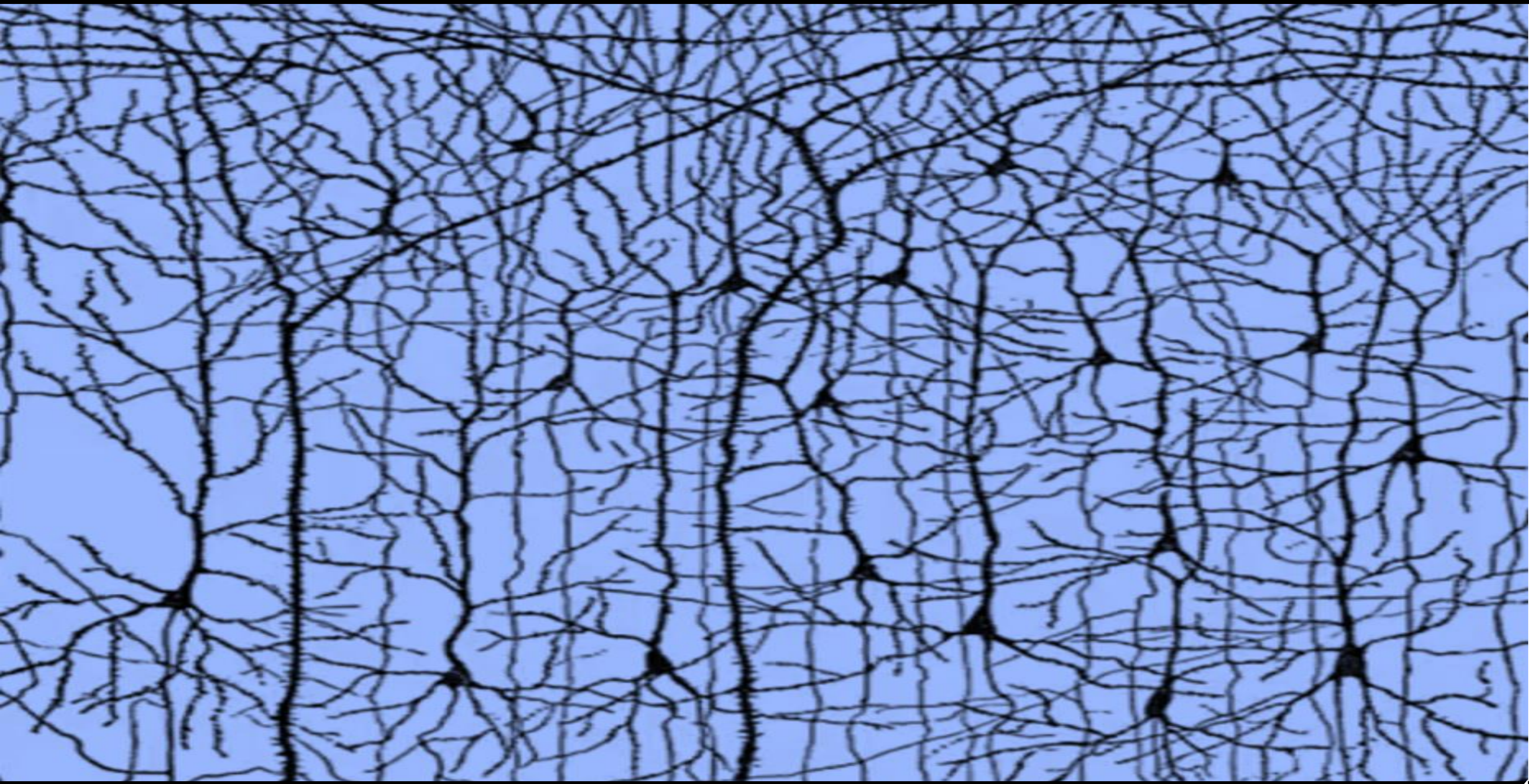
Neuroscience of Learning, Memory, Cognition

Part I: Neuronal Networks



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Network Models

Set I

Course Syllabus

Part I: Neuronal Networks

1. Neuron models
2. Network models (feedforward & recurrent networks)
3. Synaptic plasticity & learning

Part II: The Neural Code

4. Encoding of information
5. Decoding of spike events
6. Information and entropy

Part III: Learning & Memory

7. Reinforcement learning
8. Associative memory

Outline

- Modeling synaptic inputs
- Spiking and firing-rate based network models
- Feedforward networks
- Recurrent networks

Some slides credit:

- Adrienne Fairhall, Rajesh Rao, UW course material 2013-2017
- Wulfram Gerstner, EPFL course material 2018

Other credits as noted on slides

Cover slide drawing: Santiago Ramon Y Cajal

Textbooks:

- Peter Dayan & Larry Abbott “Theoretical Neuroscience”, 2005
- Wulfram Gerstner “Neuronal Dynamics”, 2014
- Eugene Izhikevich “Dynamical Systems in Neuroscience”, 2010

Reference book:

- Paul Miller “An Introductory Course in Computational Neuroscience”, 2018

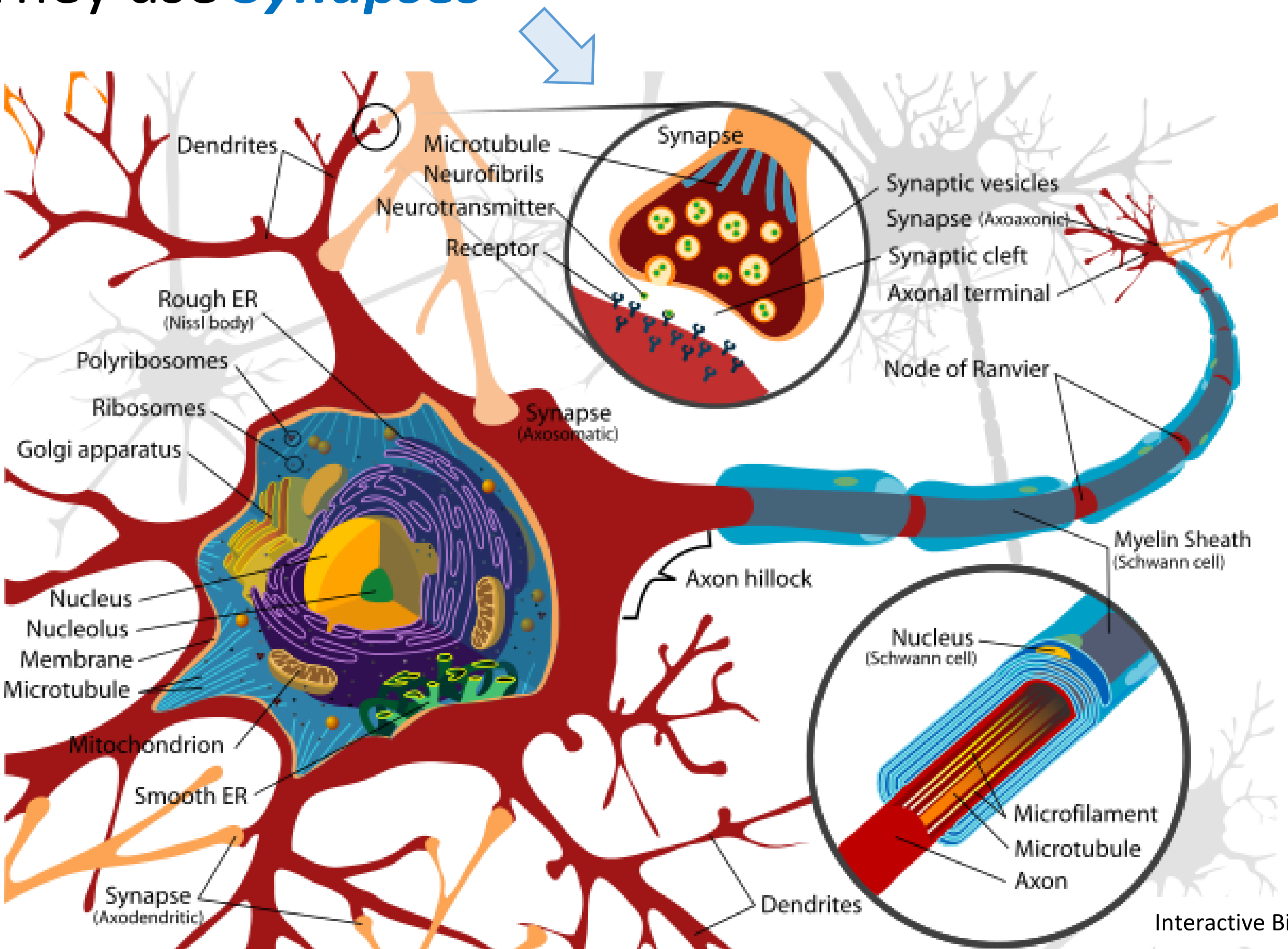
Outline

- Modeling synaptic inputs
  - Excitatory and inhibitory synapses
  - Modeling the effects of a synapse
  - Linear filter model of a synapse
- From spiking to firing-rate-based network
  - Multiple synapses
  - Firing-rate-based network
- Feedforward networks
  - Linear feedforward networks
  - Large networks: Continuous model
  - Mexican hat model
- Recurrent networks
  - Network stability
  - Application: Memory
  - Nonlinear recurrent networks
  - Excitatory–inhibitory networks
  - Phase plane stability analysis
  - Oscillations in olfactory system

Excitatory and Inhibitory Synapses

What is a Synapse?

