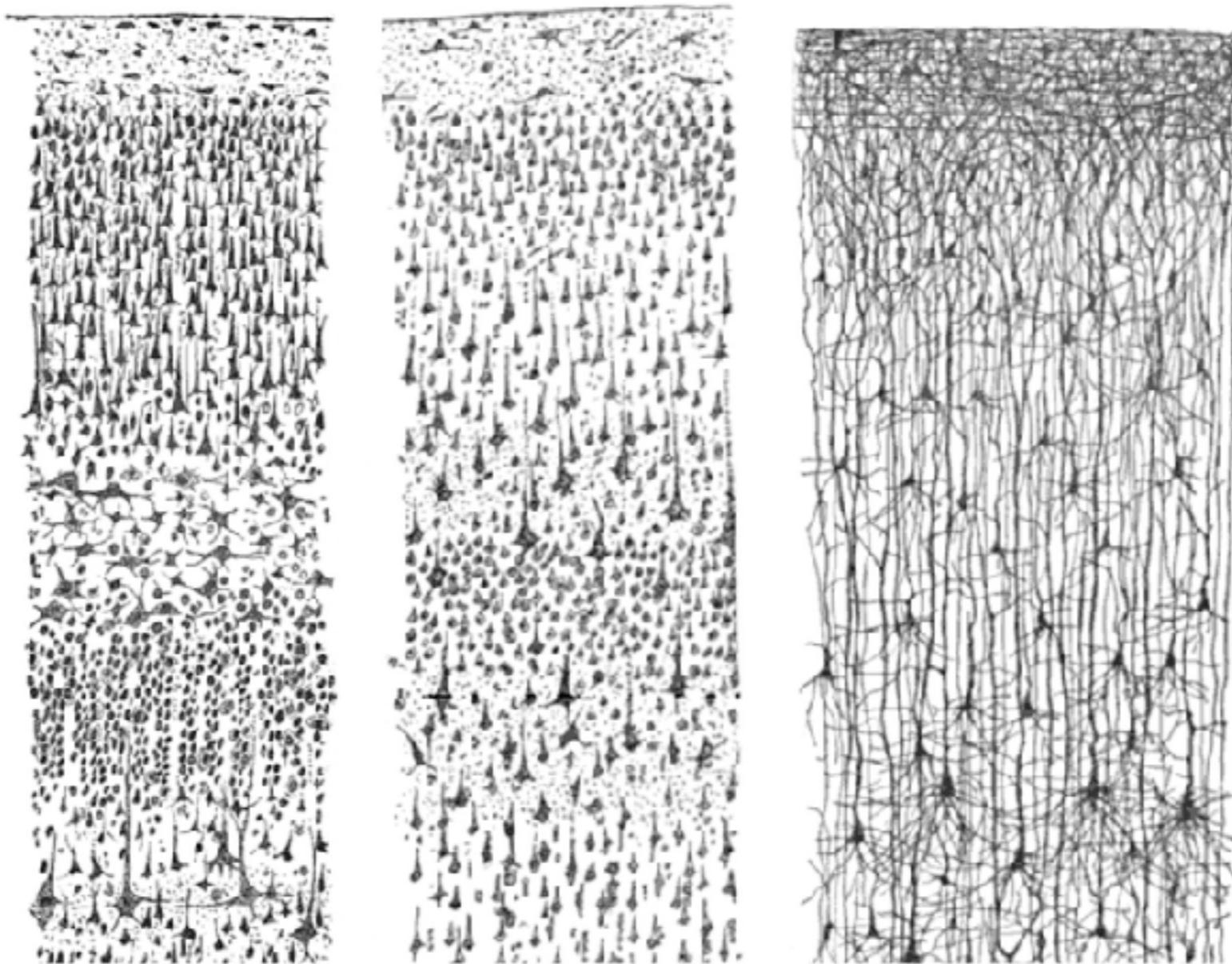


Lecture 9: Biophysical neuron models & the LIF

What is the brain made of exactly ?



Joseph von Gerlach (1871), Camillo Golgi

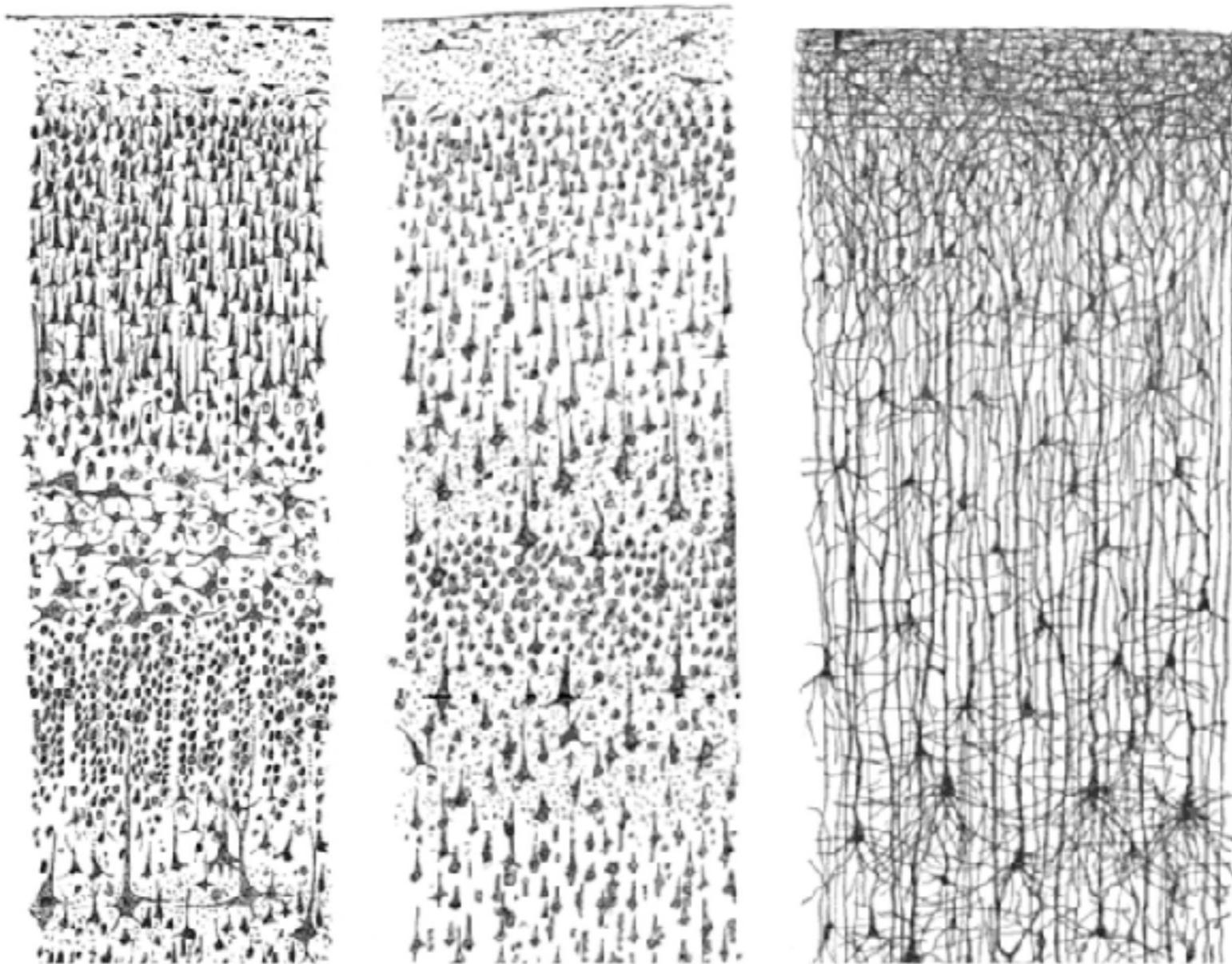
→ reticular theory

Santiago Ramon y Cajal, Wilhelm Waldeyer

→ neuronal theory

prix Nobel 1906

What is the brain made of exactly ?



Joseph von Gerlach (1871), Camillo Golgi



~~reticular theory~~

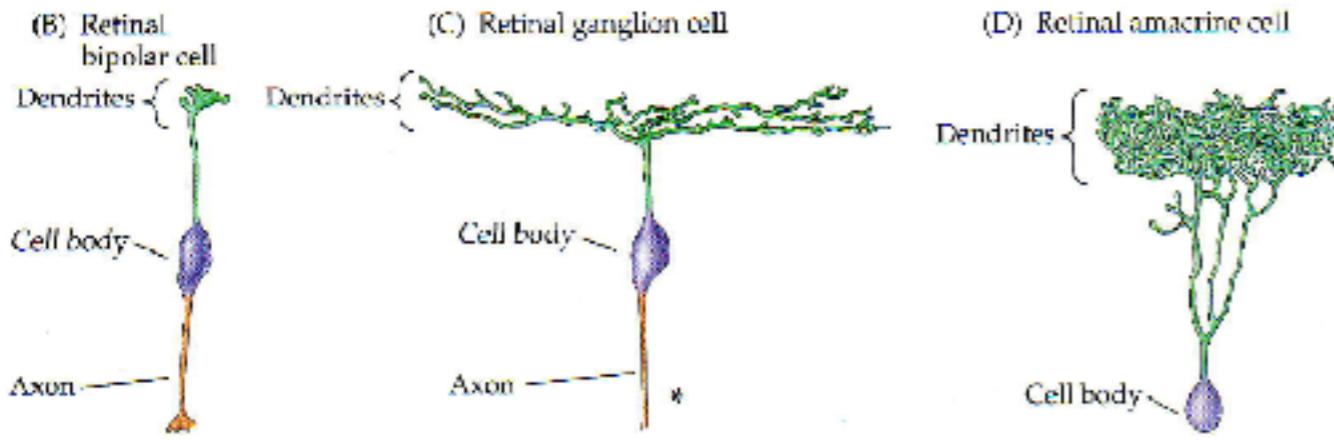
Santiago Ramon y Cajal, Wilhelm Waldeyer



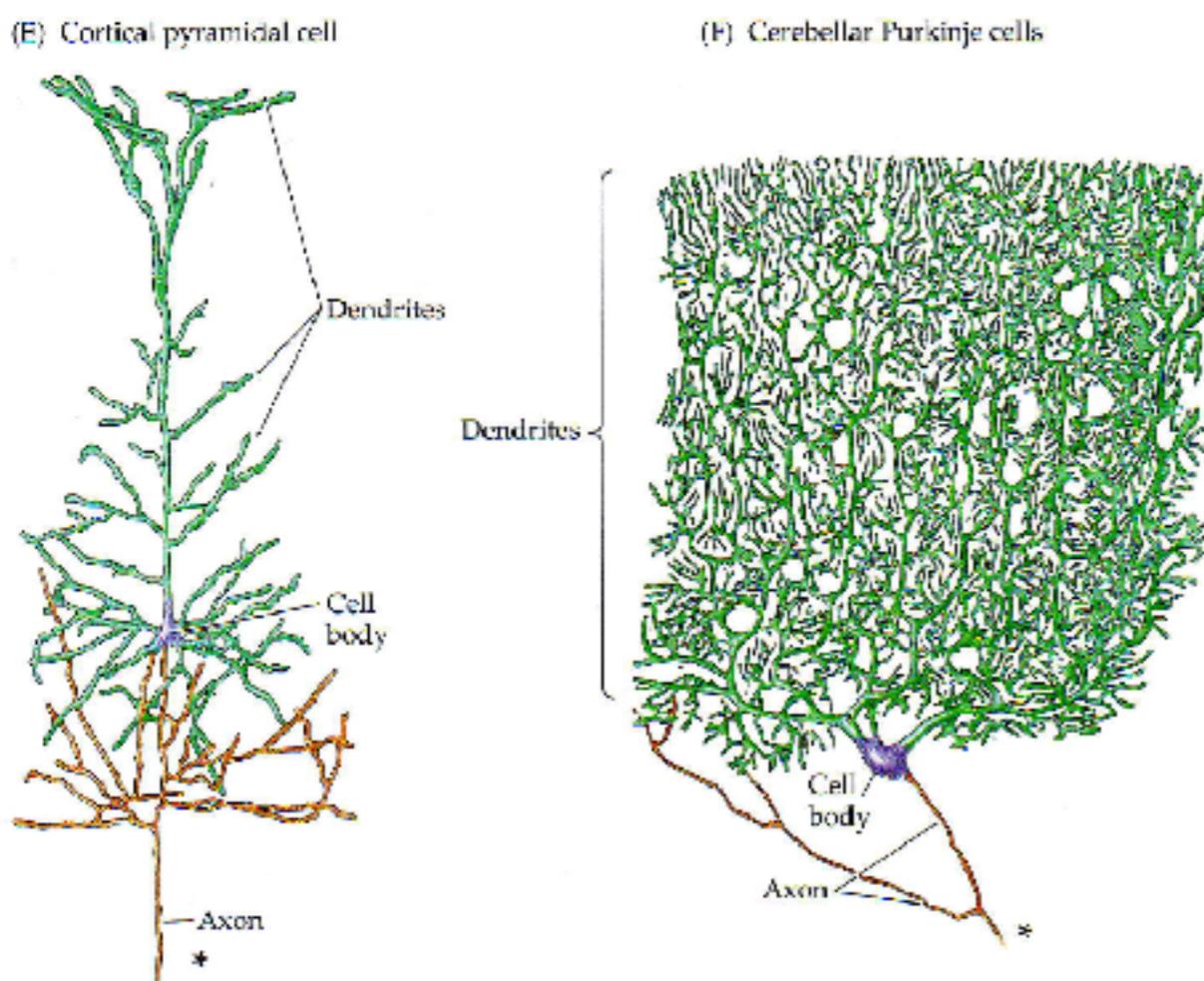
neuronal theory

prix Nobel 1906

Neurons = basic units of computation



dendrites

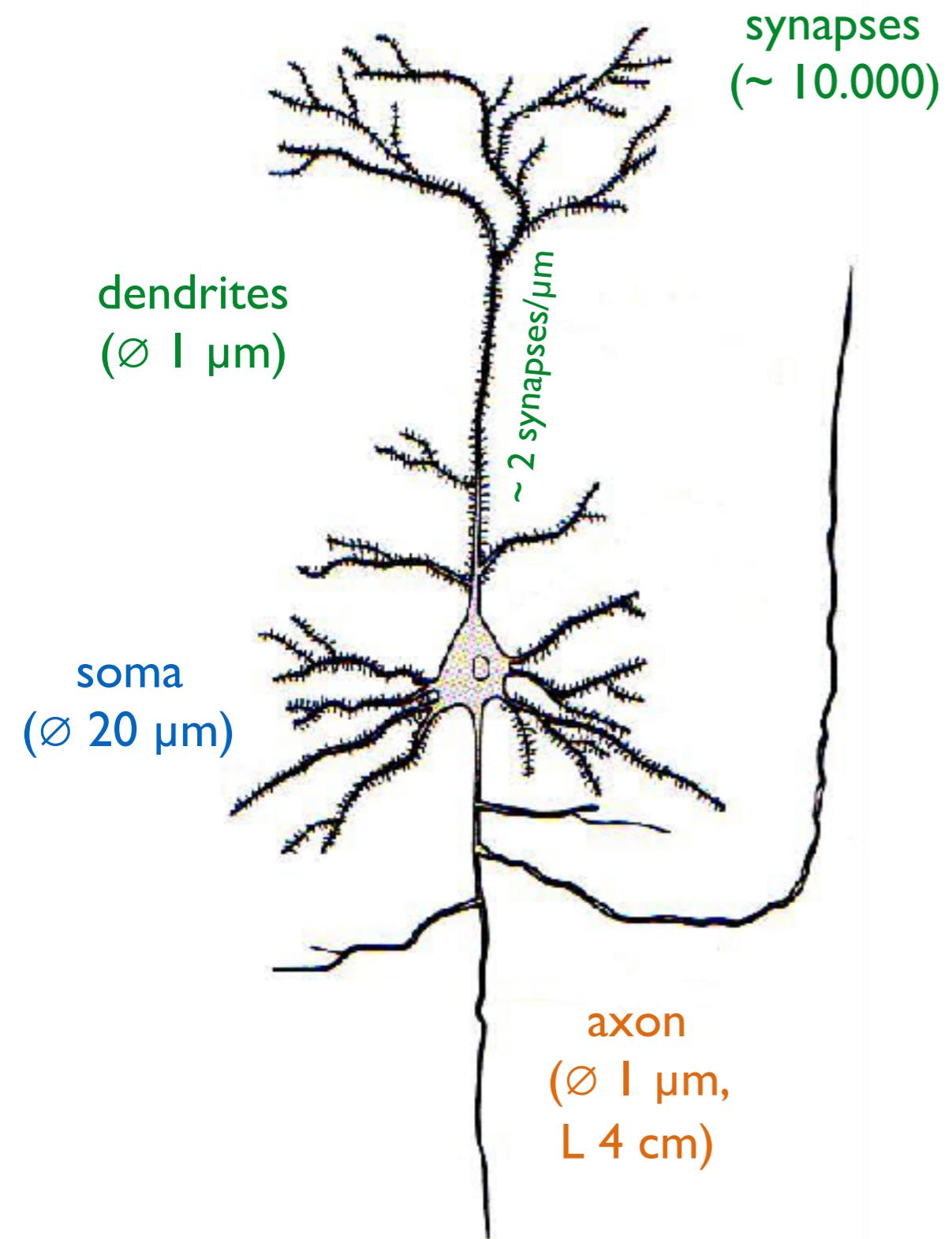


soma

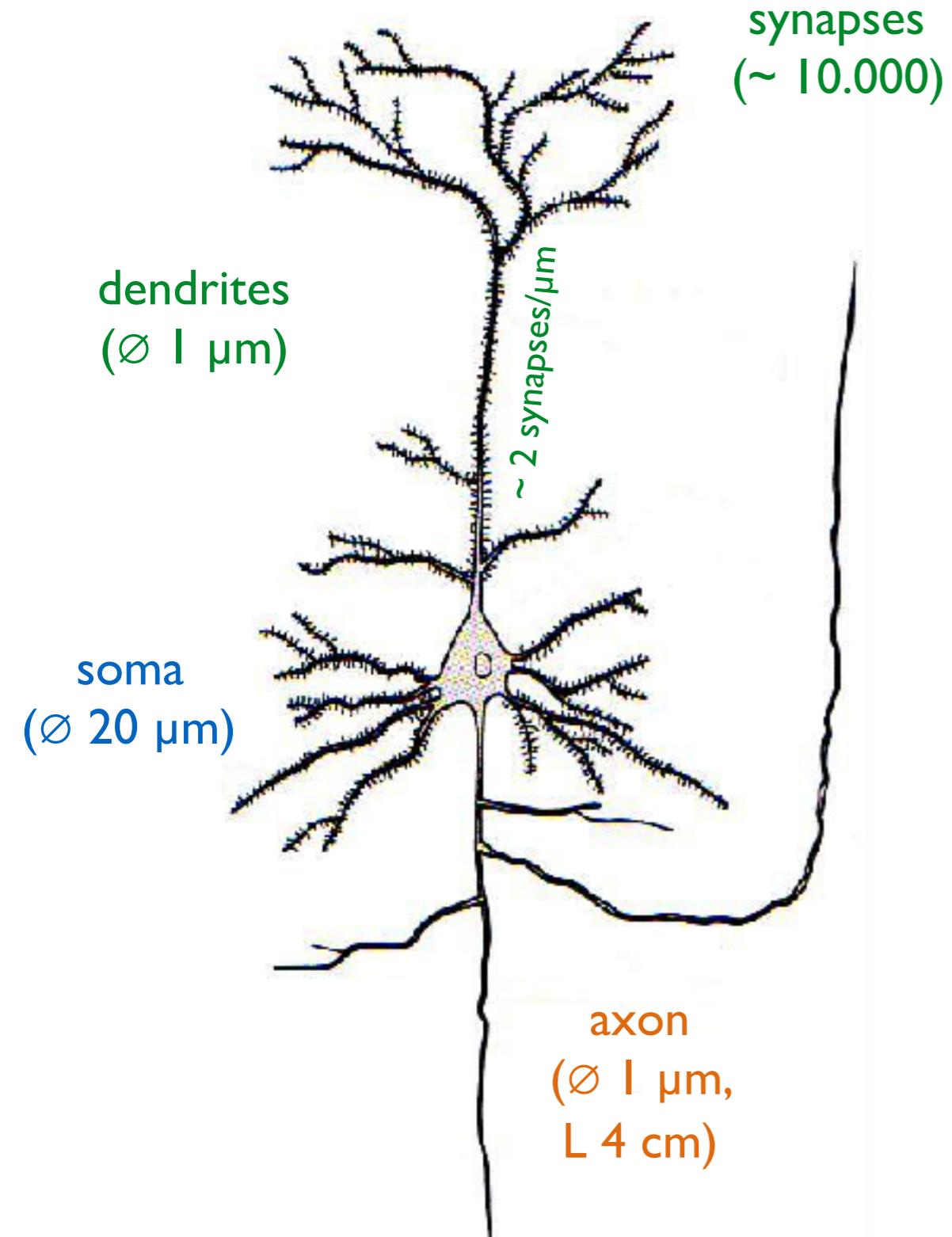
axon

information flux

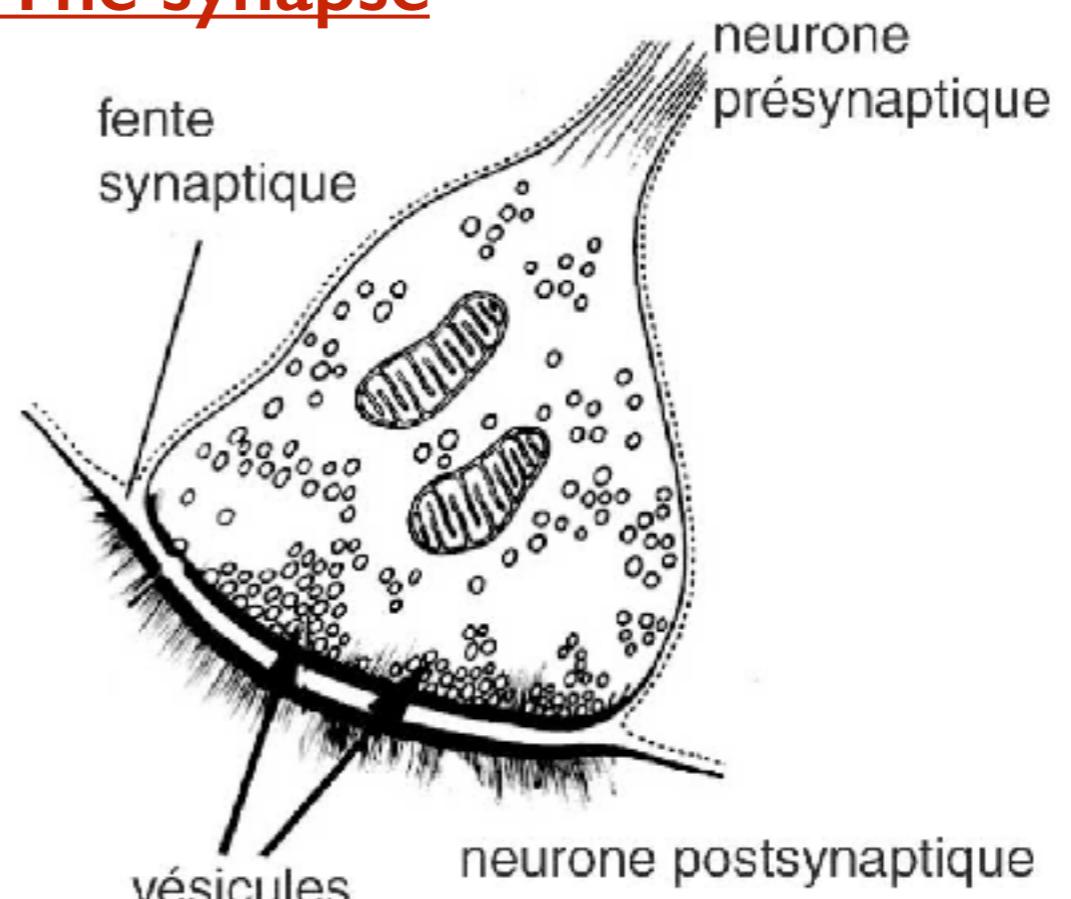
A typical cortical neuron



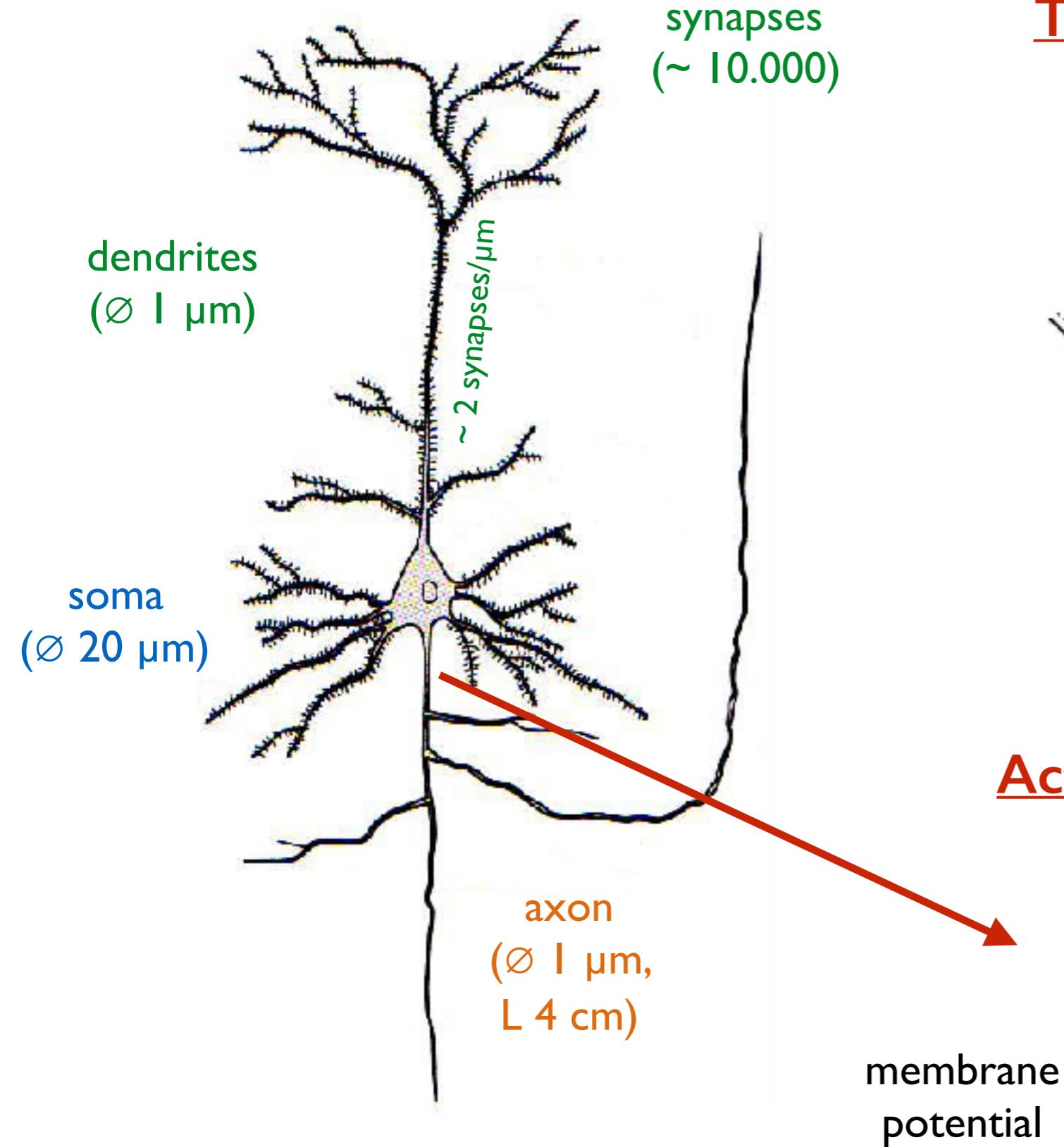
A typical cortical neuron



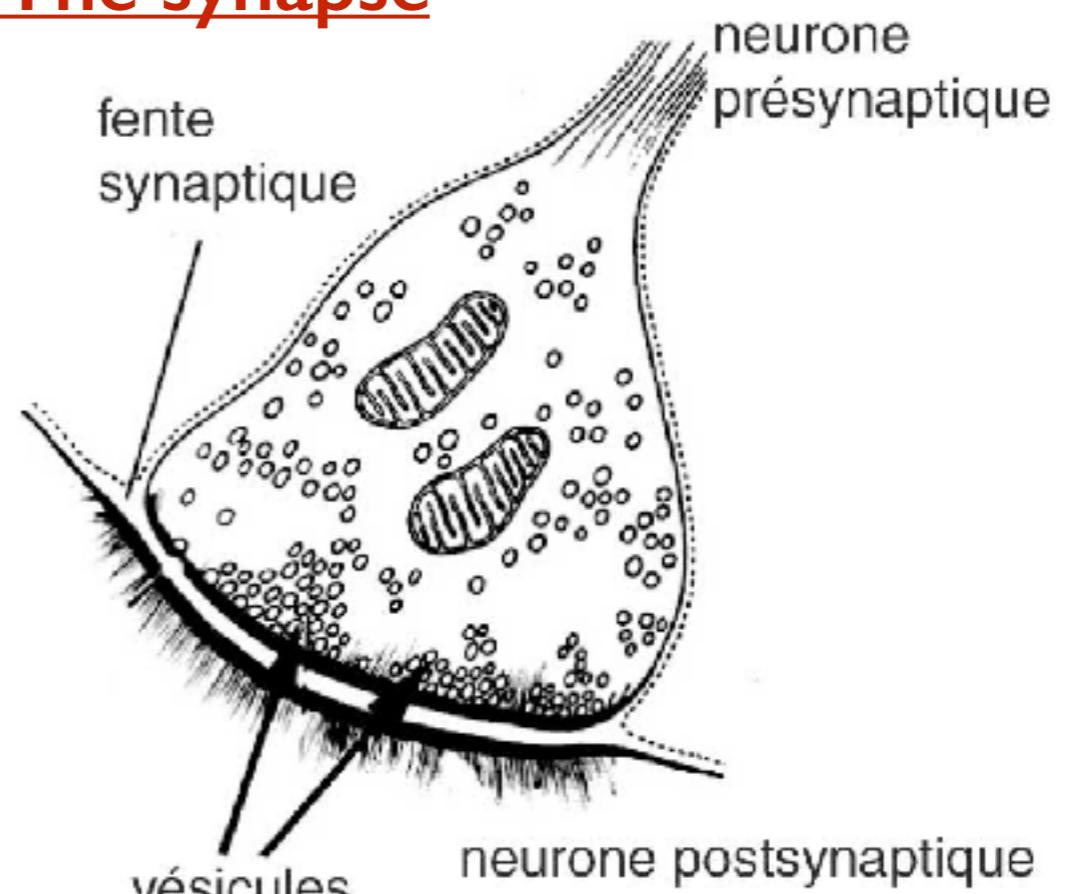
The synapse



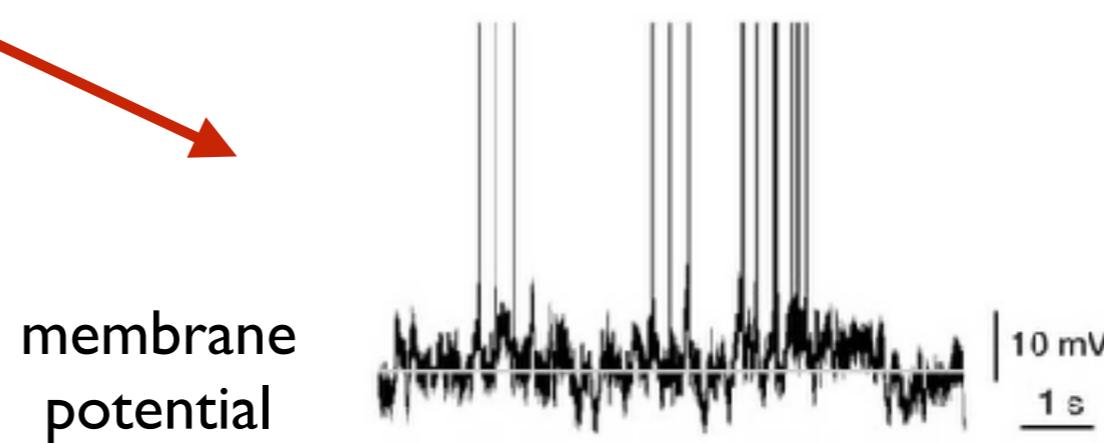
A typical cortical neuron



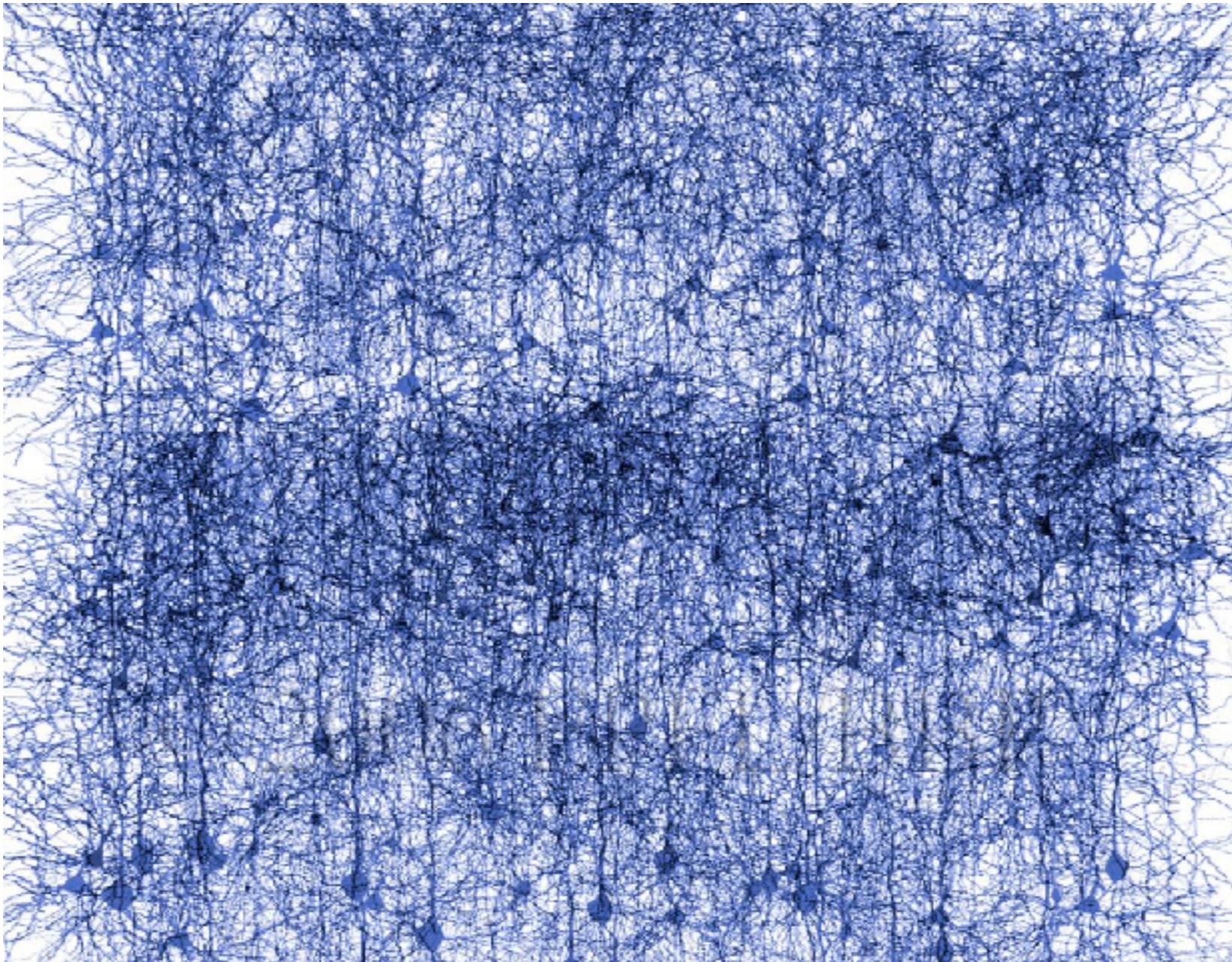
The synapse



Action potentials (spikes)

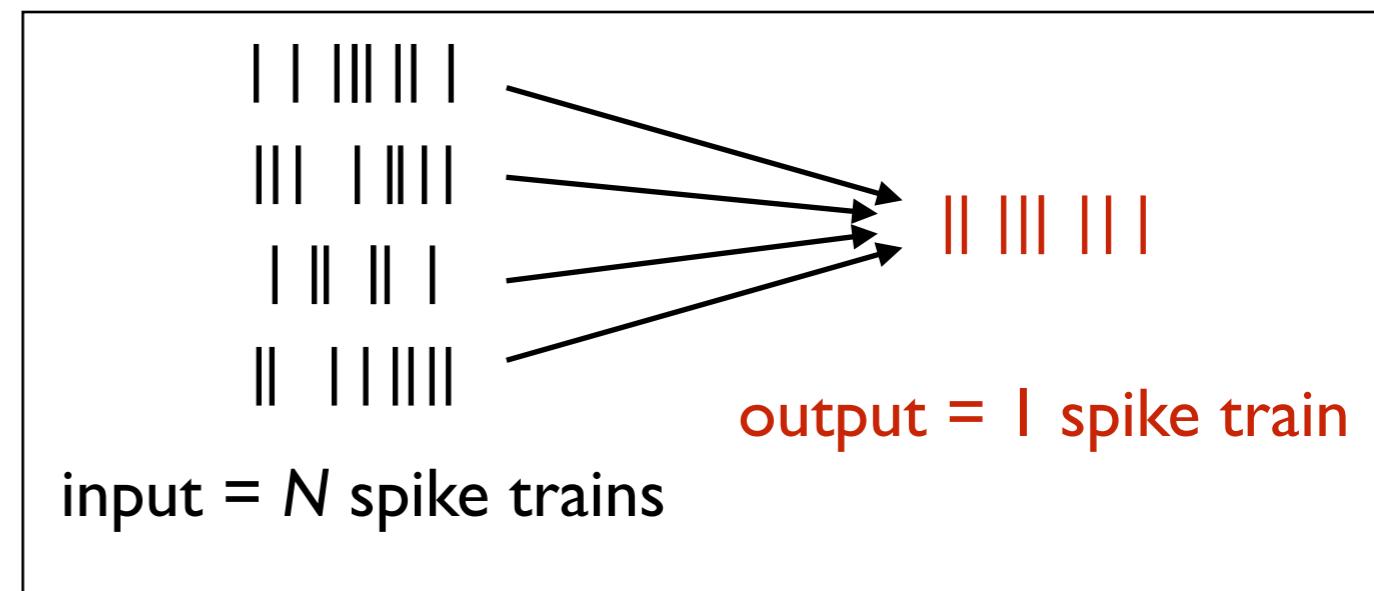
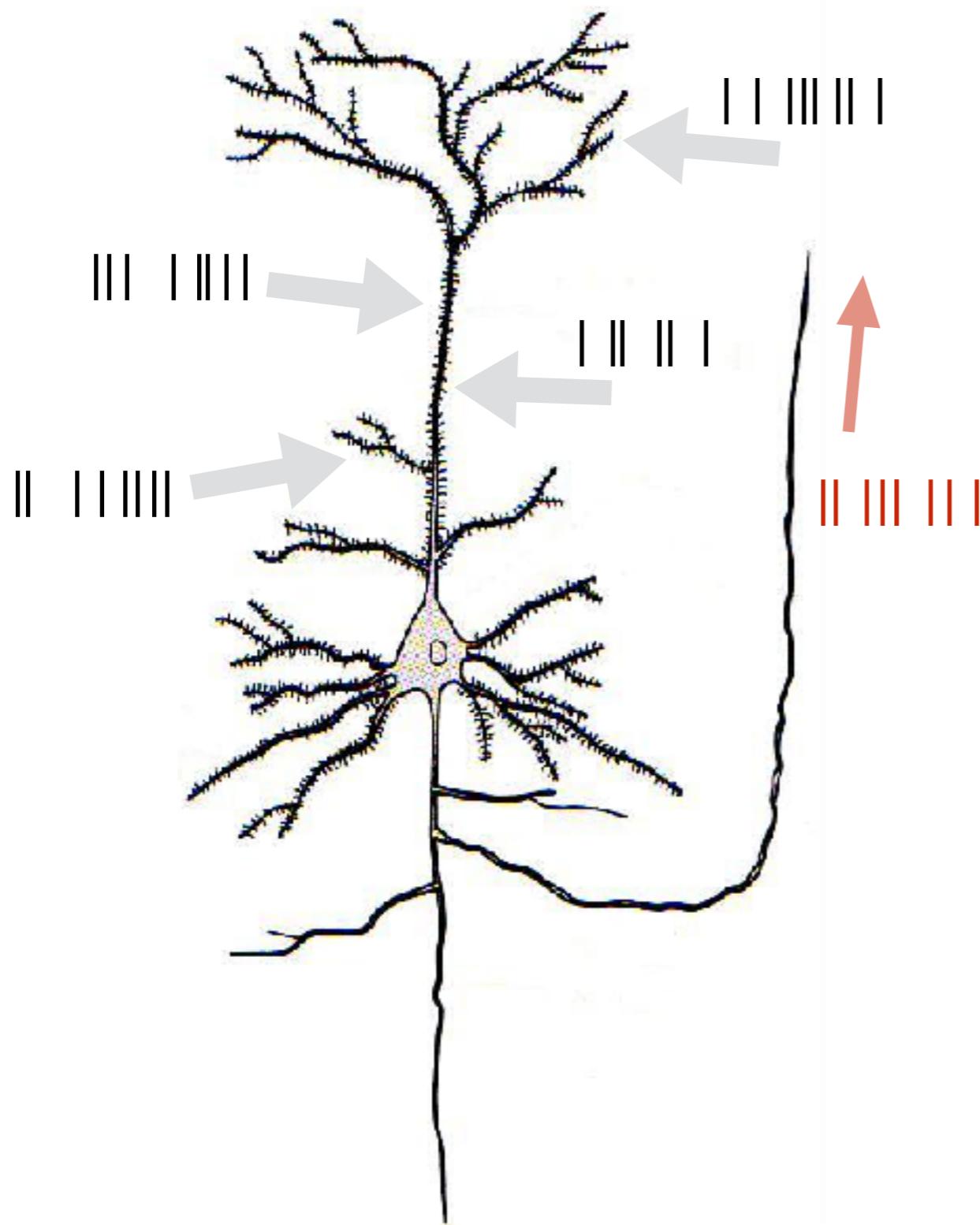


Neurons combine to form networks

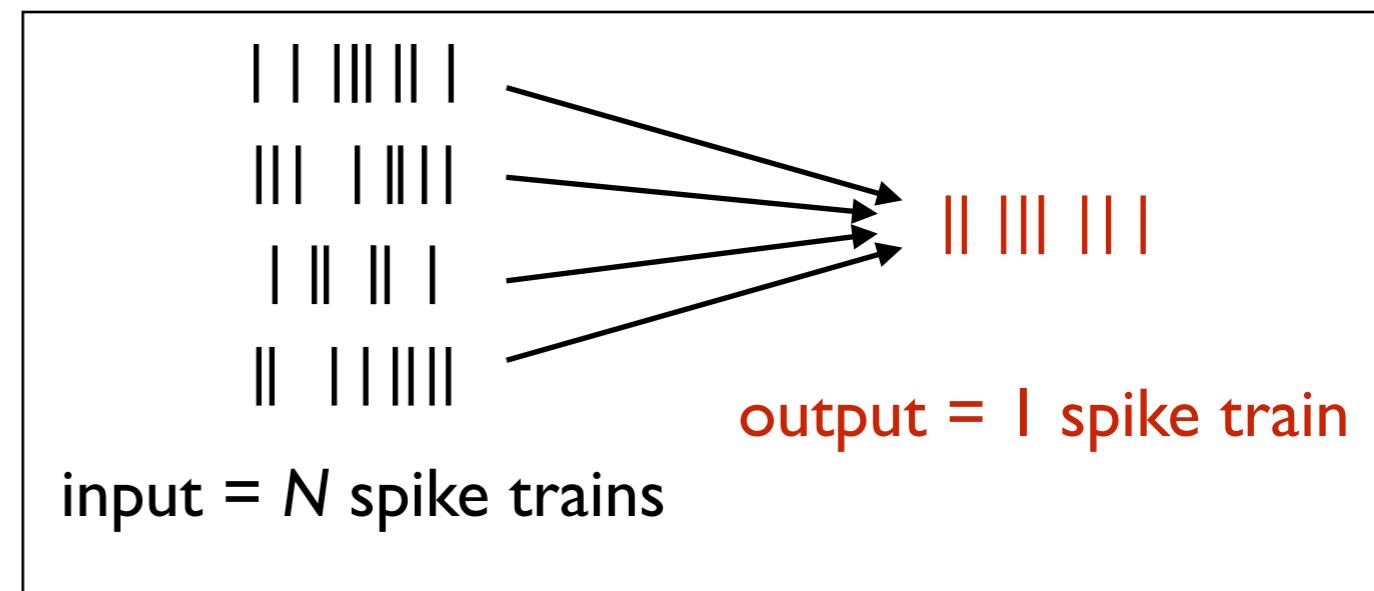
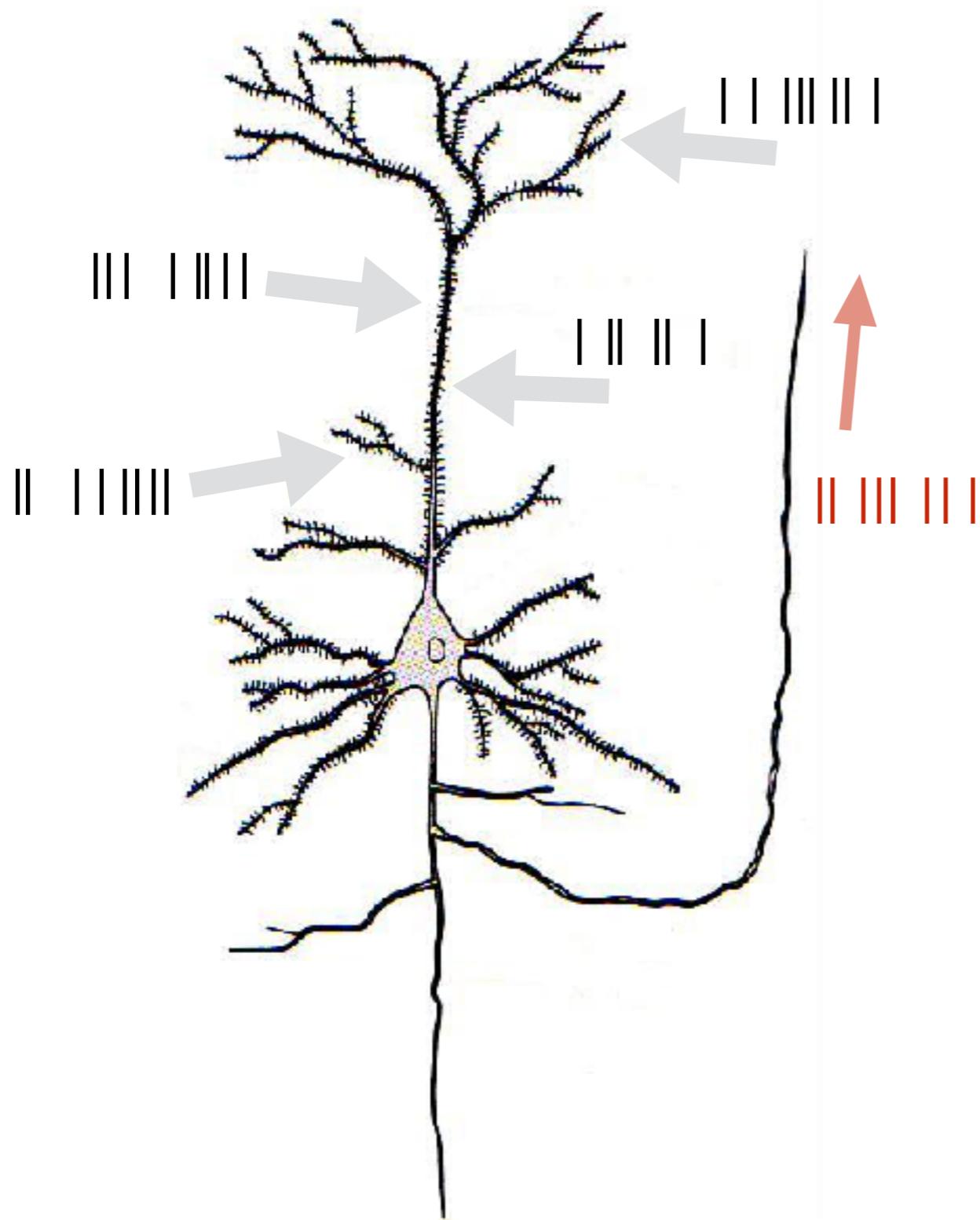


The human brain : 10^{11} neurons connected by 10^{15} synapses

Neuronal integration



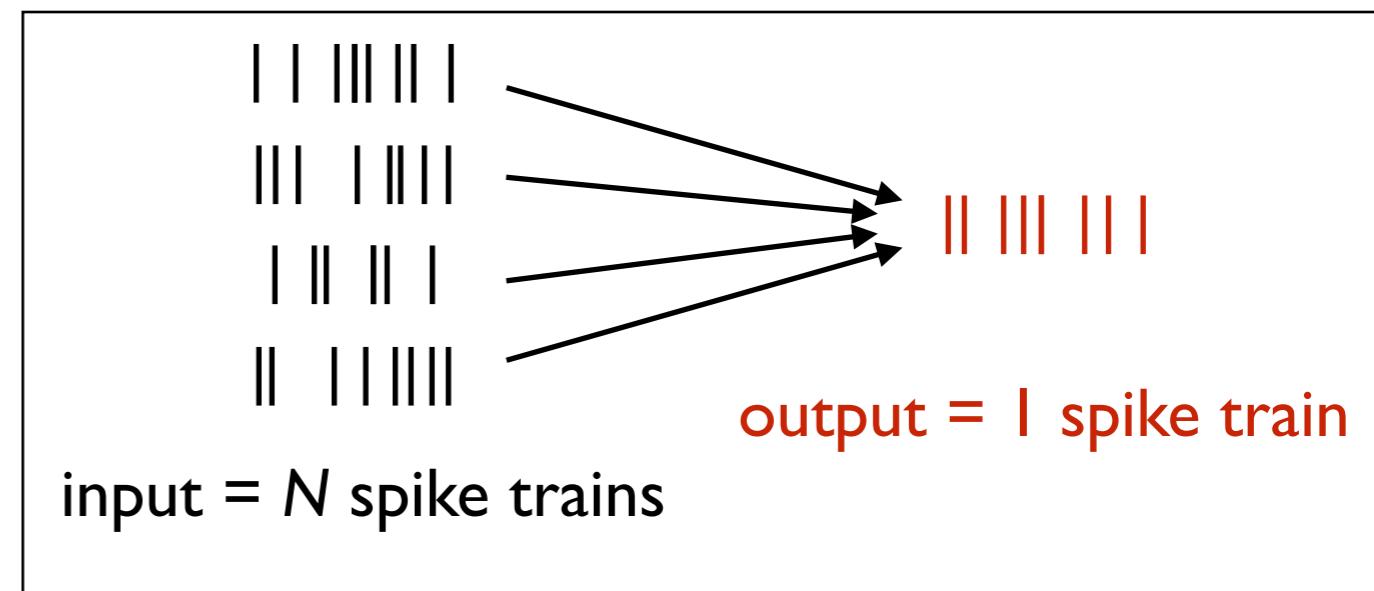
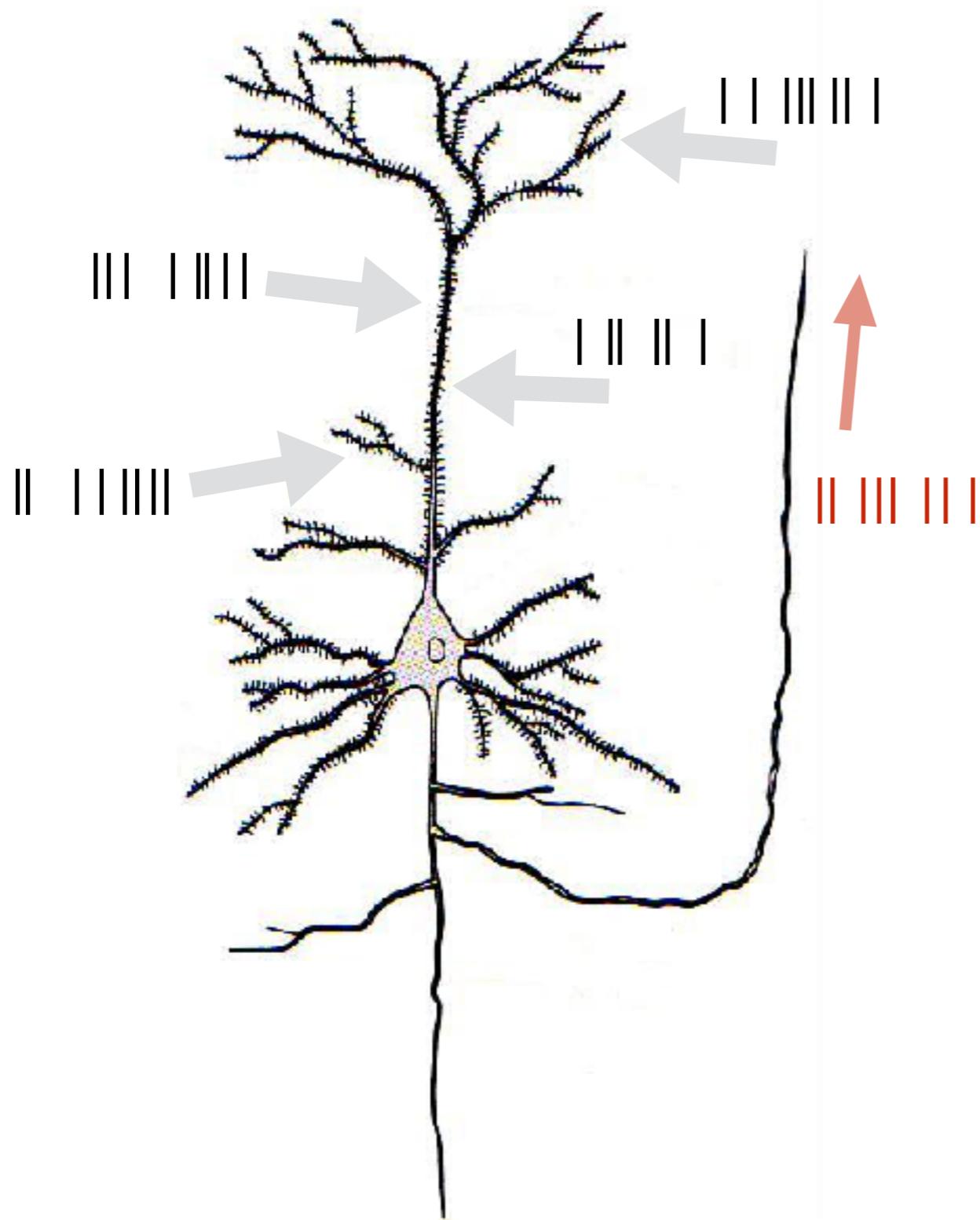
Neuronal integration



Synaptic current after a spike:

$$I_{\text{syn}} = g_{\max}(E_{\text{syn}} - V)\alpha(t) \simeq w_{ij}\alpha(t)$$

Neuronal integration

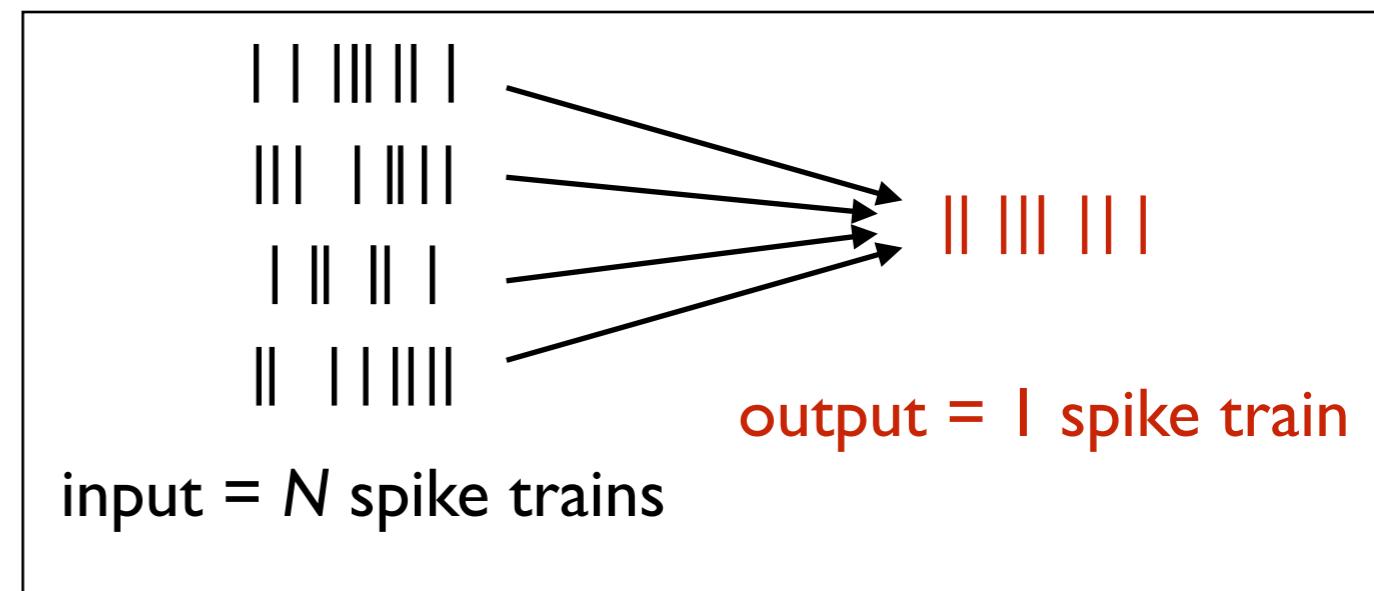
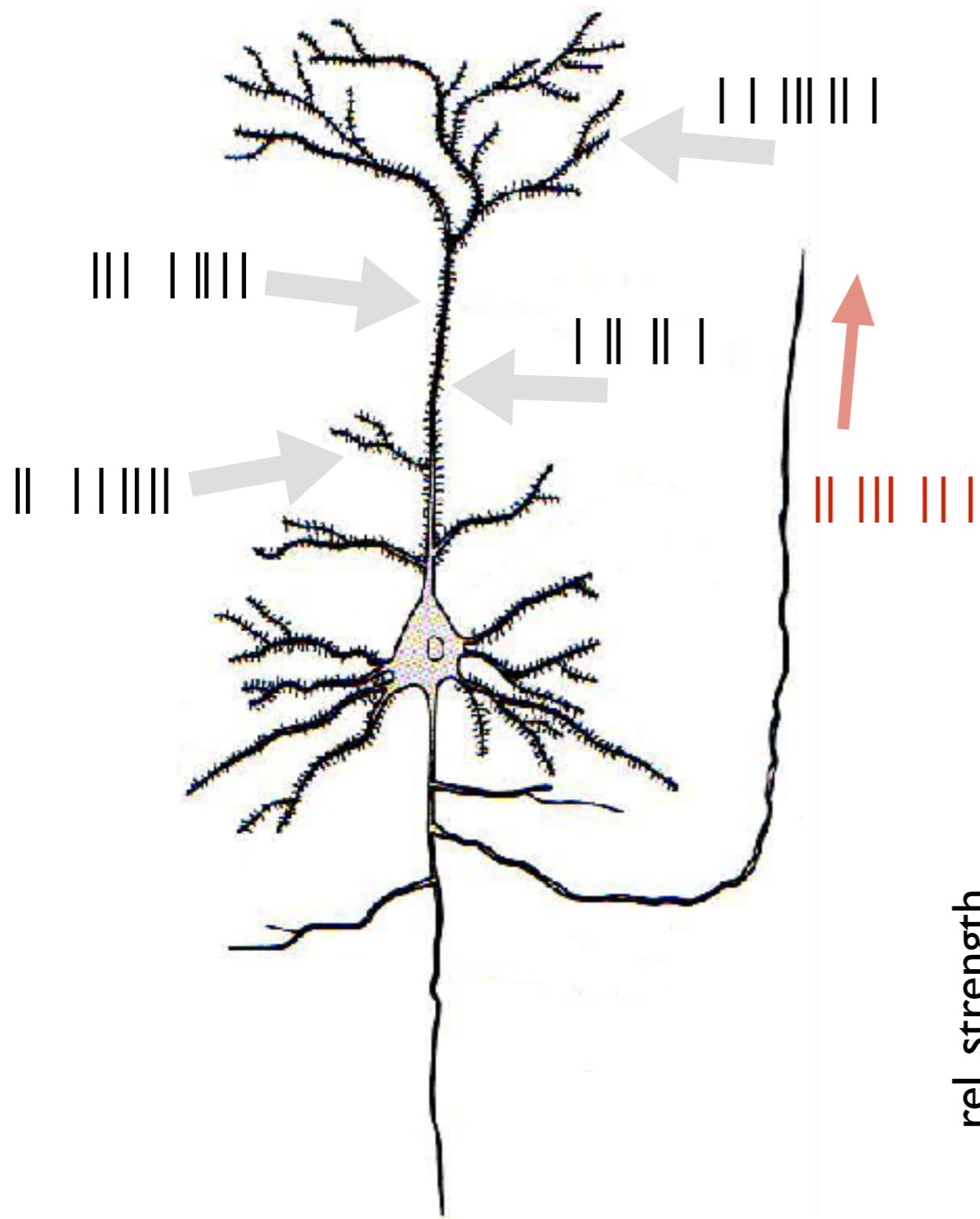


Synaptic current after a spike:

$$I_{\text{syn}} = g_{\max}(E_{\text{syn}} - V)\alpha(t) \simeq w_{ij}\alpha(t)$$

↑
effective syn. weight $j \rightarrow i$

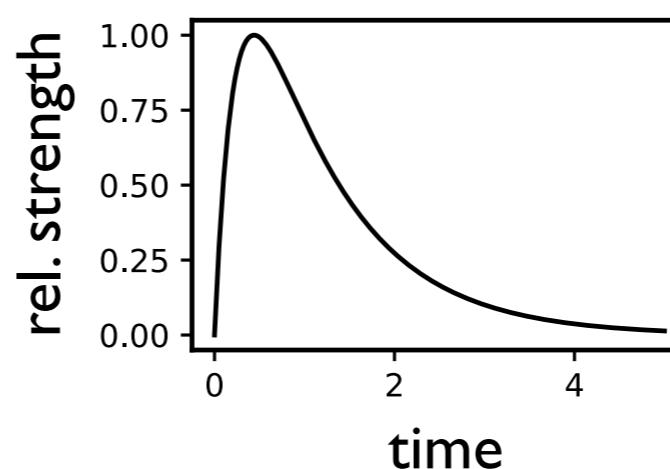
Neuronal integration



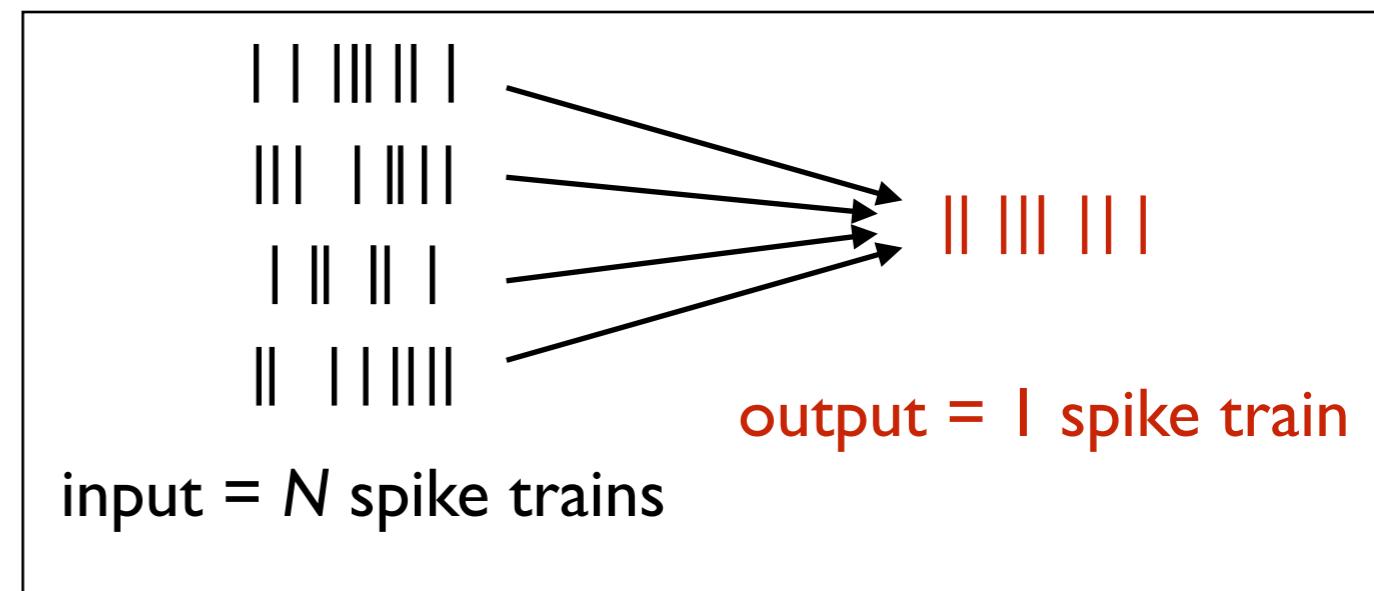
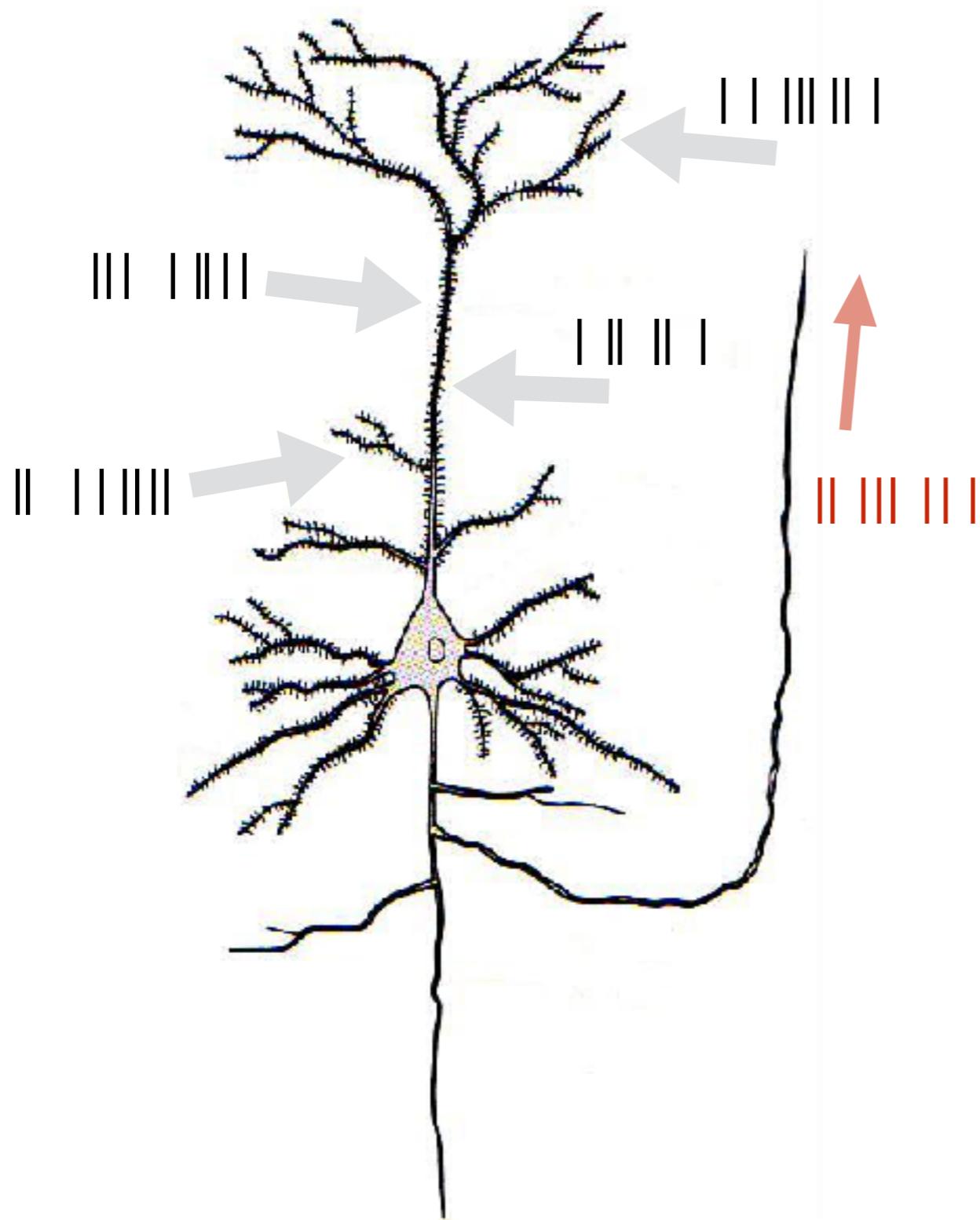
Synaptic current after a spike:

$$I_{\text{syn}} = g_{\max}(E_{\text{syn}} - V)\alpha(t) \simeq w_{ij}\alpha(t)$$

↑
effective syn. weight $j \rightarrow i$



Neuronal integration

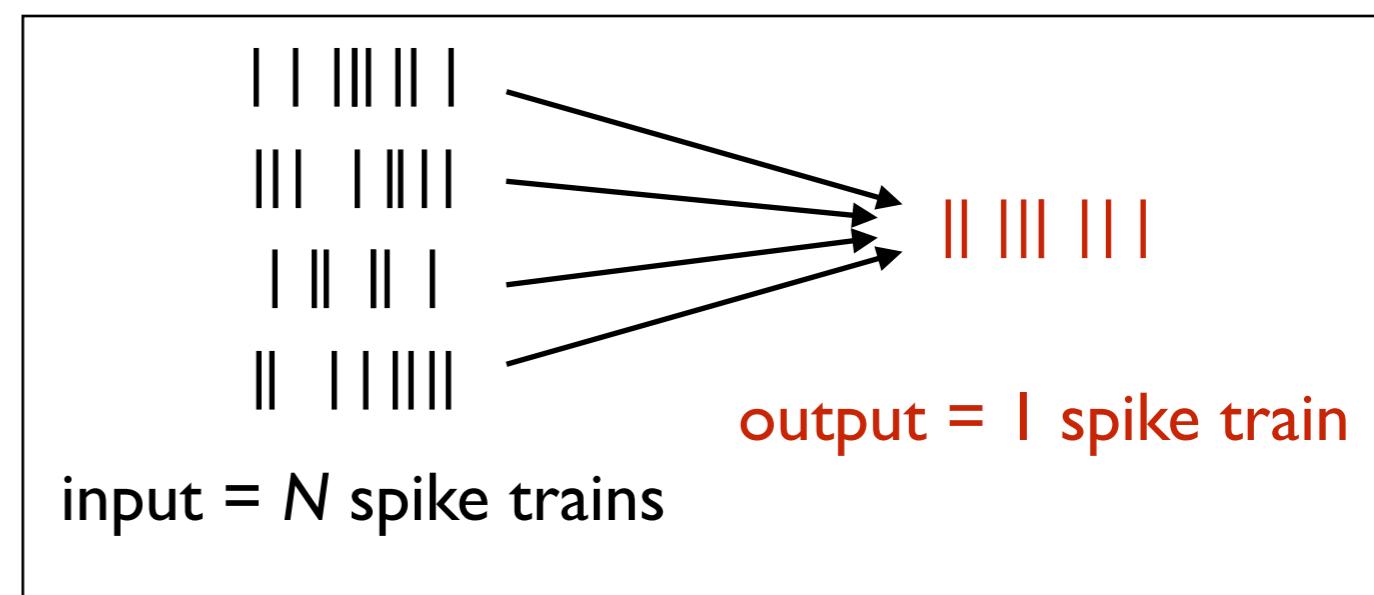
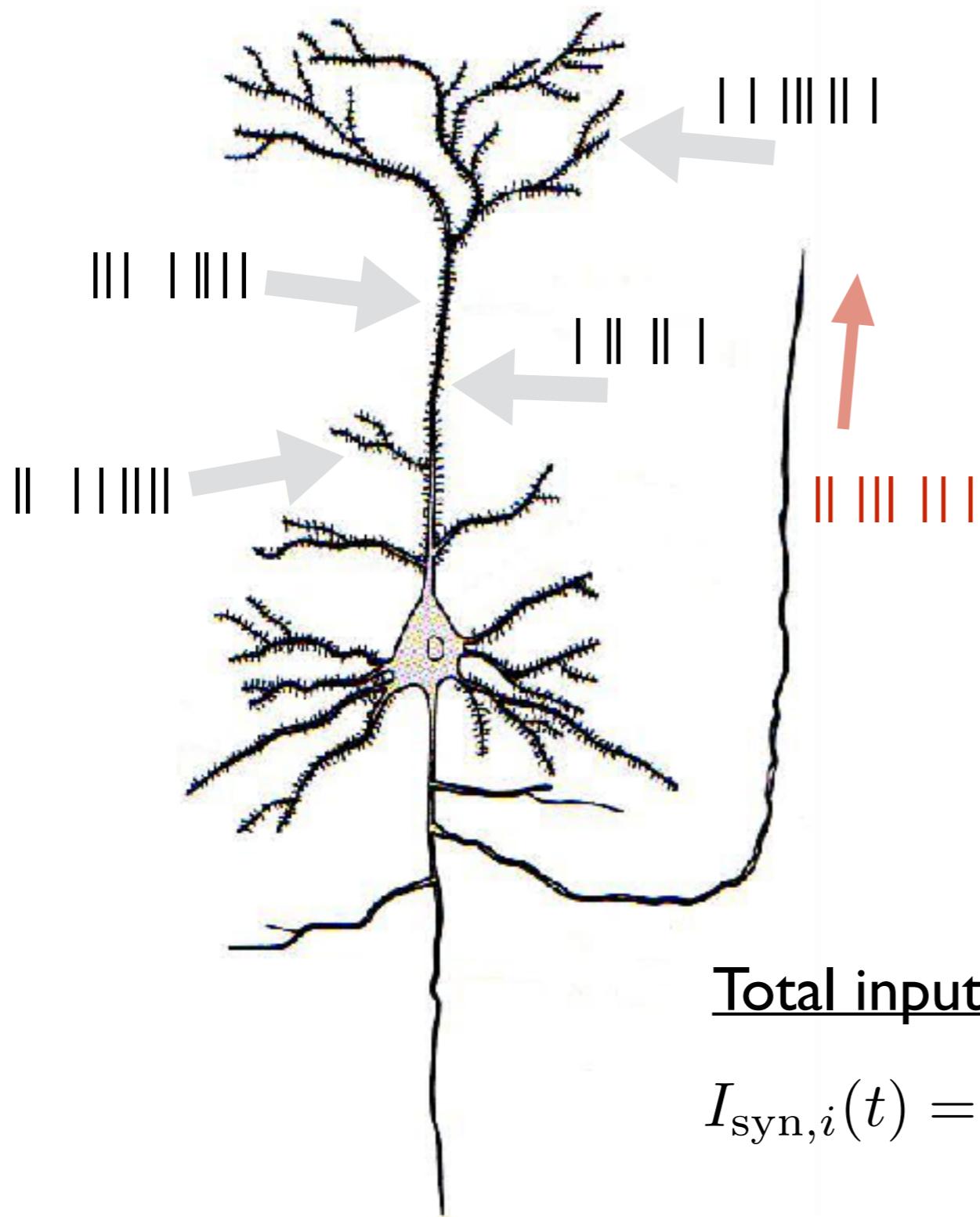


Synaptic current after a spike:

$$I_{\text{syn}} = g_{\max}(E_{\text{syn}} - V)\alpha(t) \simeq w_{ij}\alpha(t)$$

↑
effective syn. weight $j \rightarrow i$

Neuronal integration



Synaptic current after a spike:

$$I_{\text{syn}} = g_{\max}(E_{\text{syn}} - V)\alpha(t) \simeq w_{ij}\alpha(t)$$

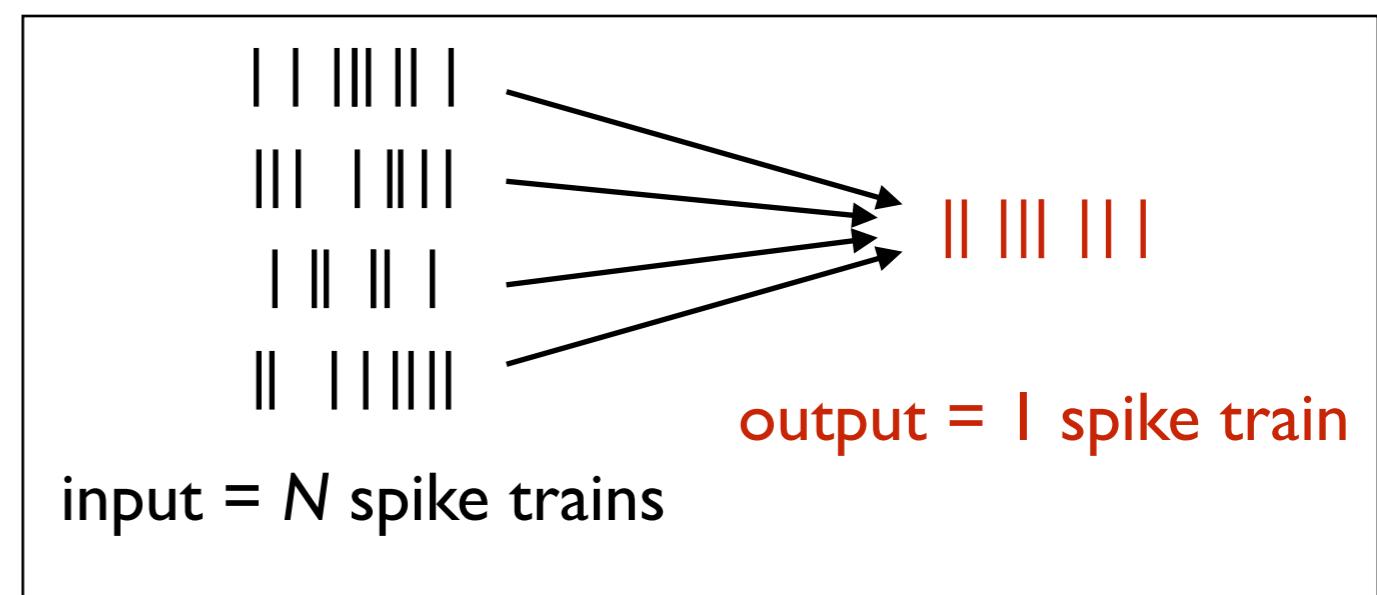
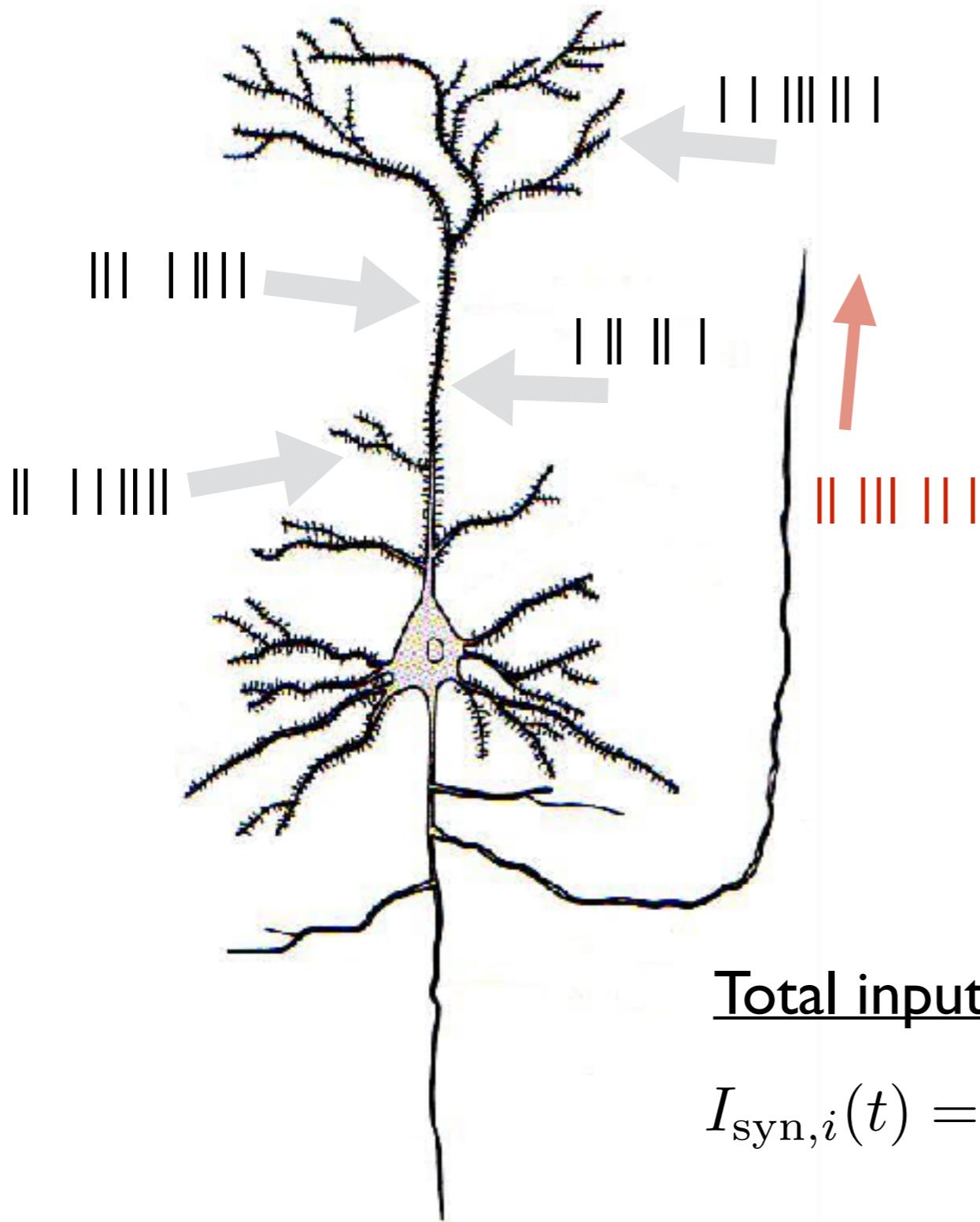
↑
effective syn. weight $j \rightarrow i$

Total input synaptic current for neuron i :

$$I_{\text{syn},i}(t) = \sum_j w_{ij} \sum_k \alpha(t - t_j^{(k)})$$

← time of k -th spike
of neuron j

Neuronal integration



Synaptic current after a spike:

$$I_{\text{syn}} = g_{\max}(E_{\text{syn}} - V)\alpha(t) \simeq w_{ij}\alpha(t)$$

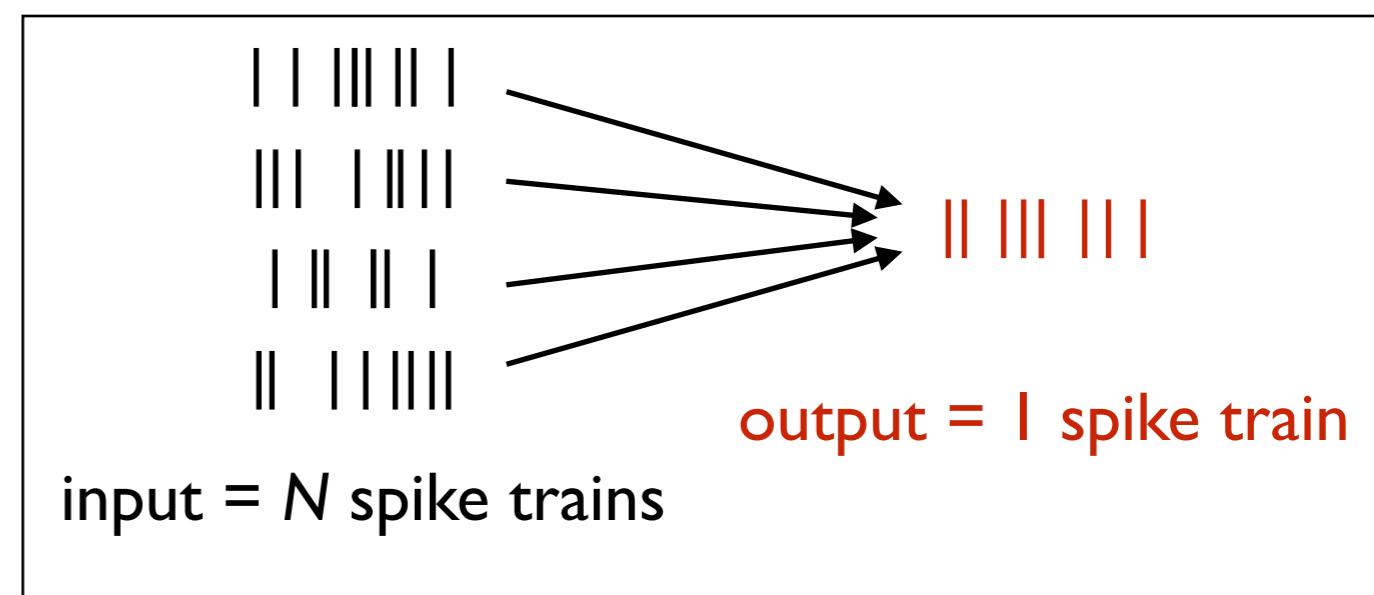
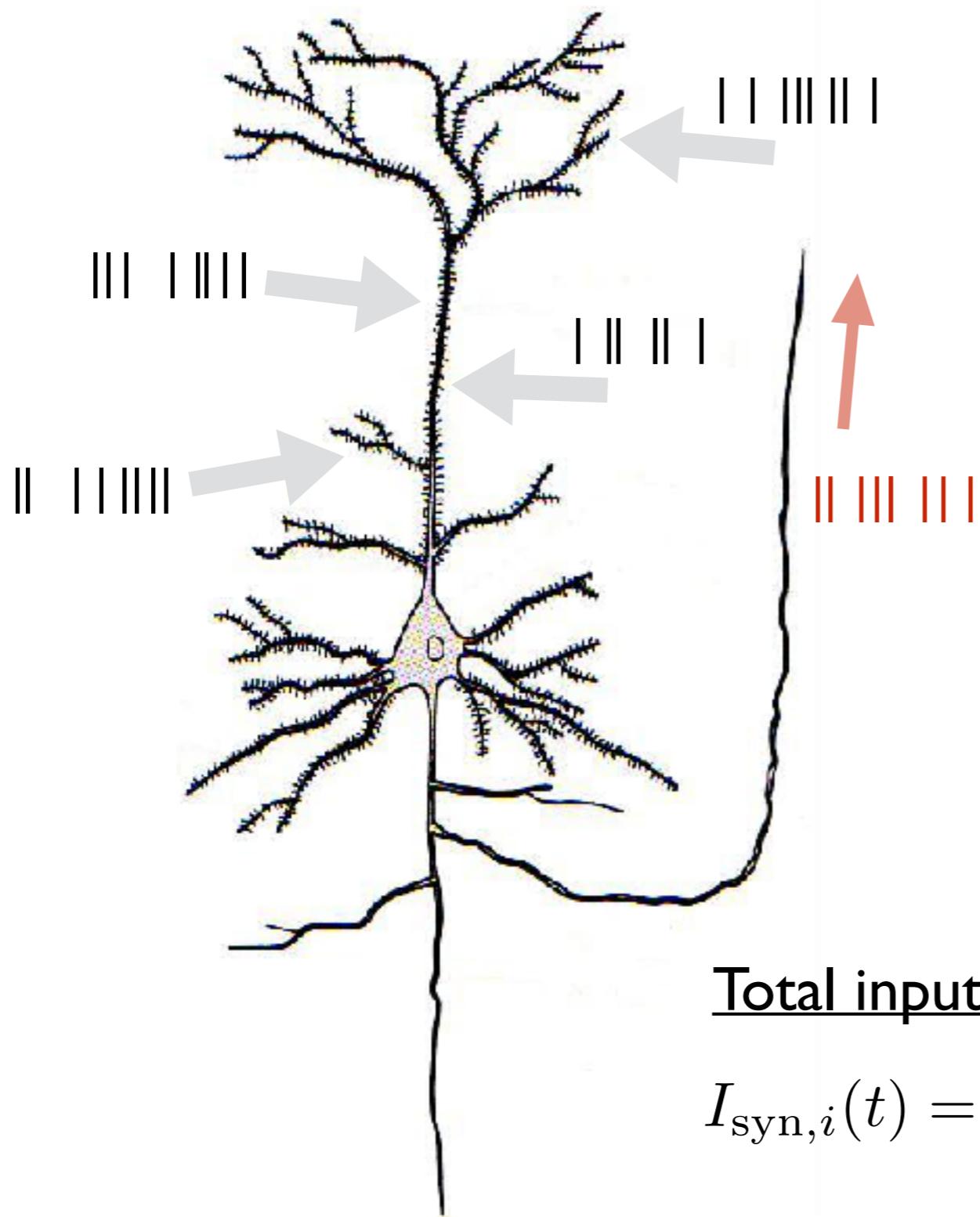
↑
effective syn. weight $j \rightarrow i$

Total input synaptic current for neuron i :

$$I_{\text{syn},i}(t) = \sum_j w_{ij} \sum_k \alpha(t - t_j^{(k)})$$

presynaptic neurons ↙
time of k -th spike
of neuron j

Neuronal integration



Synaptic current after a spike:

$$I_{\text{syn}} = g_{\max}(E_{\text{syn}} - V)\alpha(t) \simeq w_{ij}\alpha(t)$$

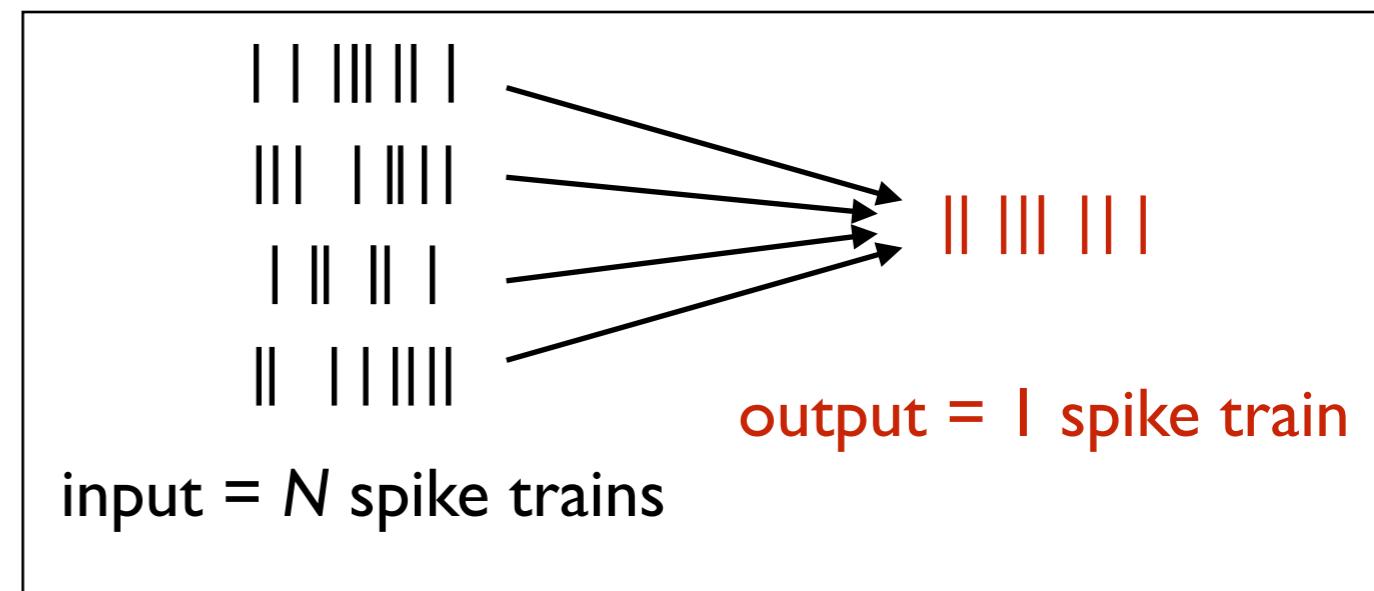
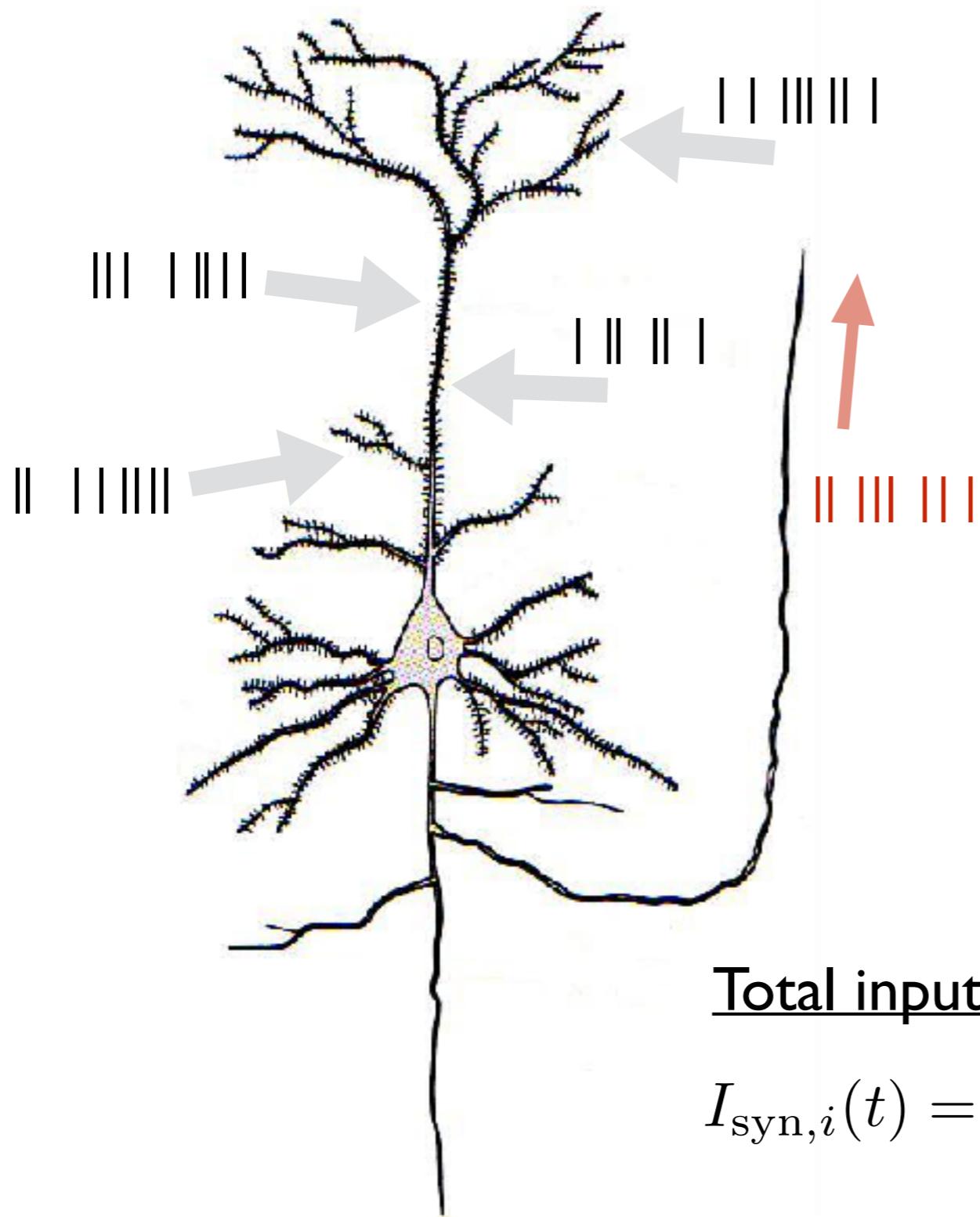
↑
effective syn. weight $j \rightarrow i$

Total input synaptic current for neuron i :

$$I_{\text{syn},i}(t) = \sum_j w_{ij} \sum_k \alpha(t - t_j^{(k)})$$

↓
spikes
time of k -th spike
of neuron j

Neuronal integration



Synaptic current after a spike:

$$I_{\text{syn}} = g_{\max}(E_{\text{syn}} - V)\alpha(t) \simeq w_{ij}\alpha(t)$$

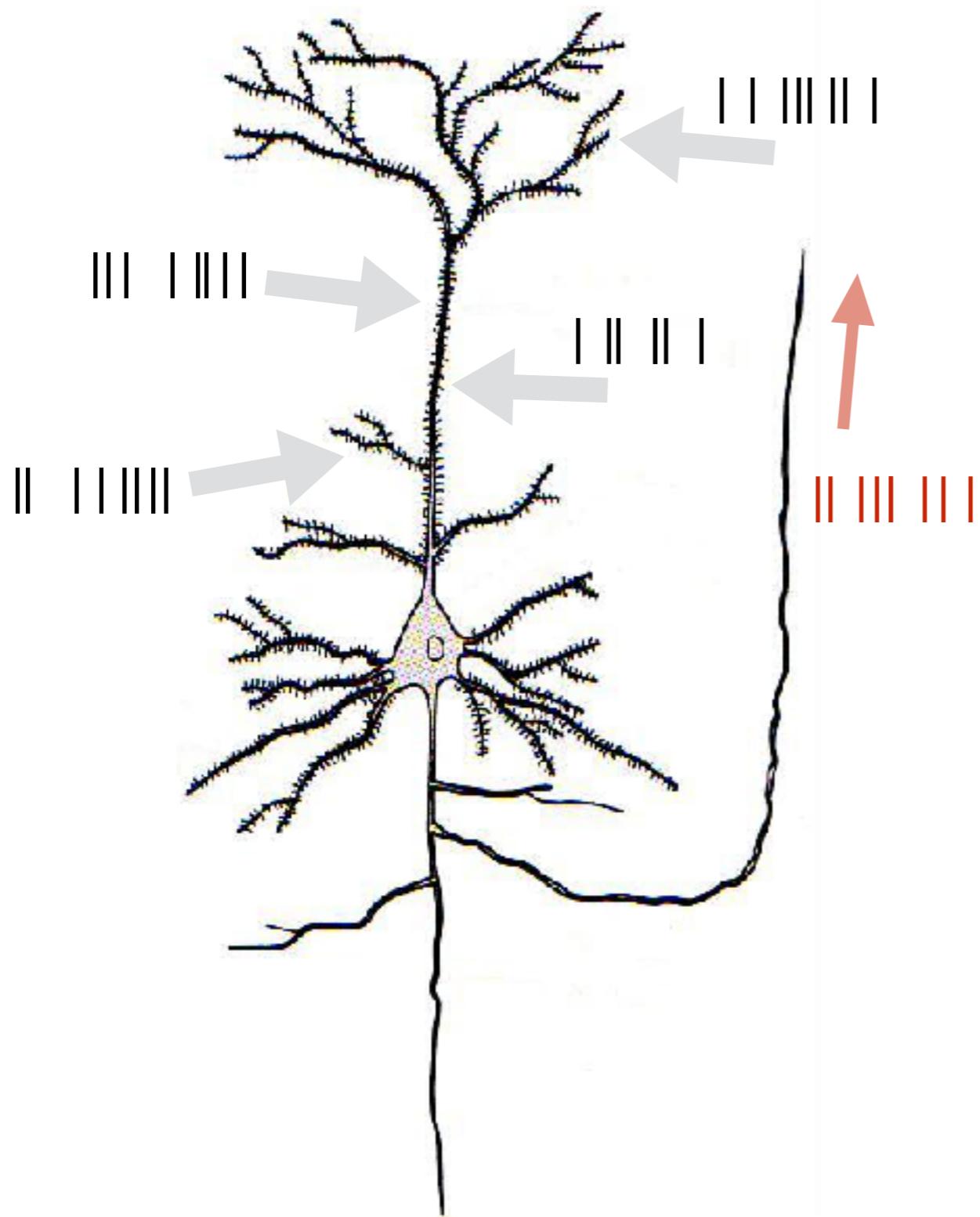
↑
effective syn. weight $j \rightarrow i$

Total input synaptic current for neuron i :

$$I_{\text{syn},i}(t) = \sum_j w_{ij} \sum_k \alpha(t - t_j^{(k)})$$

← time of k -th spike
of neuron j

Neuronal integration

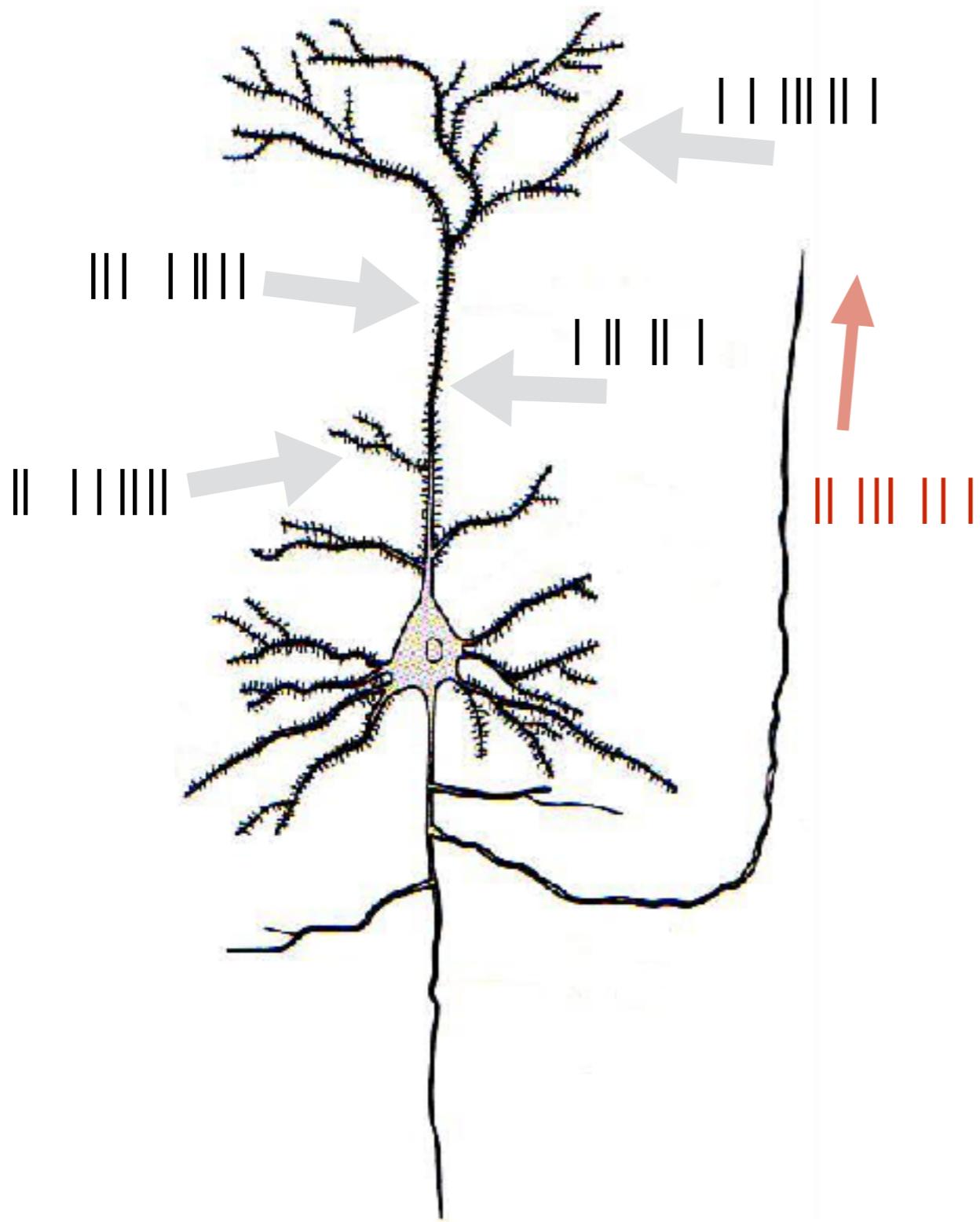


Total synaptic current:

$$I_{\text{syn},i}(t) = \sum_j w_{ij} \sum_k \alpha(t - t_j^{(k)})$$

Integrated at the level of the membrane potential:

Neuronal integration

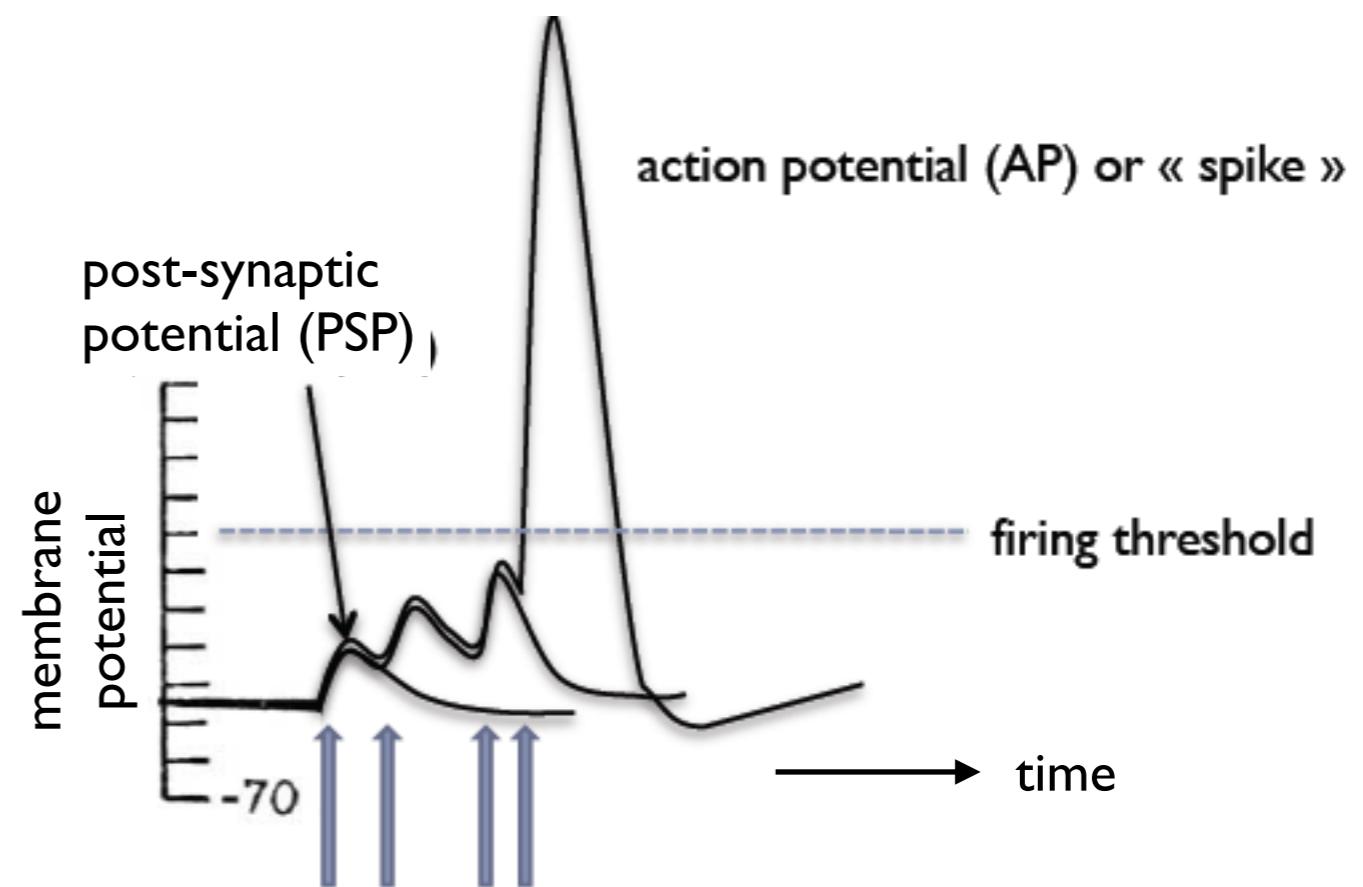


Total synaptic current:

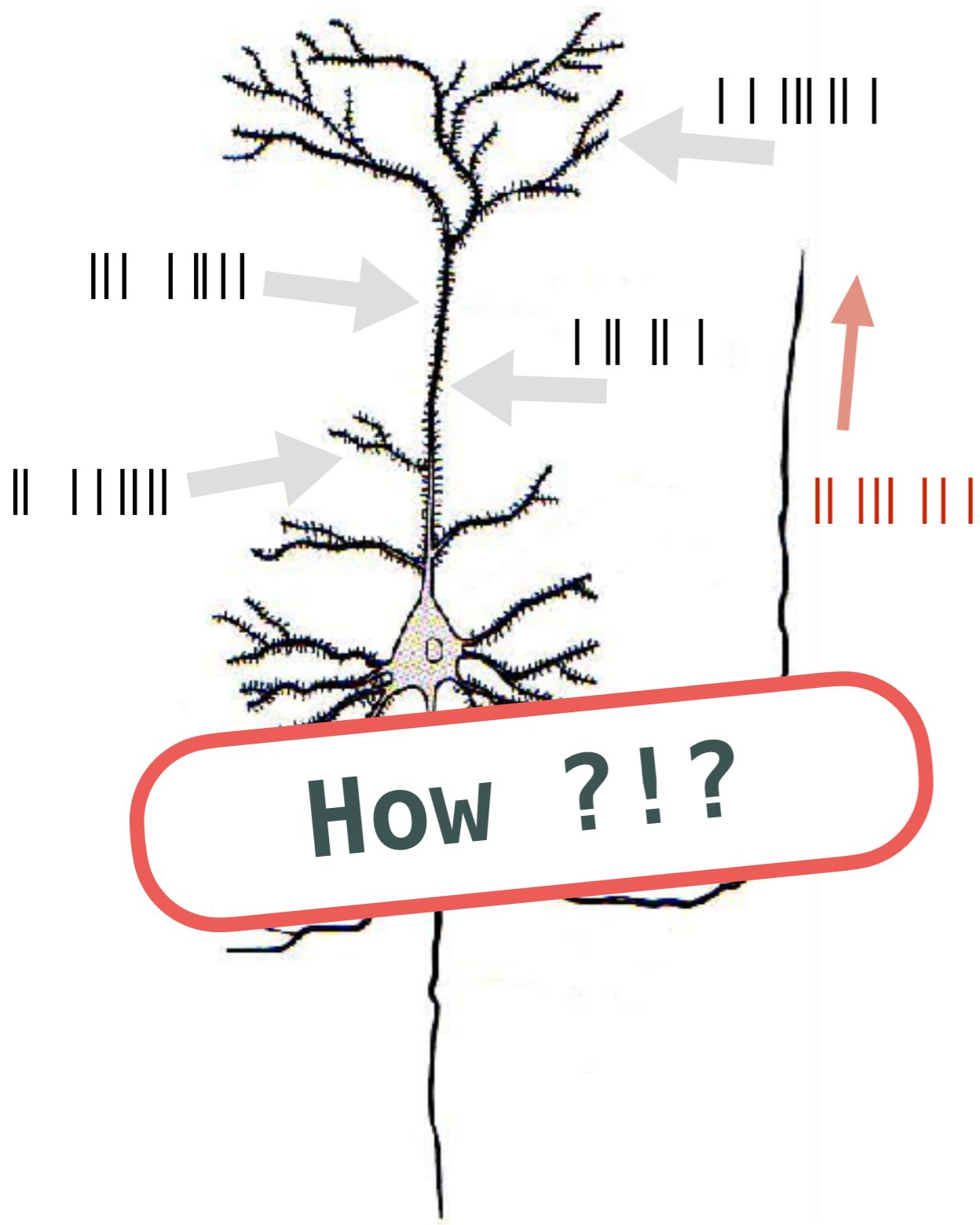
$$I_{\text{syn},i}(t) = \sum_j w_{ij} \sum_k \alpha(t - t_j^{(k)})$$

↑
time of k -th spike
of neuron j

Integrated at the level of the membrane potential:



Neuronal integration

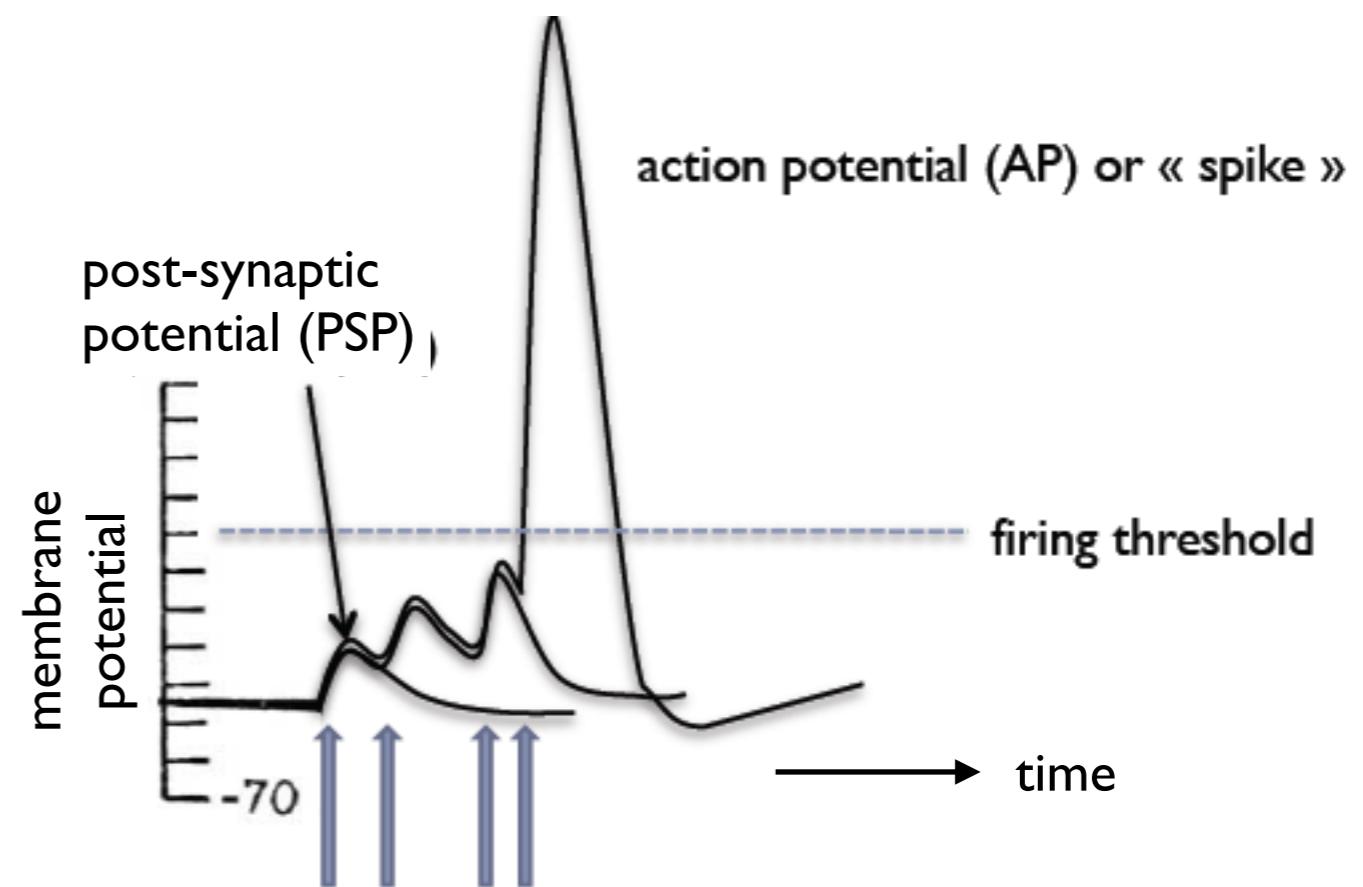


Total synaptic current:

$$I_{\text{syn},i}(t) = \sum_j w_{ij} \sum_k \alpha(t - t_j^{(k)})$$

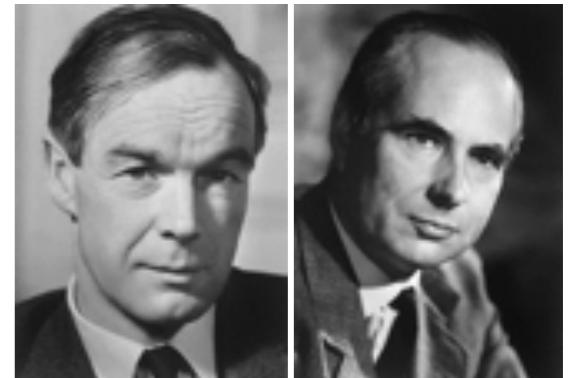
↑
time of k -th spike
of neuron j

Integrated at the level of the membrane potential:



Neuron models

- Hodgkin-Huxley model (1952):
detailed description of ion channel dynamics



Hodgkin Huxley

- Integrate-and-fire model (1907):
simplified model of neuronal integration



Lapicque

- Firing-rate model:
description of mean firing rate

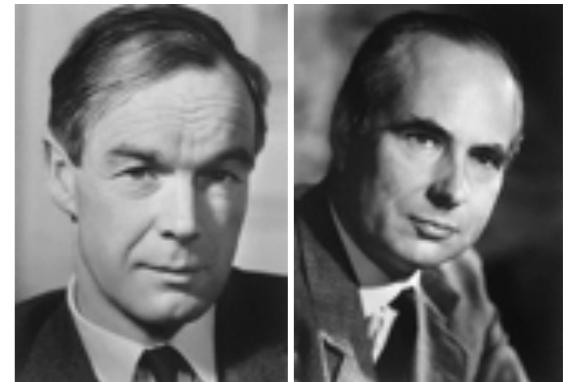


Rall

- Cable theory (1962):
description of the spatial dependence of responses
to dendritic inputs

Neuron models

- Hodgkin-Huxley model (1952):
detailed description of ion channel dynamics



Hodgkin Huxley

- Integrate-and-fire model (1907):
simplified model of neuronal integration



Lapicque

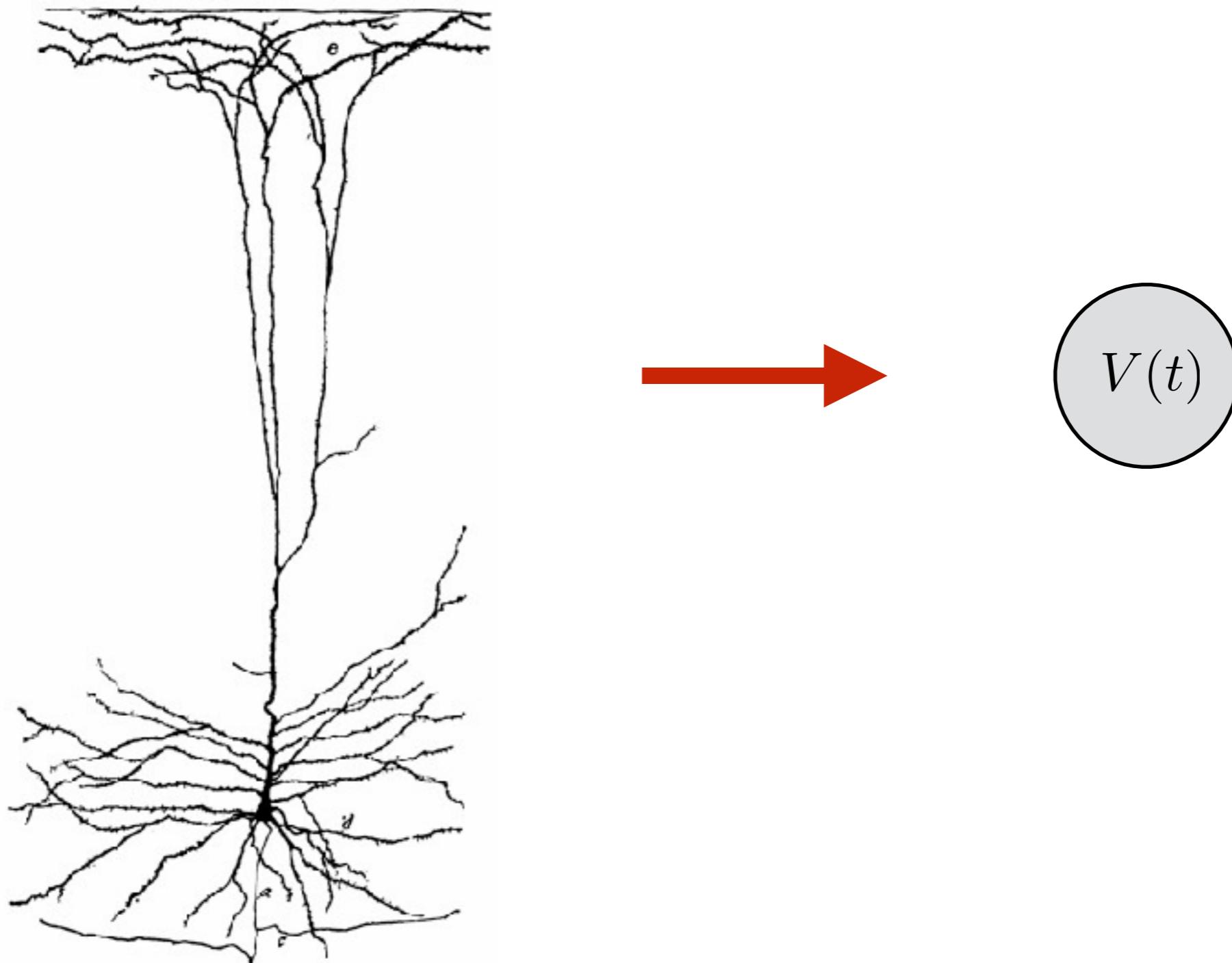
- Firing-rate model:
description of mean firing rate



Rall

- Cable theory (1962):
description of the spatial dependence of responses
to dendritic inputs

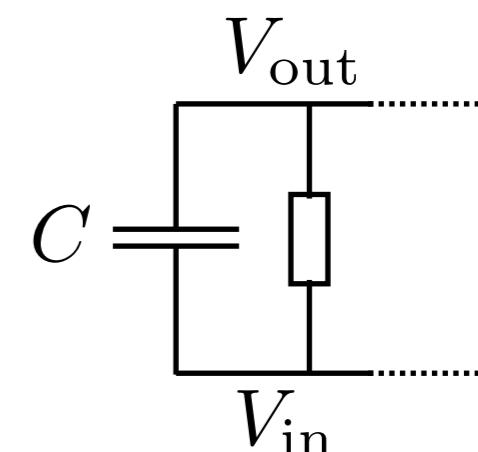
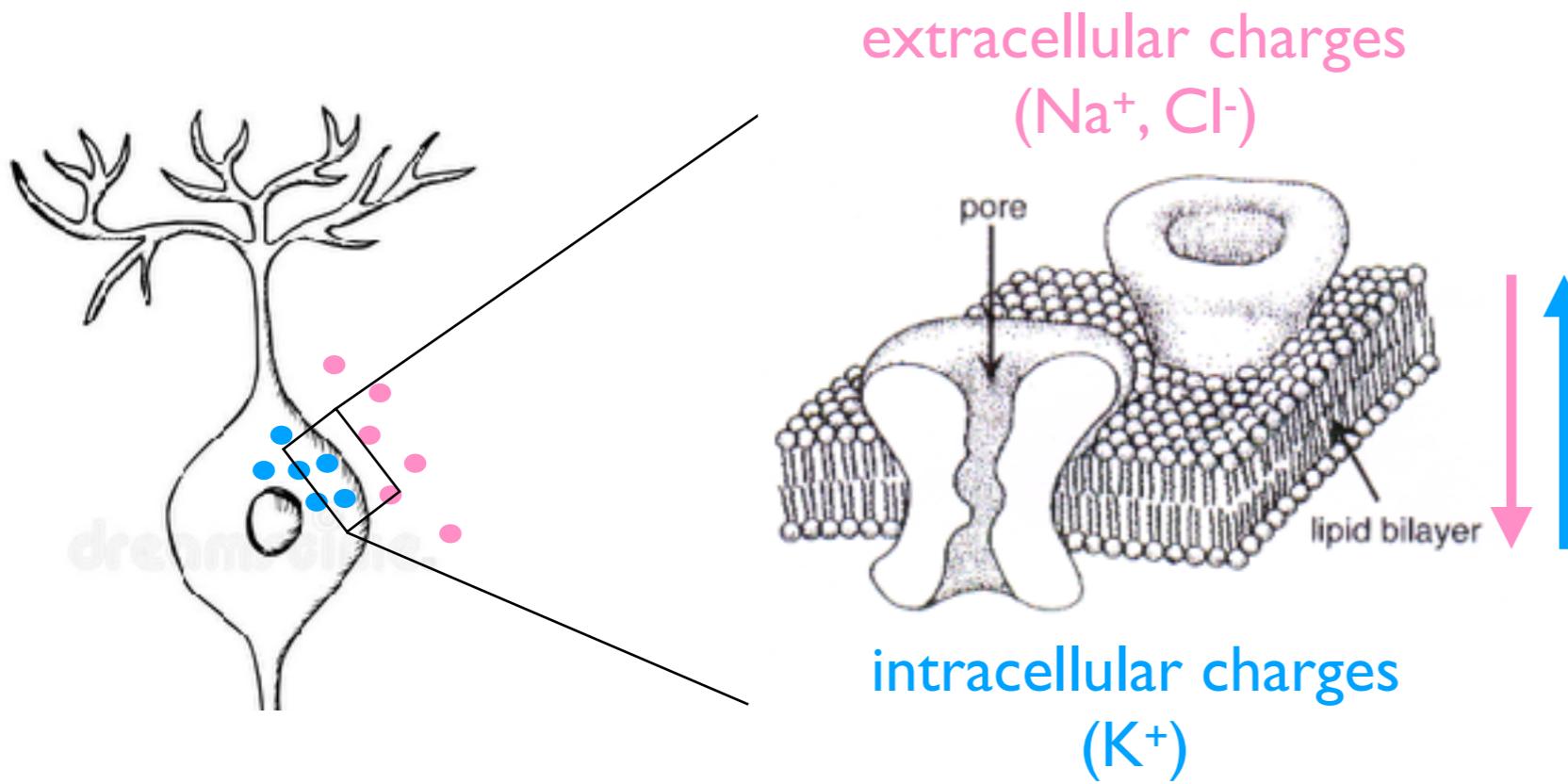
Simplified models: a single compartment



The membrane as an electrical circuit

The cell membrane is a lipid bilayer with inclusions (proteins), and has specific electrophysiological properties :

- separates intra- and extracellular charges → capacitance
- lets some charges pass (canaux) → electric conductance



$$\text{specific capacitance} = 1 \mu\text{F}/\text{cm}^2$$

$$\text{total capacitance} = \text{specific capacitance} \times \text{surface}$$

Physics reminder

Fundamental laws governing electrical circuits:

- **Ohm's law:** The current across a resistance is directly proportional to the voltage difference across the resistance.

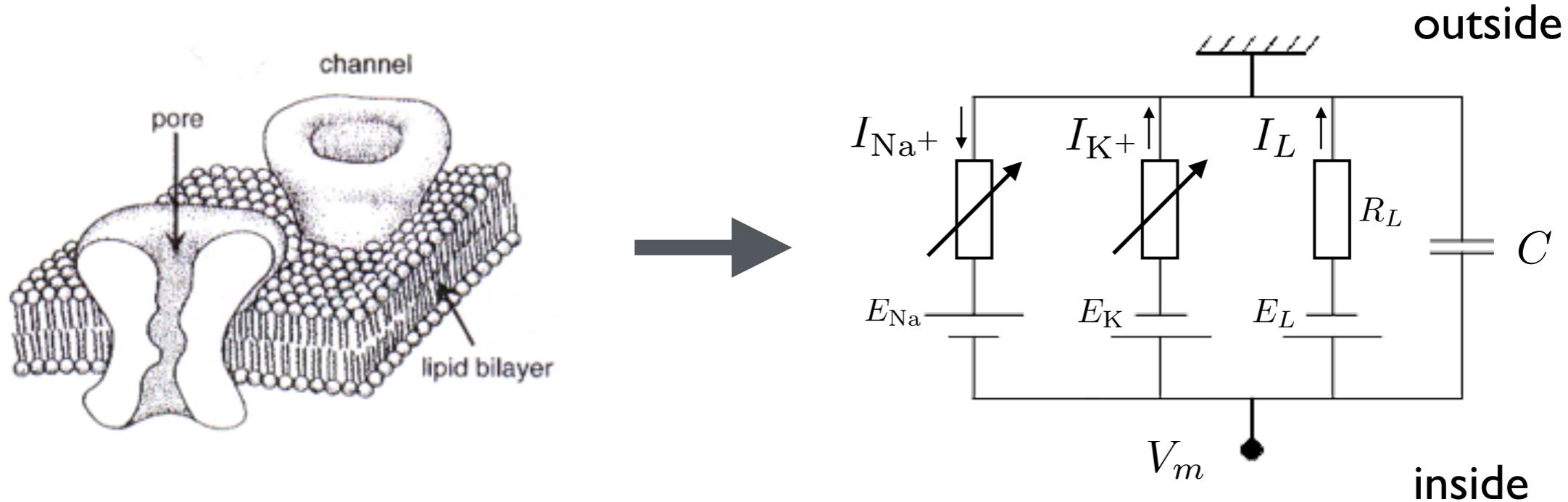
$$I = \frac{V}{R} \qquad R = \frac{1}{g}$$

- **Kirchhoff's law:** The sum of all currents into a point vanishes (i.e., positive and negative currents have to balance).

$$I_1 + I_2 + I_3 + \dots = 0$$

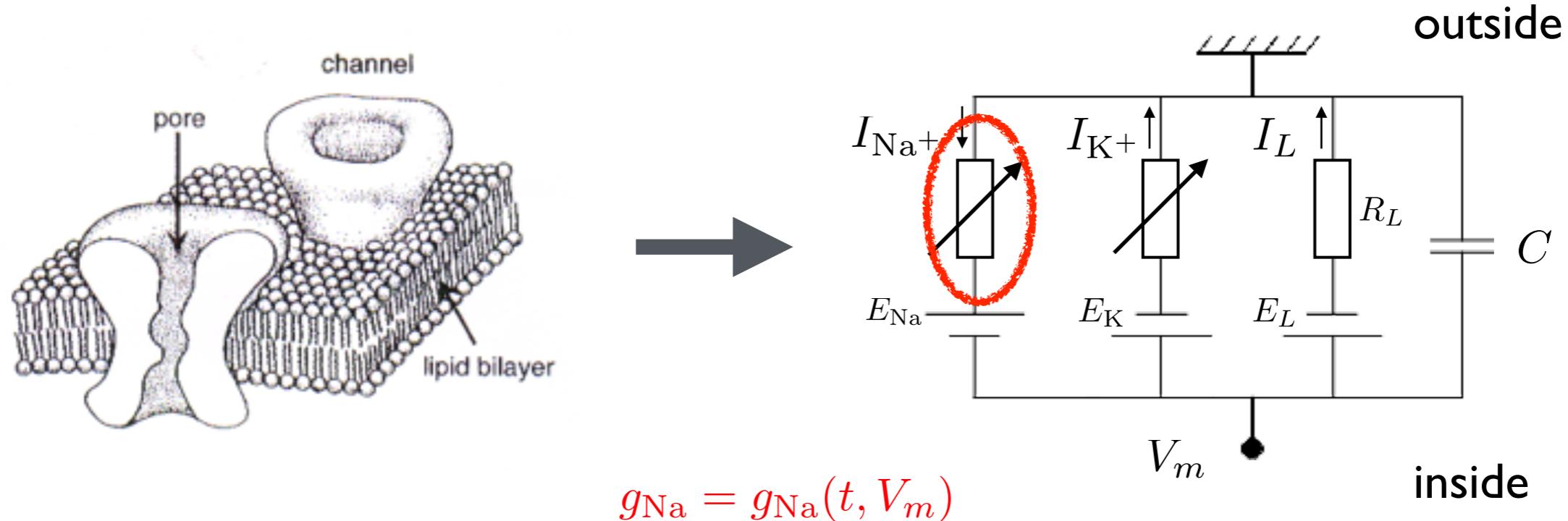
“Active” membrane properties

- The membrane potential V_m varies depending on the opening/closing of different types of ion channels.
- The membrane is “active”: The conductances (the opening) of ion channels *varies as a function of the membrane potential!*



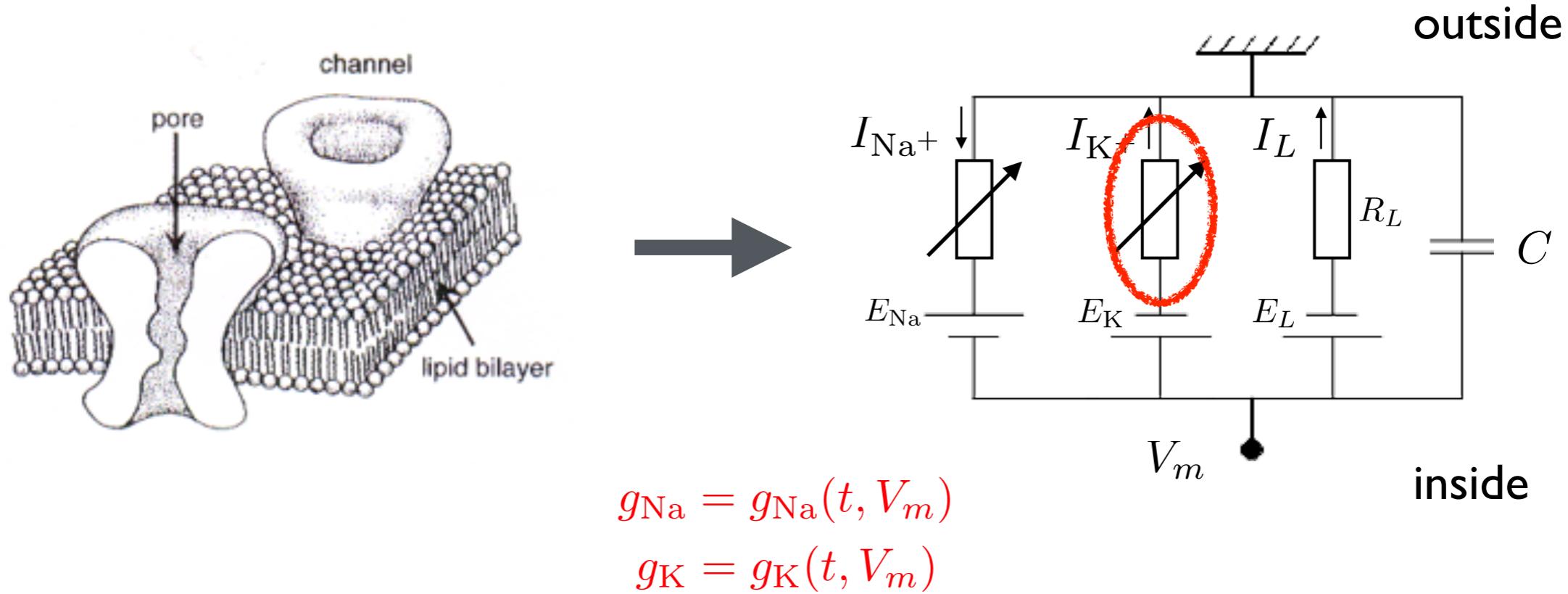
“Active” membrane properties

- The membrane potential V_m varies depending on the opening/closing of different types of ion channels.
- The membrane is “active”: The conductances (the opening) of ion channels *varies as a function of the membrane potential!*



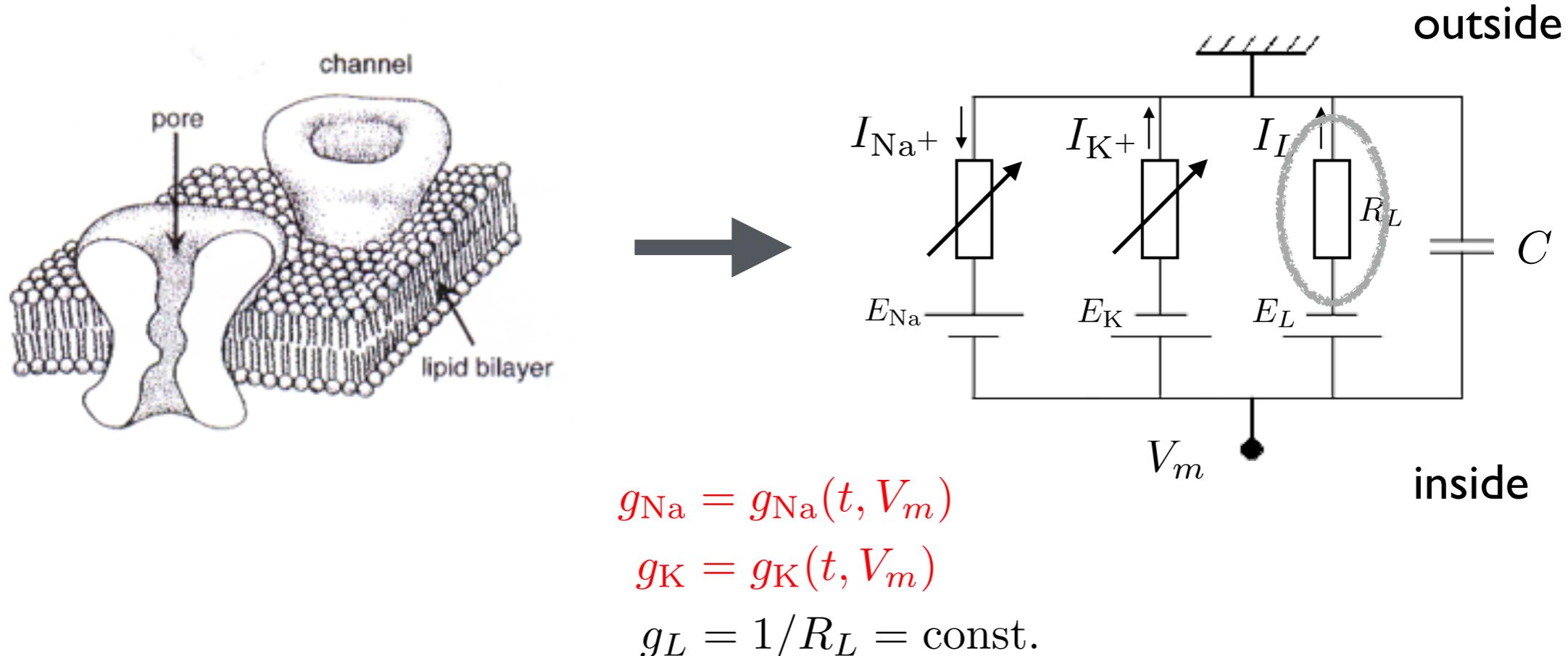
“Active” membrane properties

- The membrane potential V_m varies depending on the opening/closing of different types of ion channels.
- The membrane is “active”: The conductances (the opening) of ion channels *varies as a function of the membrane potential!*

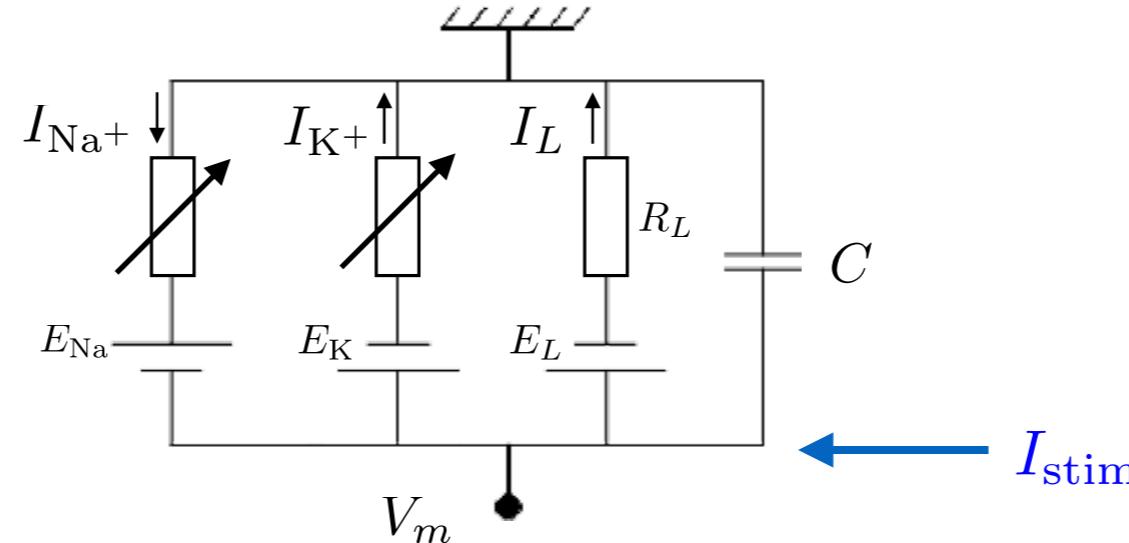


“Active” membrane properties

- The membrane potential V_m varies depending on the opening/closing of different types of ion channels.
- The membrane is “active”: The conductances (the opening) of ion channels *varies as a function of the membrane potential!*



Hodgkin–Huxley: Equation for the membrane potential



■ Kirchhoff's law: $I_C + I_L + I_{\text{Na}^+} + I_{\text{K}^+} - I_{\text{stim}} = 0$

■ Ohm's law: $I_X = \frac{\Delta V}{R} = g_X(V - V_{\text{reversion},X}) \quad X = L, \text{Na}^+, \text{K}^+$

■ Capacitive current: $I_C = C \frac{dV}{dt}$

evolution eq. for membrane potential

→
$$C \frac{dV}{dt} = g_L(E_L - V) + g_{\text{Na}}(E_{\text{Na}} - V) + g_{\text{K}}(E_{\text{K}} - V) + I_{\text{stim}}$$

Hodgkin-Huxley model: *detailed description* of the dynamics of g_{Na} , g_{K}

The complete equations of the Hodgkin–Huxley model

$$C \frac{dV}{dt} = g_L(E_L - V) + \bar{g}_{\text{Na}} m(t)^3 h(t)(E_{\text{Na}} - V) + \bar{g}_{\text{K}} n(t)^4 (E_{\text{K}} - V) + I_{\text{stim}}$$

$$\tau_n \frac{dn}{dt} = n_\infty - n$$

$$\tau_n = \frac{1}{\alpha_n + \beta_n}$$

$$n_\infty = \frac{\alpha_n}{\alpha_n + \beta_n}$$

$$\tau_m \frac{dm}{dt} = m_\infty - m$$

$$\tau_m = \frac{1}{\alpha_m + \beta_m}$$

$$m_\infty = \frac{\alpha_m}{\alpha_m + \beta_m}$$

$$\tau_h \frac{dh}{dt} = h_\infty - h$$

$$\tau_h = \frac{1}{\alpha_h + \beta_h}$$

$$h_\infty = \frac{\alpha_h}{\alpha_h + \beta_h}$$

The complete equations of the Hodgkin–Huxley model

$$C \frac{dV}{dt} = g_L(E_L - V) + \bar{g}_{\text{Na}}m(t)^3h(t)(E_{\text{Na}} - V) + \bar{g}_{\text{K}}n(t)^4(E_{\text{K}} - V) + I_{\text{stim}}$$

$$\tau_n \frac{dn}{dt} = n_\infty - n$$

$$\tau_n = \frac{1}{\alpha_n + \beta_n}$$

$$n_\infty = \frac{\alpha_n}{\alpha_n + \beta_n}$$

$$\tau_m \frac{dm}{dt} = m_\infty - m$$

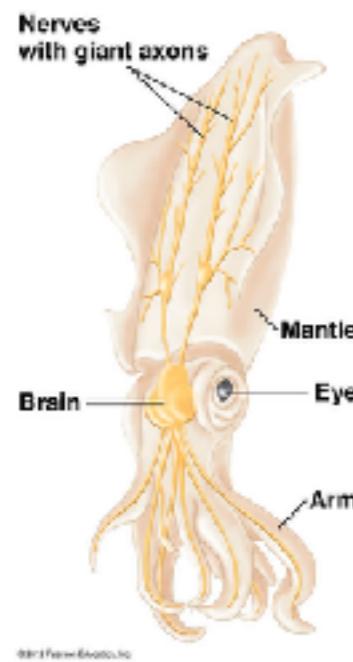
$$\tau_m = \frac{1}{\alpha_m + \beta_m}$$

$$m_\infty = \frac{\alpha_m}{\alpha_m + \beta_m}$$

$$\tau_h \frac{dh}{dt} = h_\infty - h$$

$$\tau_h = \frac{1}{\alpha_h + \beta_h}$$

$$h_\infty = \frac{\alpha_h}{\alpha_h + \beta_h}$$



The complete equations of the Hodgkin–Huxley model

$$C \frac{dV}{dt} = g_L(E_L - V) + \bar{g}_{\text{Na}} m(t)^3 h(t)(E_{\text{Na}} - V) + \bar{g}_{\text{K}} n(t)^4 (E_{\text{K}} - V) + I_{\text{stim}}$$

$$\tau_n \frac{dn}{dt} = n_\infty - n$$

$$\tau_n = \frac{1}{\alpha_n + \beta_n}$$

$$n_\infty = \frac{\alpha_n}{\alpha_n + \beta_n}$$

$$\tau_m \frac{dm}{dt} = m_\infty - m$$

$$\tau_m = \frac{1}{\alpha_m + \beta_m}$$

$$m_\infty = \frac{\alpha_m}{\alpha_m + \beta_m}$$

$$\tau_h \frac{dh}{dt} = h_\infty - h$$

$$\tau_h = \frac{1}{\alpha_h + \beta_h}$$

$$h_\infty = \frac{\alpha_h}{\alpha_h + \beta_h}$$

Transition rates (determined for the axon of the giant squid):

$$\alpha_n(V) = \frac{(0.1 - 0.01V)}{e^{1-0.1V} - 1}$$

$$\beta_n(V) = 0.125 e^{-\frac{V}{80}}$$

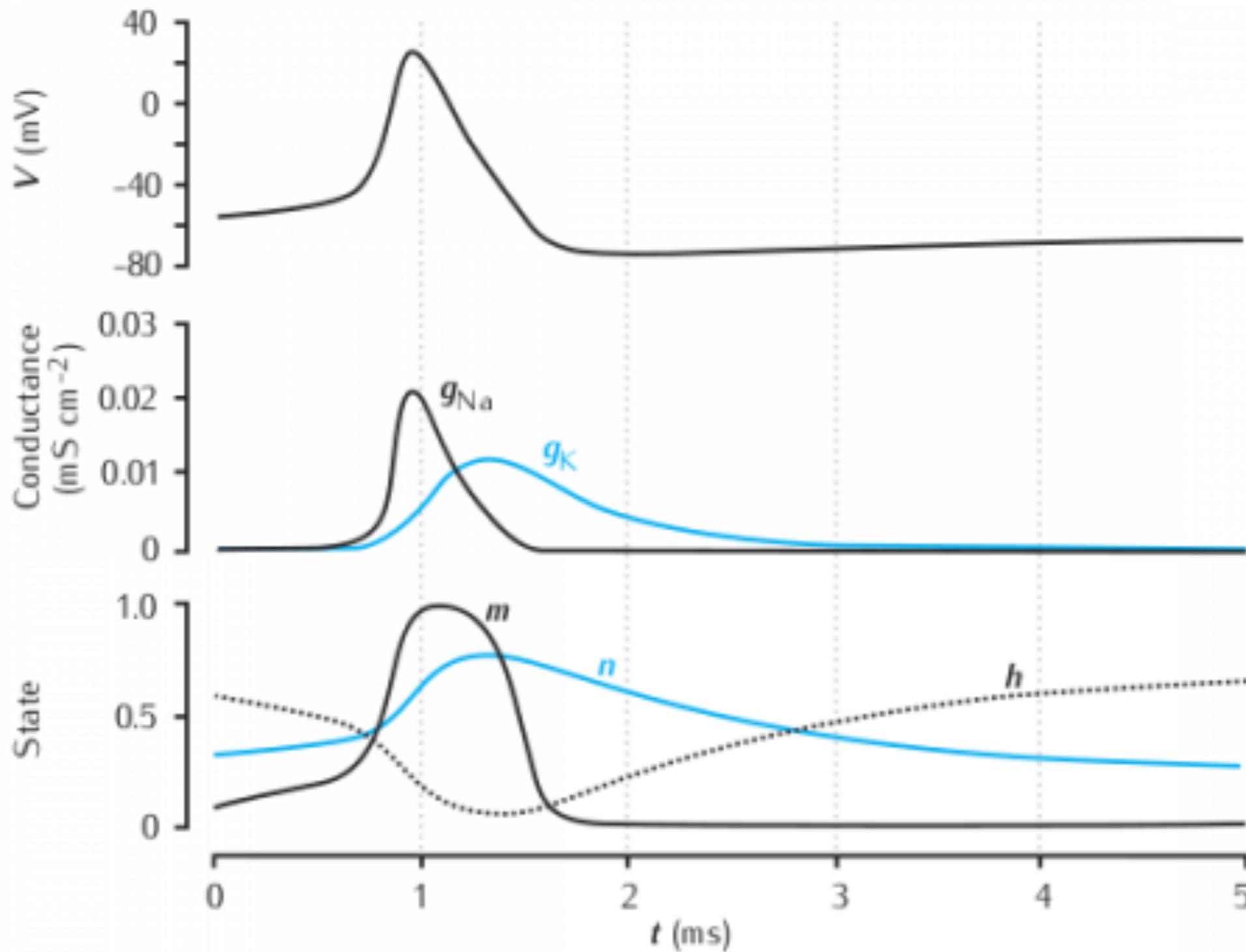
$$\alpha_m(V) = \frac{(2.5 - 0.1V)}{e^{2.5-0.1V} - 1}$$

$$\beta_m(V) = 4 e^{-\frac{V}{18}}$$

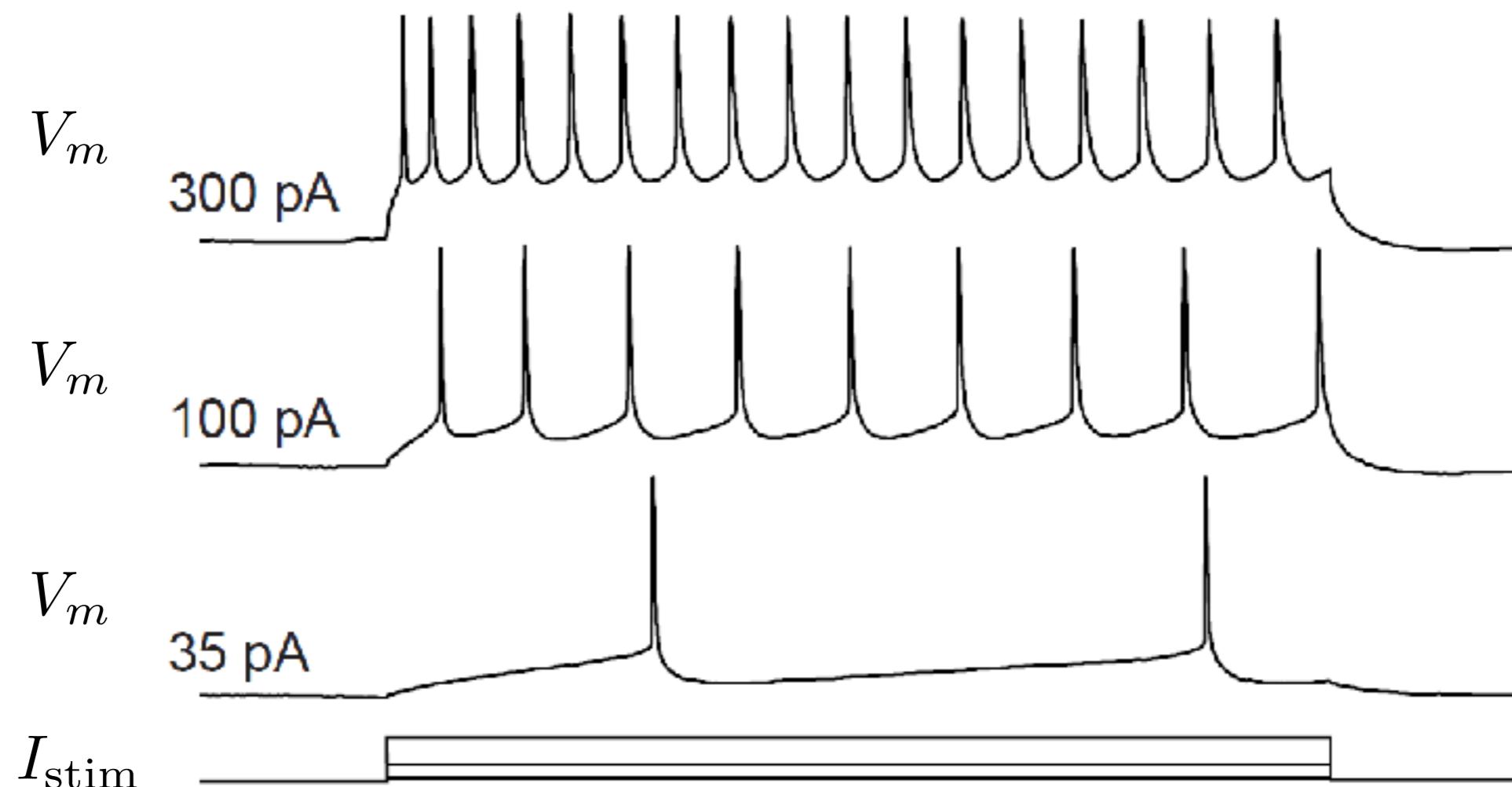
$$\alpha_h(V) = 0.07 e^{-\frac{V}{20}}$$

$$\beta_h(V) = \frac{1}{e^{3-0.1V} + 1}$$

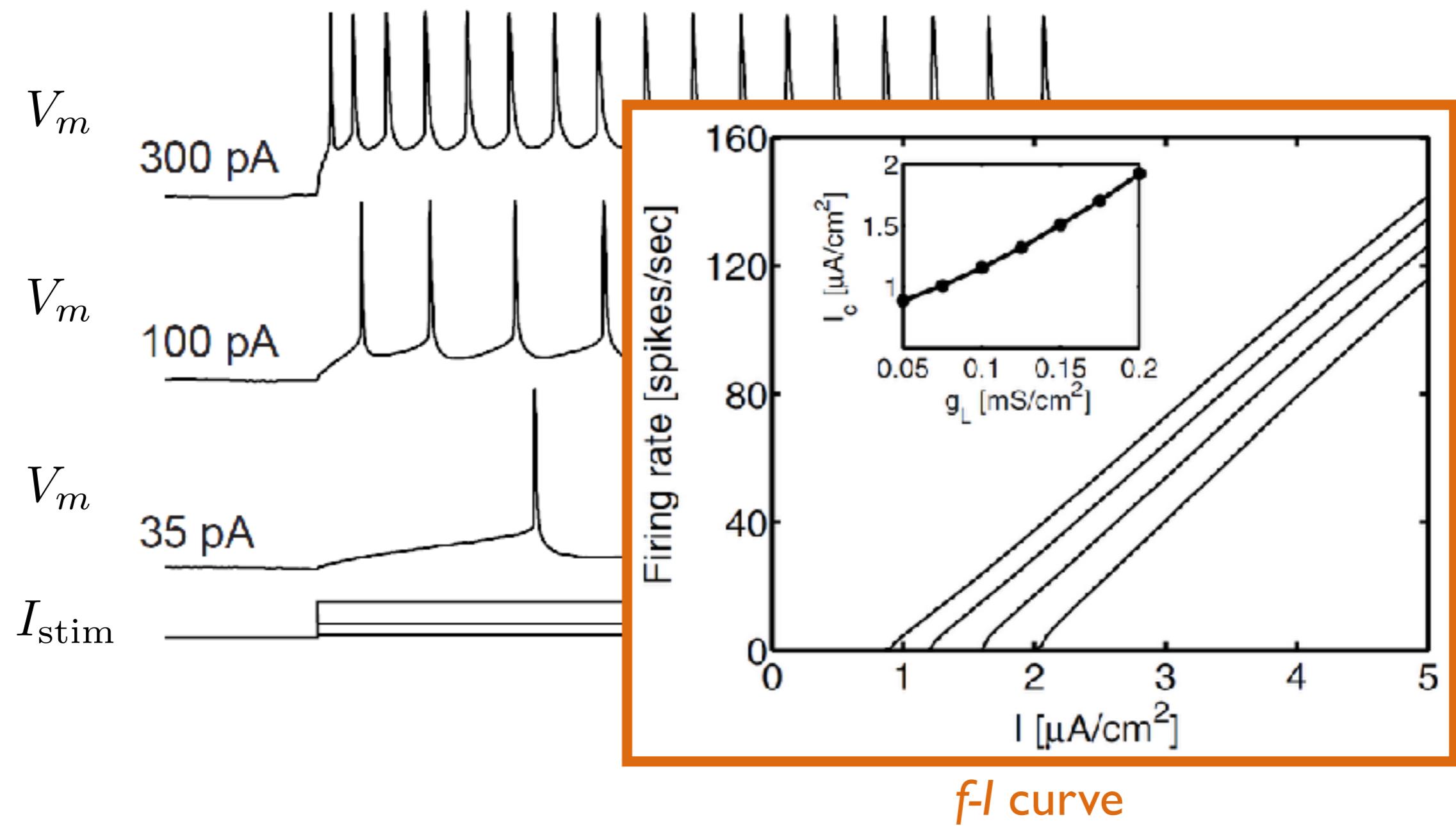
Hodgkin–Huxley model explains the spike shape!



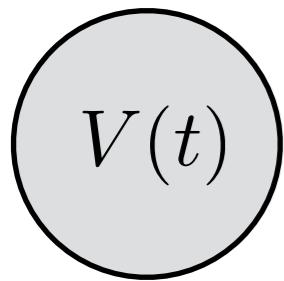
Hodgkin–Huxley in response to current injection



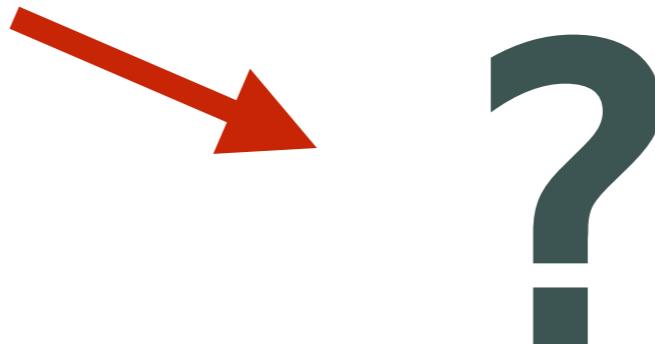
Hodgkin–Huxley in response to current injection



Beyond Hodgkin–Huxley: going simpler or more complex ?

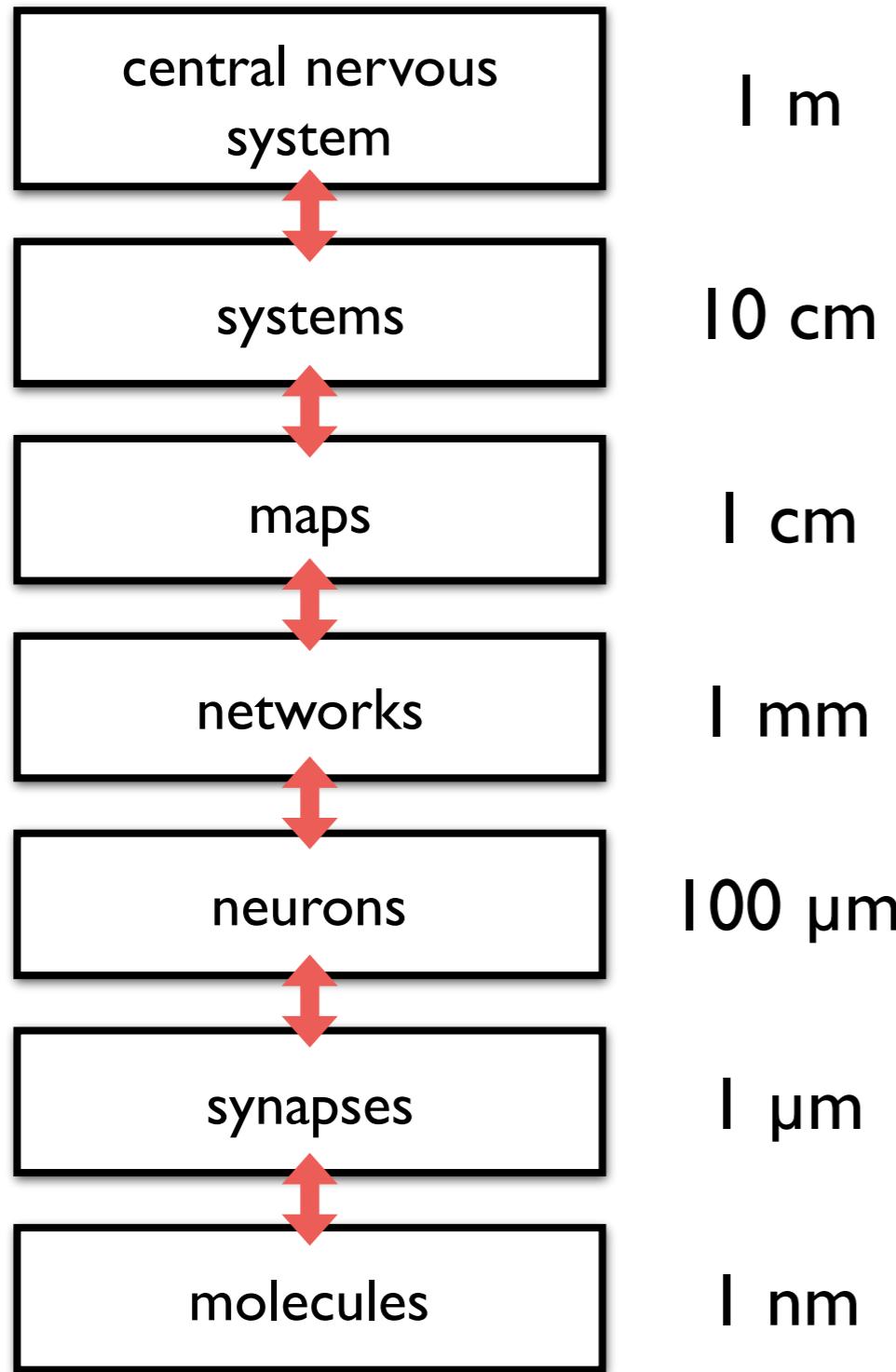


Hodgkin-Huxley
“complete” model of spike generation and
membrane potential dynamics



?

The level of detail depends on the scale we wish to study



1 m

10 cm

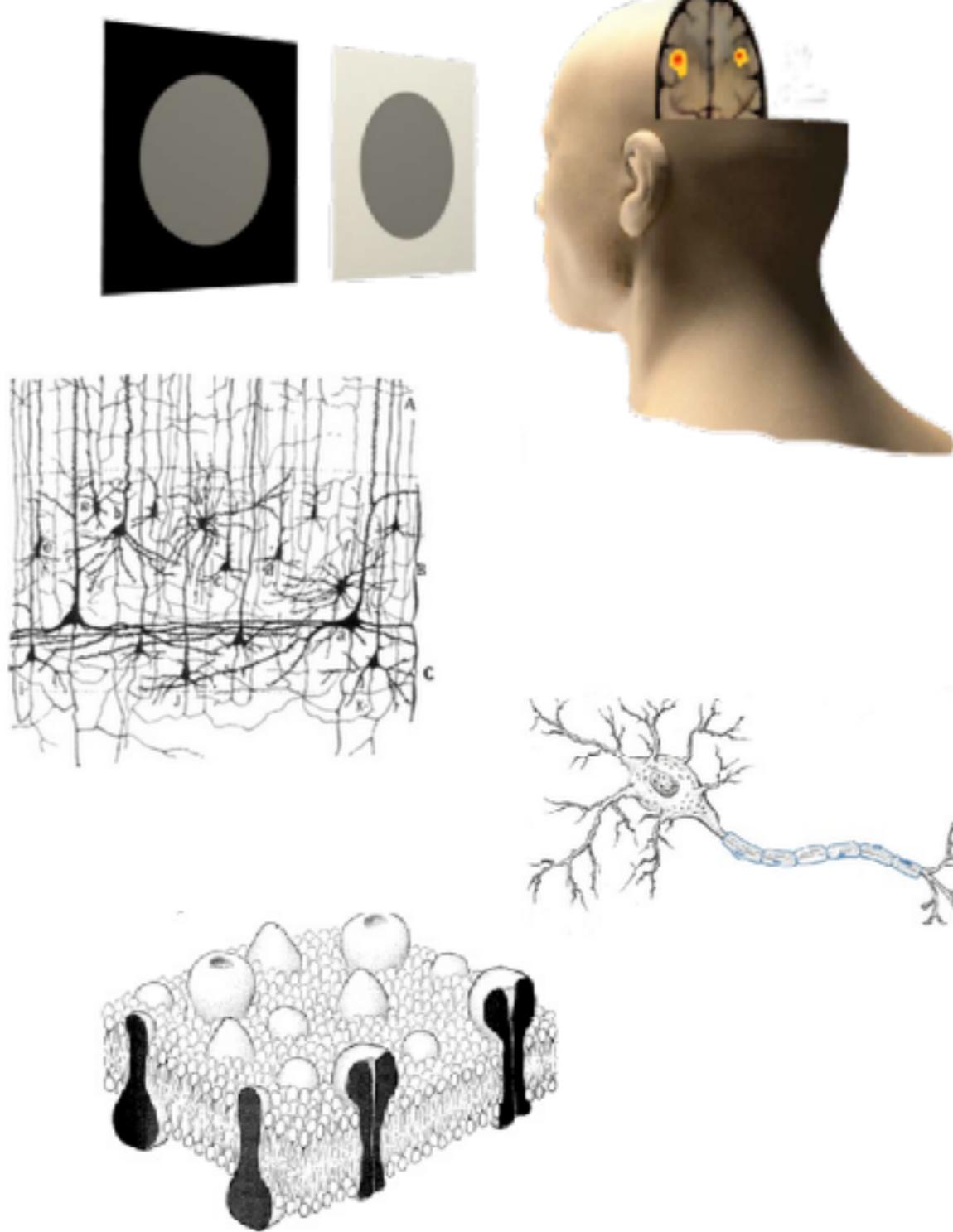
1 cm

1 mm

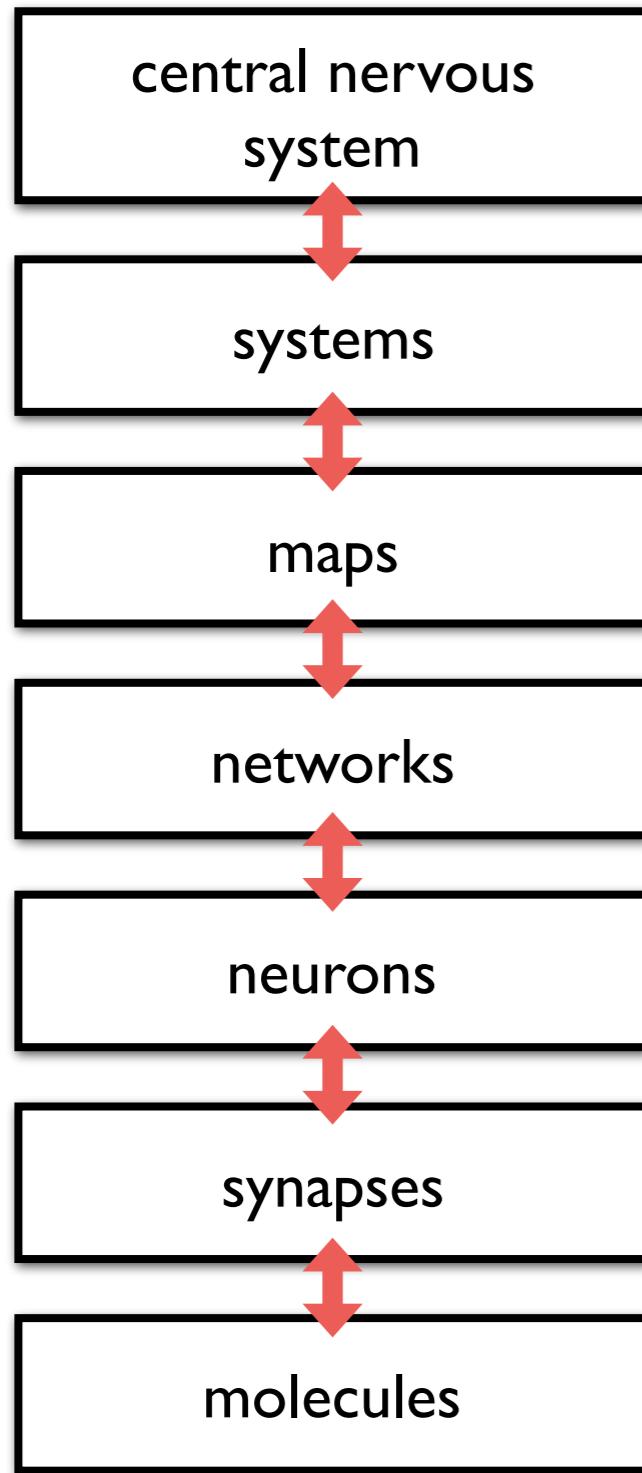
100 μm

1 μm

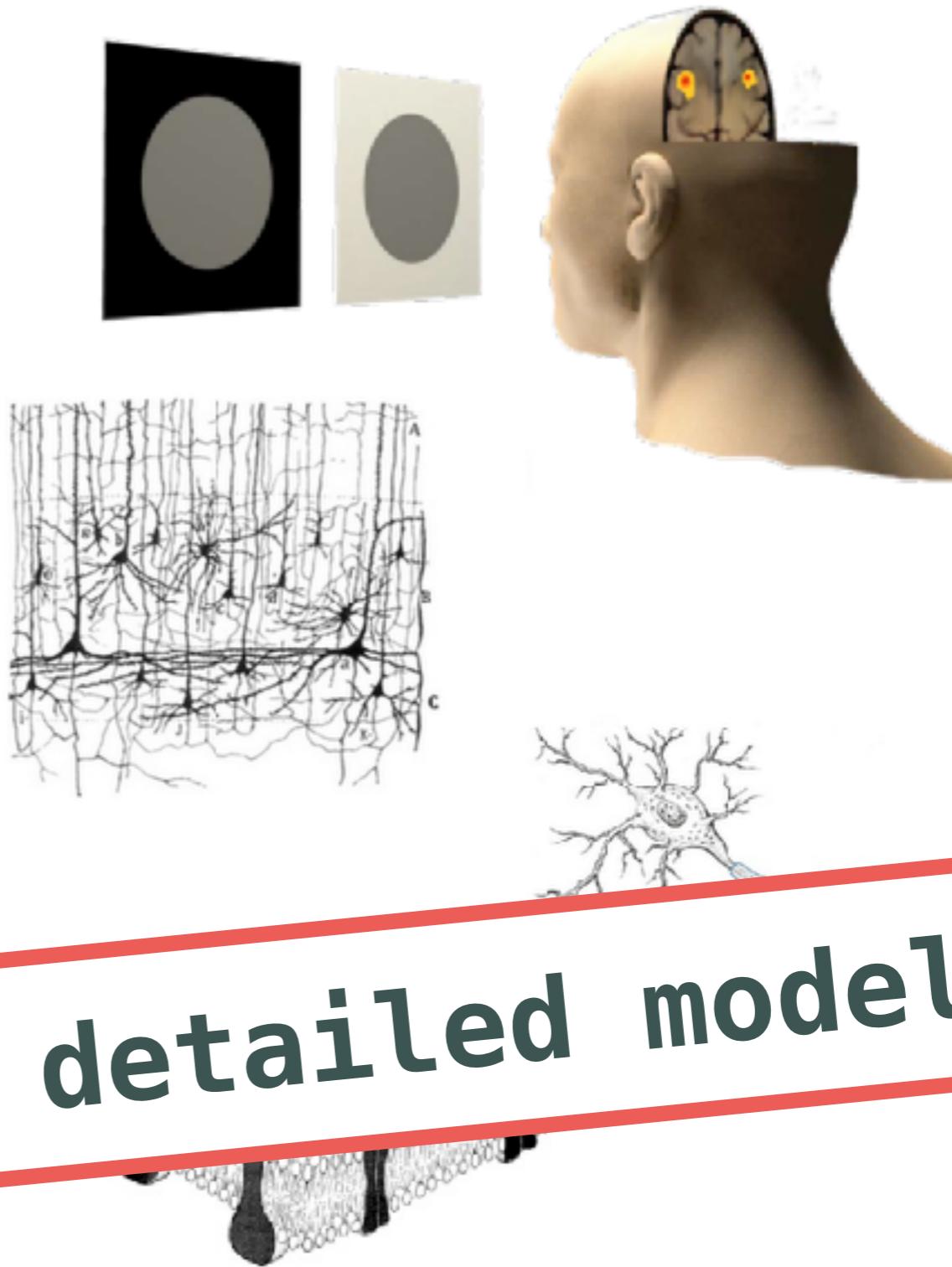
1 nm



The level of detail depends on the scale we wish to study

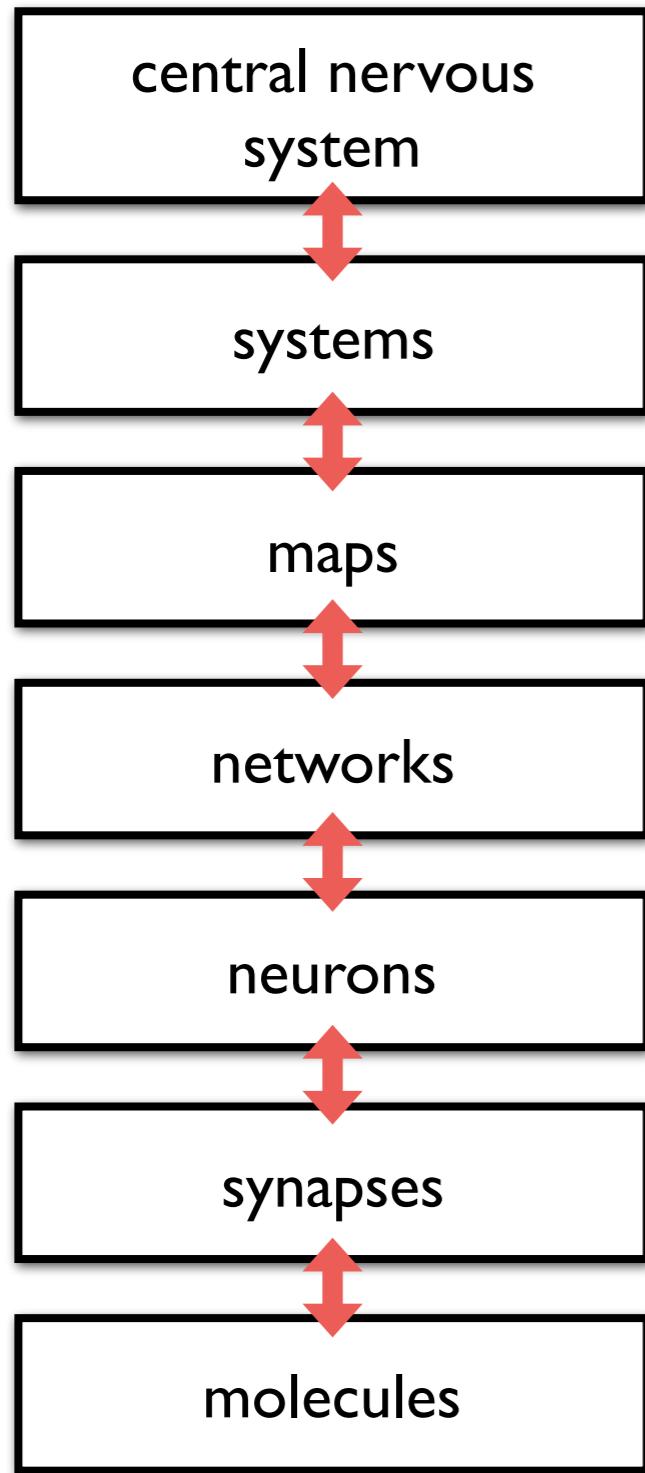


1 m
10 cm
1 cm
1 mm
100 μm
1 μm
1 nm

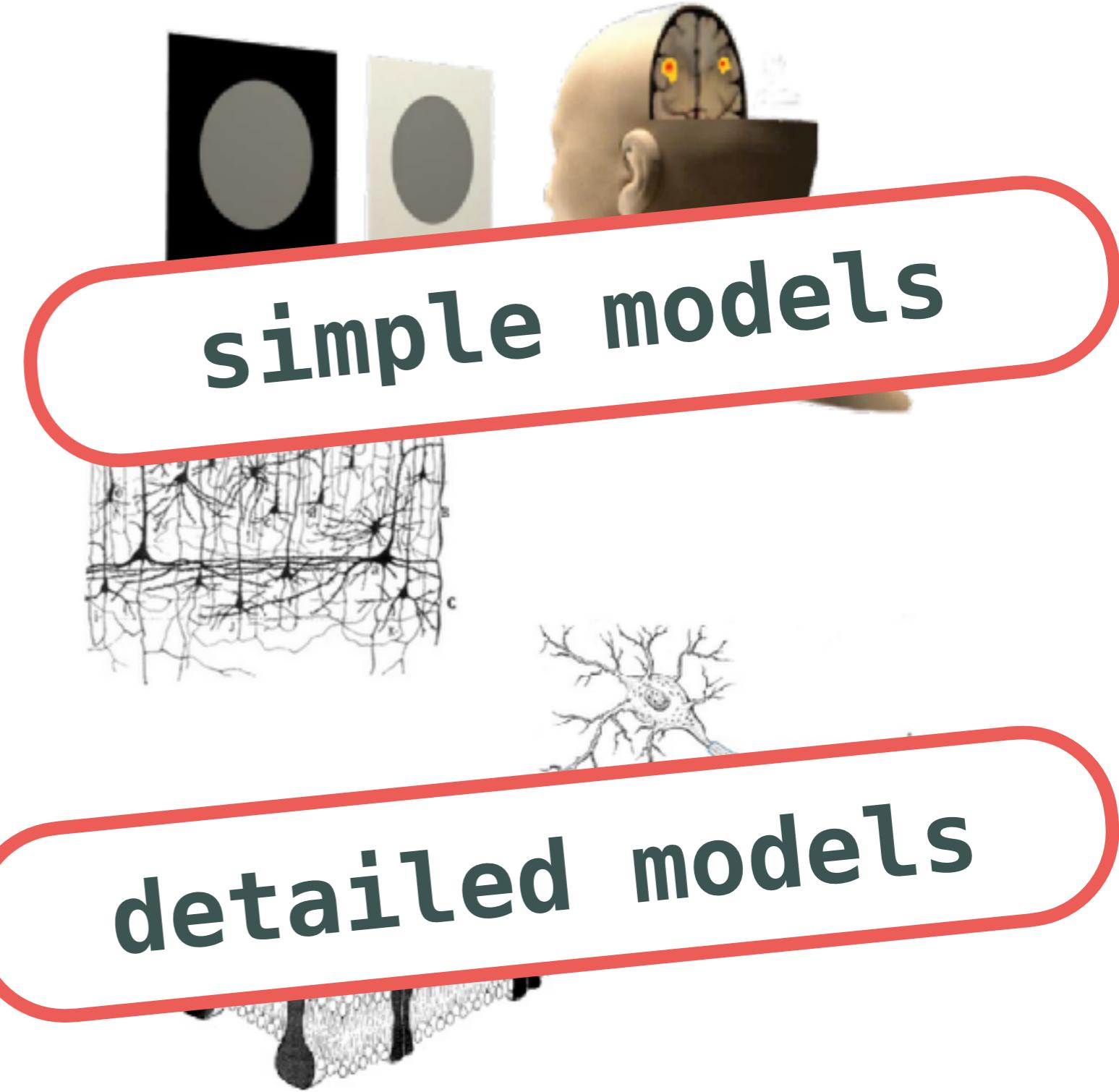


detailed models

The level of detail depends on the scale we wish to study

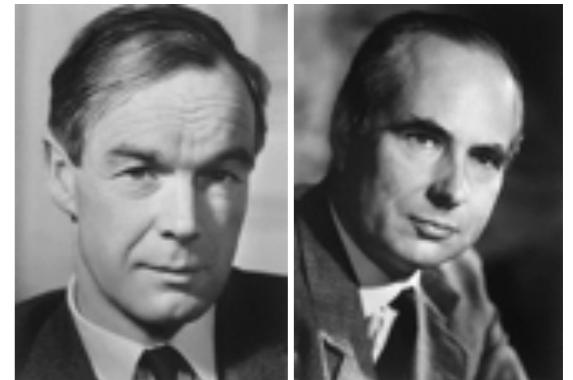


1 m
10 cm
1 cm
1 mm
100 μ m
1 μ m
1 nm



Neuron models

- Hodgkin-Huxley model (1952):
detailed description of ion channel dynamics



Hodgkin Huxley

- Integrate-and-fire model (1907):
simplified model of neuronal integration



Lapicque

- Firing-rate model:
description of mean firing rate



Rall

- Cable theory (1962):
description of the spatial dependence of responses
to dendritic inputs

Neuron models

- Hodgkin-Huxley model (1952):
detailed description of ion channel dynamics



Hodgkin Huxley

- Integrate-and-fire model (1907):
simplified model of neuronal integration



Lapicque

- Firing-rate model:
description of mean firing rate



Rall

- Cable theory (1962):
description of the spatial dependence of responses
to dendritic inputs

Integrate-and-Fire model: motivation

- In the Hodgkin-Huxley model, the active conductances (Na^+ and K^+) explain the *spike generation and the repolarisation of the membrane*.
The model (and biology!) model tells us:
 - I. Each time the membrane potential crosses a threshold potential, an action potential is generated.
The spike time course is stereotypical and doesn't contain information about the signal (the input current).
 2. Far from threshold, the active conductances are basically closed.
- “Integrate-and-fire” model: keep passive sub-threshold dynamics, include spike generation without caring about precise mechanism...

$$C \frac{dV}{dt} = g_L(E_L - V) + g_{\text{Na}}(E_{\text{Na}} - V) + g_K(E_K - V) + I_{\text{stim}}$$

Integrate-and-Fire model: motivation

- In the Hodgkin-Huxley model, the active conductances (Na^+ and K^+) explain the *spike generation and the repolarisation of the membrane*.
The model (and biology!) model tells us:
 - I. Each time the membrane potential crosses a threshold potential, an action potential is generated.
The spike time course is stereotypical and doesn't contain information about the signal (the input current).
 2. Far from threshold, the active conductances are basically closed.
- “Integrate-and-fire” model: keep passive sub-threshold dynamics, include spike generation without caring about precise mechanism...

$$C \frac{dV}{dt} = g_L(E_L - V) + \cancel{g_{\text{Na}}(E_{\text{Na}} - V)} + g_K(E_K - V) + I_{\text{stim}}$$

Integrate-and-Fire model: motivation

- In the Hodgkin-Huxley model, the active conductances (Na^+ and K^+) explain the *spike generation and the repolarisation of the membrane*.
The model (and biology!) model tells us:
 - I. Each time the membrane potential crosses a threshold potential, an action potential is generated.
The spike time course is stereotypical and doesn't contain information about the signal (the input current).
 2. Far from threshold, the active conductances are basically closed.
- “Integrate-and-fire” model: keep passive sub-threshold dynamics, include spike generation without caring about precise mechanism...

$$C \frac{dV}{dt} = g_L(E_L - V) + \cancel{g_{\text{Na}}(E_{\text{Na}} - V)} + \cancel{g_{\text{K}}(E_{\text{K}} - V)} + I_{\text{stim}}$$

Integrate-and-Fire model: motivation

- In the Hodgkin-Huxley model, the active conductances (Na^+ and K^+) explain the *spike generation and the repolarisation of the membrane*.
The model (and biology!) model tells us:
 - I. Each time the membrane potential crosses a threshold potential, an action potential is generated.
The spike time course is stereotypical and doesn't contain information about the signal (the input current).
 2. Far from threshold, the active conductances are basically closed.
- “Integrate-and-fire” model: keep passive sub-threshold dynamics, include spike generation without caring about precise mechanism...

$$C \frac{dV}{dt} = g_L(E_L - V) + \cancel{g_{\text{Na}}(E_{\text{Na}} - V)} + \cancel{g_{\text{K}}(E_{\text{K}} - V)} + I_{\text{stim}}$$

“integrate”

Integrate-and-Fire model: motivation

- In the Hodgkin-Huxley model, the active conductances (Na^+ and K^+) explain the *spike generation and the repolarisation of the membrane*.
The model (and biology!) model tells us:
 - I. Each time the membrane potential crosses a threshold potential, an action potential is generated.
The spike time course is stereotypical and doesn't contain information about the signal (the input current).
 2. Far from threshold, the active conductances are basically closed.
- “Integrate-and-fire” model: keep passive sub-threshold dynamics, include spike generation without caring about precise mechanism...

$$C \frac{dV}{dt} = g_L(E_L - V) + \cancel{g_{\text{Na}}(E_{\text{Na}} - V)} + \cancel{g_{\text{K}}(E_{\text{K}} - V)} + I_{\text{stim}}$$

$V(t) > V_{\text{seuil}}$:
spike + reset

“integrate”

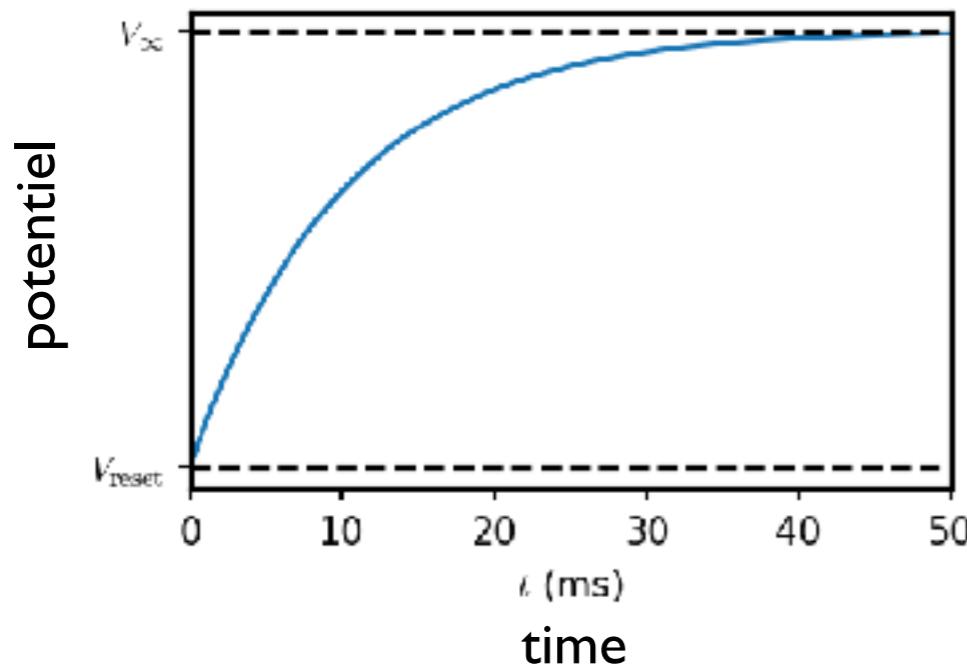
“fire”

Integrate-and-Fire neuron

- More precisely: “Leaky Integrate-and-Fire” (LIF)

$$C \frac{dV}{dt} = g_L(E_L - V) + I_{\text{syn}}$$

- *Characteristic time constant* of integration of synaptic input: $\tau_m = C/g_L$
- The simplicity of the LIF allows to analytically calculate e.g. the firing rate in *deterministic* et *stochastic* regimes.

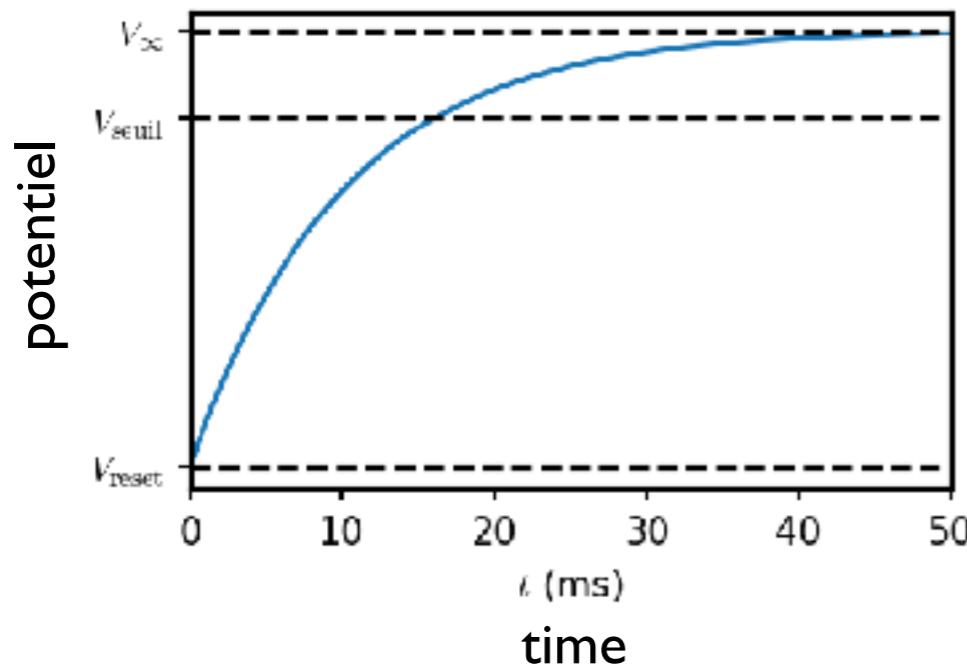


Integrate-and-Fire neuron

- More precisely: “Leaky Integrate-and-Fire” (LIF)

$$C \frac{dV}{dt} = g_L(E_L - V) + I_{\text{syn}}$$

- *Characteristic time constant* of integration of synaptic input: $\tau_m = C/g_L$
- The simplicity of the LIF allows to analytically calculate e.g. the firing rate in *deterministic* et *stochastic* regimes.

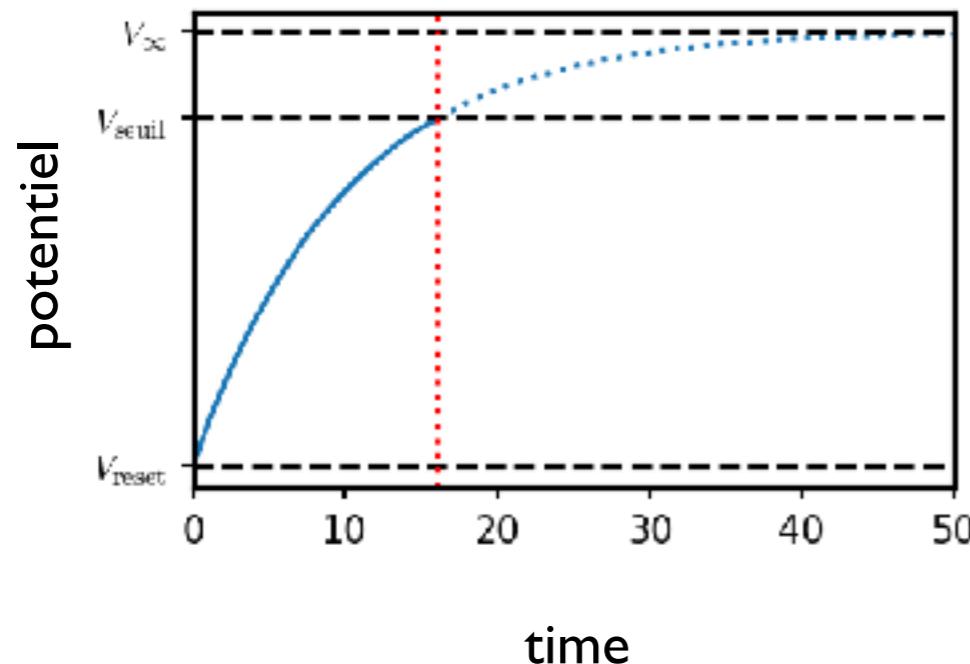


Integrate-and-Fire neuron

- More precisely: “Leaky Integrate-and-Fire” (LIF)

$$C \frac{dV}{dt} = g_L(E_L - V) + I_{\text{syn}}$$

- *Characteristic time constant* of integration of synaptic input: $\tau_m = C/g_L$
- The simplicity of the LIF allows to analytically calculate e.g. the firing rate in *deterministic* et *stochastic* regimes.

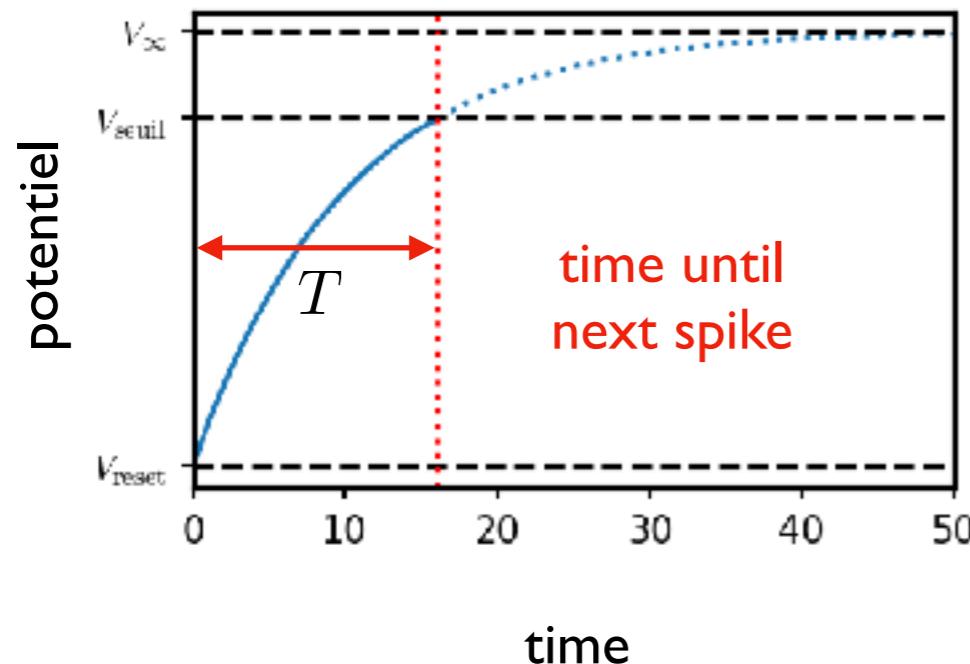


Integrate-and-Fire neuron

- More precisely: “Leaky Integrate-and-Fire” (LIF)

$$C \frac{dV}{dt} = g_L(E_L - V) + I_{\text{syn}}$$

- Characteristic time constant* of integration of synaptic input: $\tau_m = C/g_L$
- The simplicity of the LIF allows to analytically calculate e.g. the firing rate in *deterministic* et *stochastic* regimes.

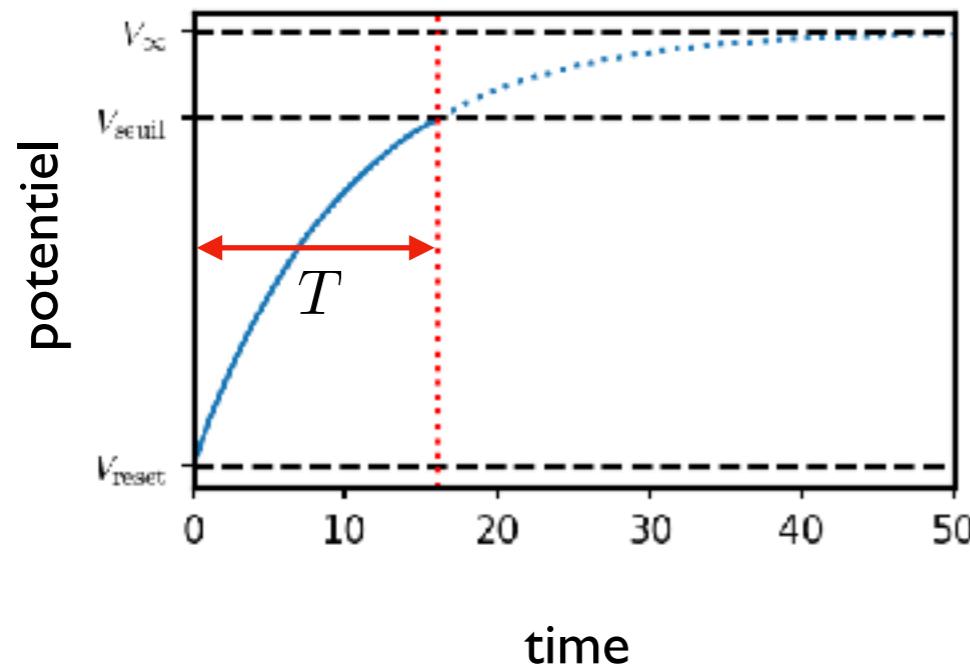


Integrate-and-Fire neuron

- More precisely: “Leaky Integrate-and-Fire” (LIF)

$$C \frac{dV}{dt} = g_L(E_L - V) + I_{\text{syn}}$$

- Characteristic time constant* of integration of synaptic input: $\tau_m = C/g_L$
- The simplicity of the LIF allows to analytically calculate e.g. the firing rate in *deterministic* et *stochastic* regimes.

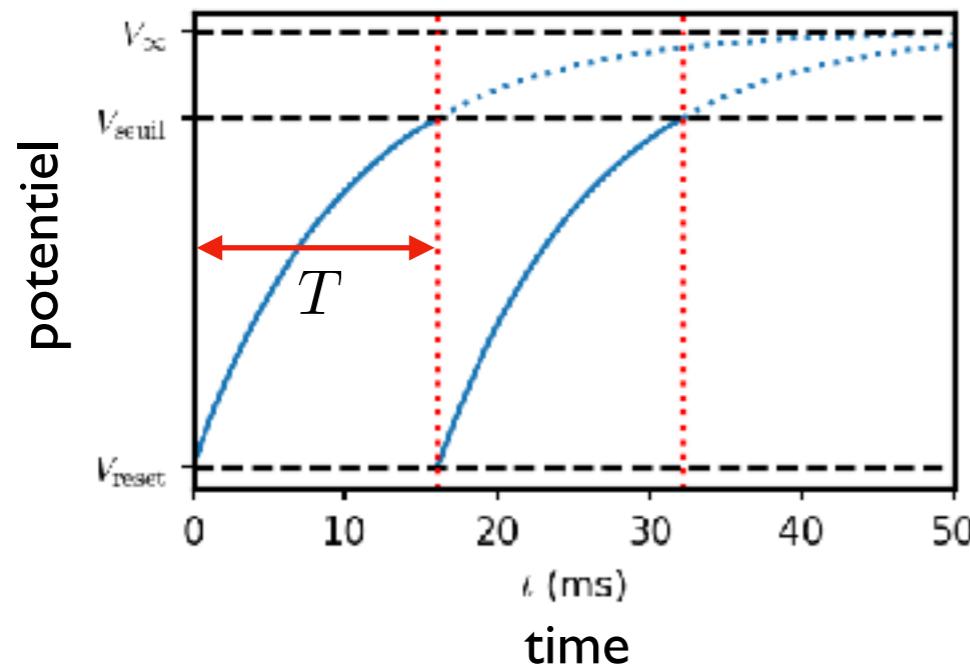


Integrate-and-Fire neuron

- More precisely: “Leaky Integrate-and-Fire” (LIF)

$$C \frac{dV}{dt} = g_L(E_L - V) + I_{\text{syn}}$$

- *Characteristic time constant* of integration of synaptic input: $\tau_m = C/g_L$
- The simplicity of the LIF allows to analytically calculate e.g. the firing rate in *deterministic* et *stochastic* regimes.

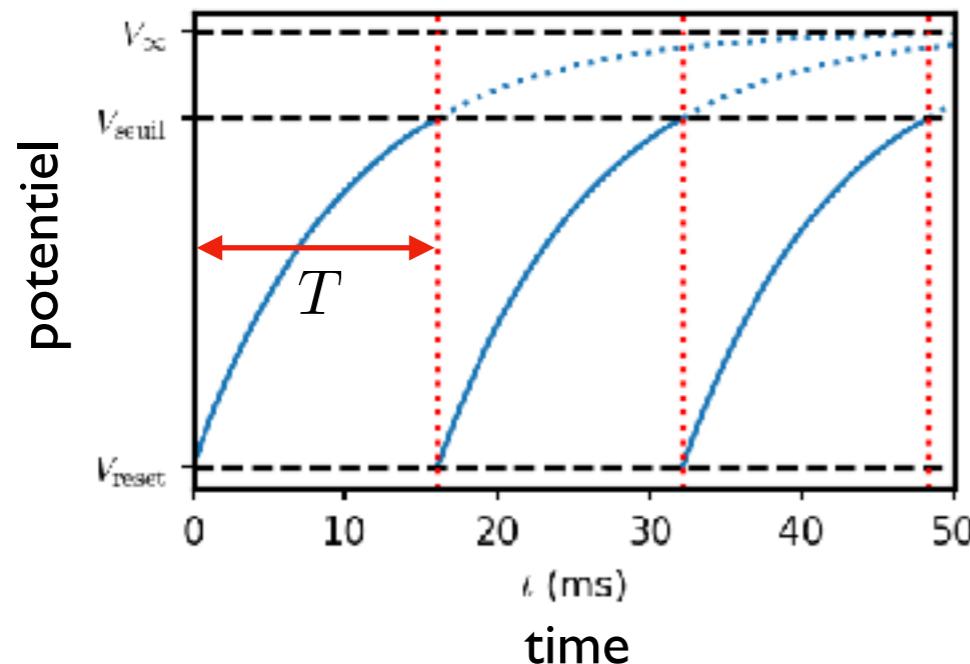


Integrate-and-Fire neuron

- More precisely: “Leaky Integrate-and-Fire” (LIF)

$$C \frac{dV}{dt} = g_L(E_L - V) + I_{\text{syn}}$$

- *Characteristic time constant* of integration of synaptic input: $\tau_m = C/g_L$
- The simplicity of the LIF allows to analytically calculate e.g. the firing rate in *deterministic* et *stochastic* regimes.

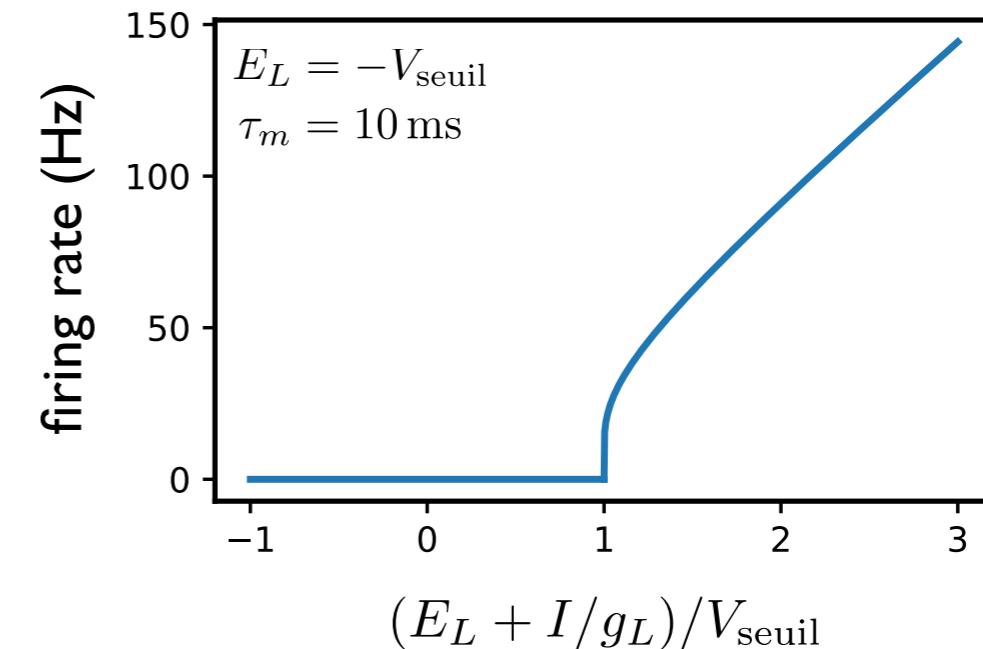
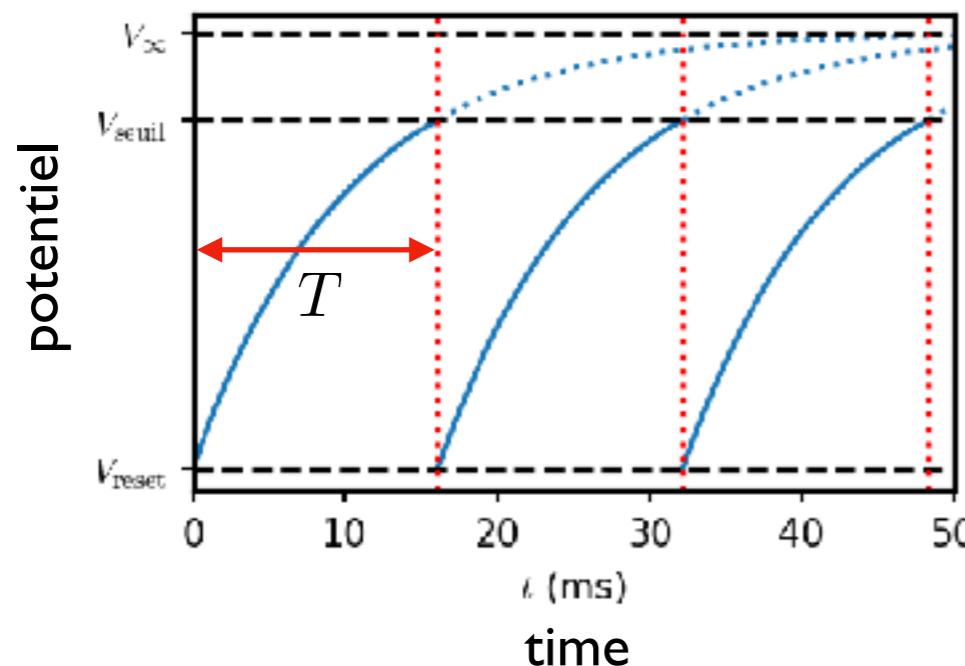


Integrate-and-Fire neuron

- More precisely: “Leaky Integrate-and-Fire” (LIF)

$$C \frac{dV}{dt} = g_L(E_L - V) + I_{\text{syn}}$$

- Characteristic time constant* of integration of synaptic input: $\tau_m = C/g_L$
- The simplicity of the LIF allows to analytically calculate e.g. the firing rate in *deterministic* et *stochastic* regimes.

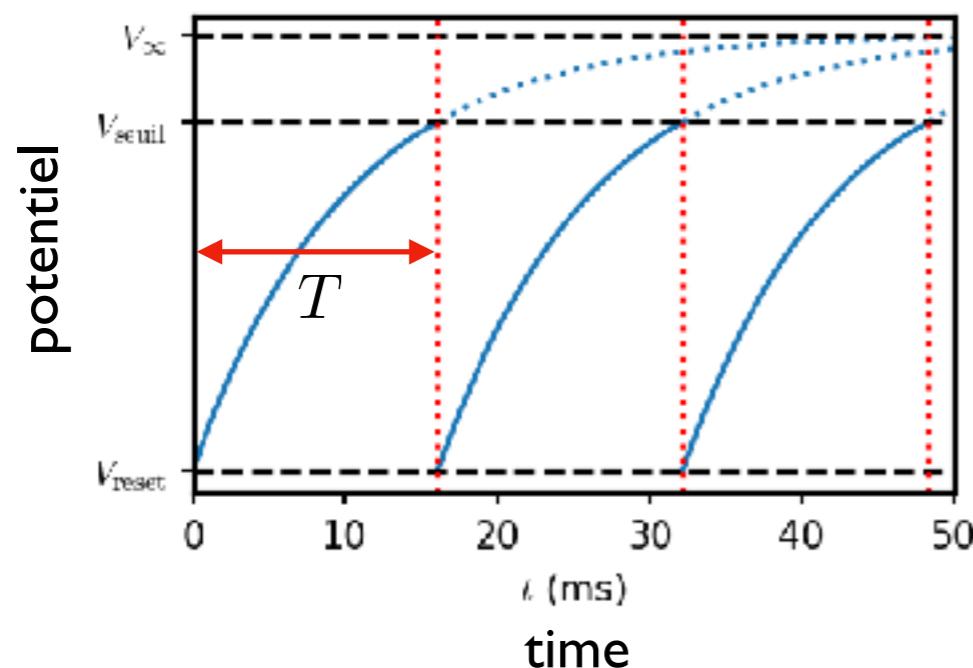


Integrate-and-Fire neuron

- More precisely: “Leaky Integrate-and-Fire” (LIF)

$$C \frac{dV}{dt} = g_L(E_L - V) + I_{\text{syn}}$$

- Characteristic time constant** of integration of synaptic input: $\tau_m = C/g_L$
- The simplicity of the LIF allows to analytically calculate e.g. the firing rate in **deterministic** et **stochastic** regimes.



$$V(T) = V_{\text{threshold}} \Rightarrow T = T(I_{\text{syn}}, \dots)$$

$$\begin{aligned} f(I) &= \frac{1}{T(I)} \\ &= \frac{1}{\tau_m} \left(\log \frac{E_L + I/g_L - V_{\text{reset}}}{E_L + I/g_L - V_{\text{threshold}}} \right)^{-1} \end{aligned}$$

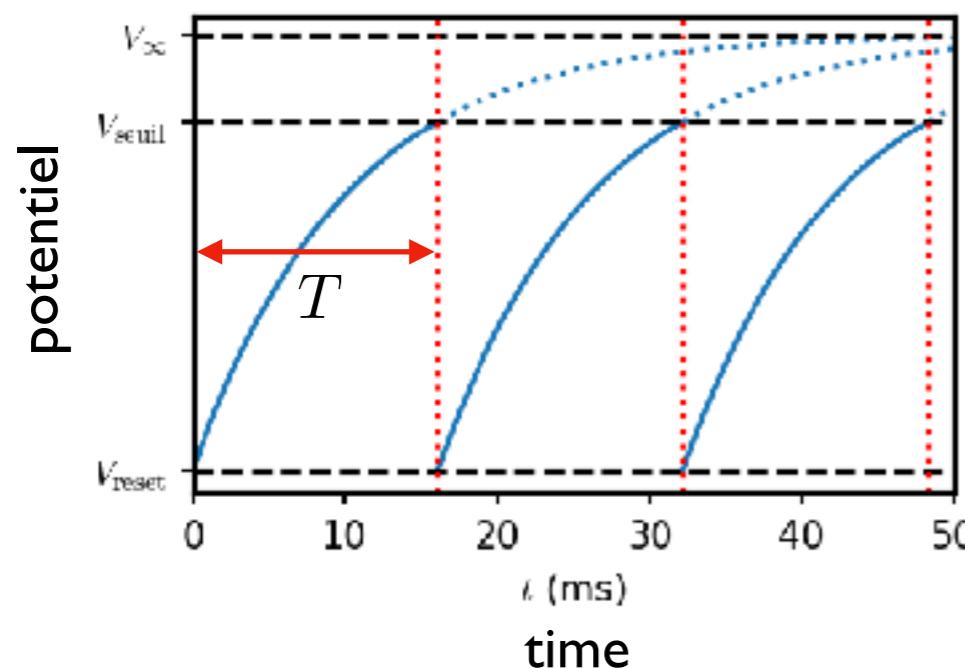
transfer function, or f-I curve

Integrate-and-Fire neuron

- More precisely: “Leaky Integrate-and-Fire” (LIF)

$$C \frac{dV}{dt} = g_L(E_L - V) + I_{\text{syn}}$$

- Characteristic time constant** of integration of synaptic input: $\tau_m = C/g_L$
- The simplicity of the LIF allows to analytically calculate e.g. the firing rate in **deterministic** et **stochastic** regimes.



$$V(T) = V_{\text{threshold}} \Rightarrow T = T(I_{\text{syn}}, \dots)$$

$$\begin{aligned} f(I) &= \frac{1}{T(I)} \\ &= \frac{1}{\tau_m} \left(\log \frac{E_L + I/g_L - V_{\text{reset}}}{E_L + I/g_L - V_{\text{threshold}}} \right)^{-1} \end{aligned}$$

transfer function, or f-I curve

- For a large number of synaptic inputs, we can approximate them by a mean synaptic current + **fluctuations** :

$$I(t) = \sum_j I_{\text{syn},j}(t) \longrightarrow I(t) = I_0 + \sigma \xi(t)$$

Networks of LIF neurons

- Because of their relative simplicity, we can use many connected LIF neurons to model *networks of spiking neurons*:

$$C \frac{dV_i}{dt} = g_L(E_L - V_i) + I_{\text{syn},i} \quad i = 1, \dots, N$$

- Cortical neurons have many ***recurrent connections***:

$$I_{\text{syn},i} = \sum_{\text{connections } j} \sum_{\text{spikes } m} J_{ij} \delta(t - t_m^{(j)} - D)$$

Networks of LIF neurons

- Because of their relative simplicity, we can use many connected LIF neurons to model *networks of spiking neurons*:

$$C \frac{dV_i}{dt} = g_L(E_L - V_i) + I_{\text{syn},i} \quad i = 1, \dots, N$$

- Cortical neurons have many *recurrent connections*:

$$I_{\text{syn},i} = \sum_{\text{connections } j} \sum_{\text{spikes } m} J_{ij} \delta(t - t_m^{(j)} - D)$$

synapse strength (weight) from neuron j to neuron i

Networks of LIF neurons

- Because of their relative simplicity, we can use many connected LIF neurons to model *networks of spiking neurons*:

$$C \frac{dV_i}{dt} = g_L(E_L - V_i) + I_{\text{syn},i} \quad i = 1, \dots, N$$

- Cortical neurons have many *recurrent connections*:

$$I_{\text{syn},i} = \sum_{\text{connections } j} \sum_{\text{spikes } m} J_{ij} \delta(t - t_m^{(j)} - D)$$

synapse strength (weight) from neuron j to neuron i

Network simulation:

Output of LIF integration → spike times → input to LIF integration

Networks of LIF neurons

- Because of their relative simplicity, we can use many connected LIF neurons to model *networks of spiking neurons*:

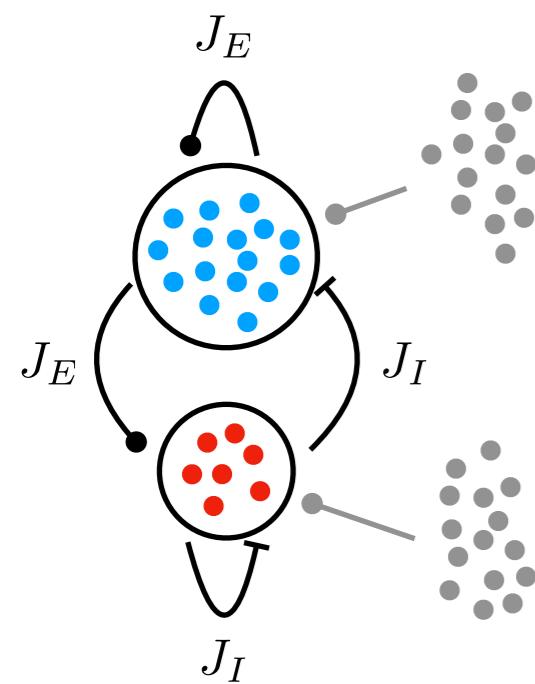
$$C \frac{dV_i}{dt} = g_L(E_L - V_i) + I_{\text{syn},i} \quad i = 1, \dots, N$$

- Cortical neurons have many *recurrent connections*:

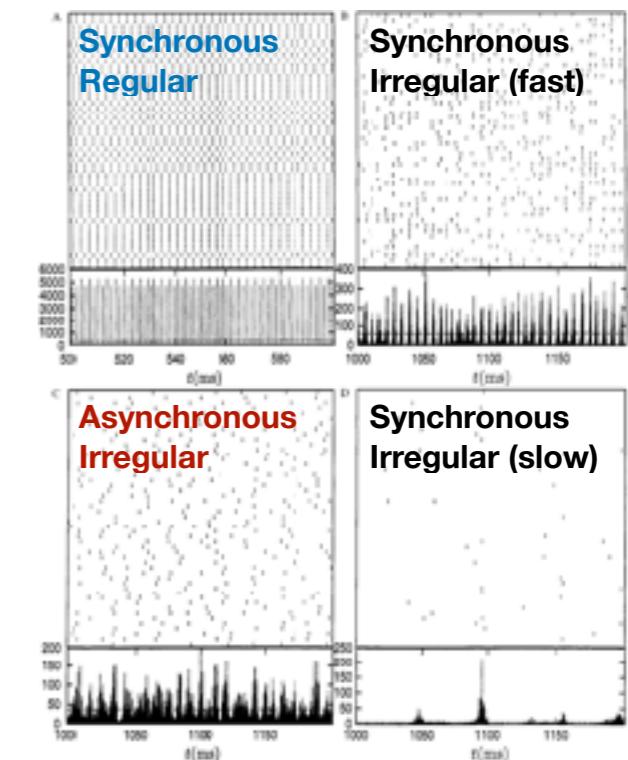
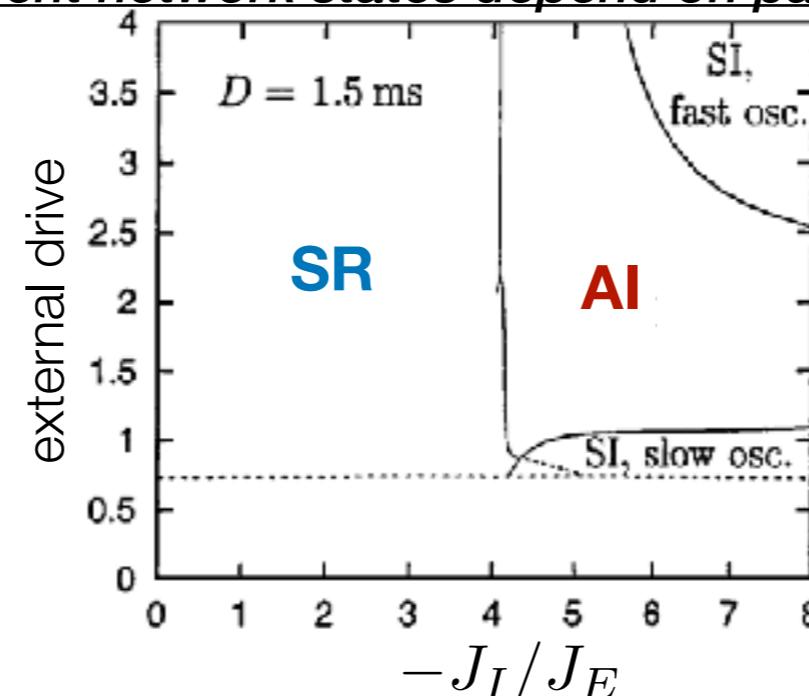
$$I_{\text{syn},i} = \sum_{\text{connections } j} \sum_{\text{spikes } m} J_{ij} \delta(t - t_m^{(j)} - D)$$

synapse strength (weight) from neuron j to neuron i

- Simplicity also allows analytical calculations (“deep” understanding):



Different network states depend on parameters



Networks of LIF neurons

- Because of their relative simplicity, we can use many connected LIF neurons to model *networks of spiking neurons*:

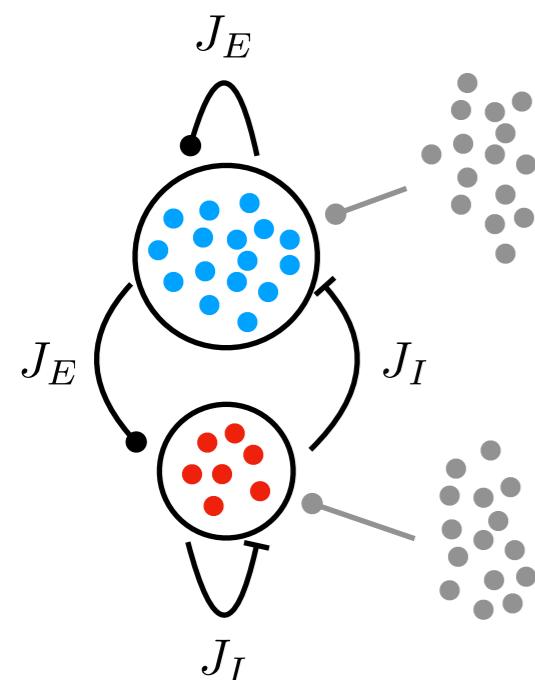
$$C \frac{dV_i}{dt} = g_L(E_L - V_i) + I_{\text{syn},i} \quad i = 1, \dots, N$$

- Cortical neurons have many *recurrent connections*:

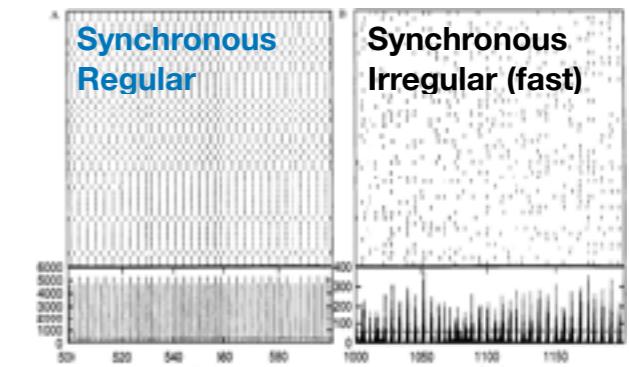
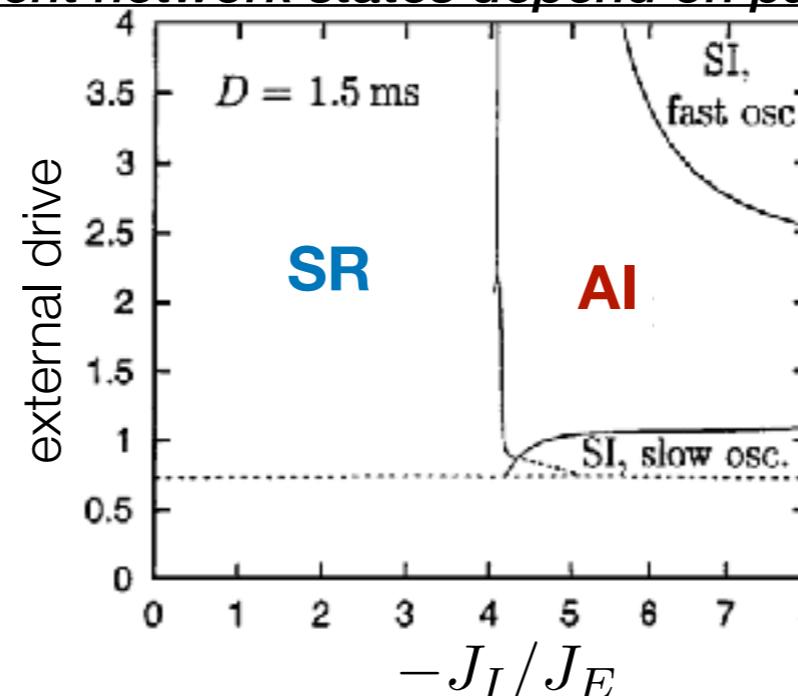
$$I_{\text{syn},i} = \sum_{\text{connections } j} \sum_{\text{spikes } m} J_{ij} \delta(t - t_m^{(j)} - D)$$

synapse strength (weight) from neuron j to neuron i

- Simplicity also allows analytical calculations (“deep” understanding):



Different network states depend on parameters



let's get
hands on !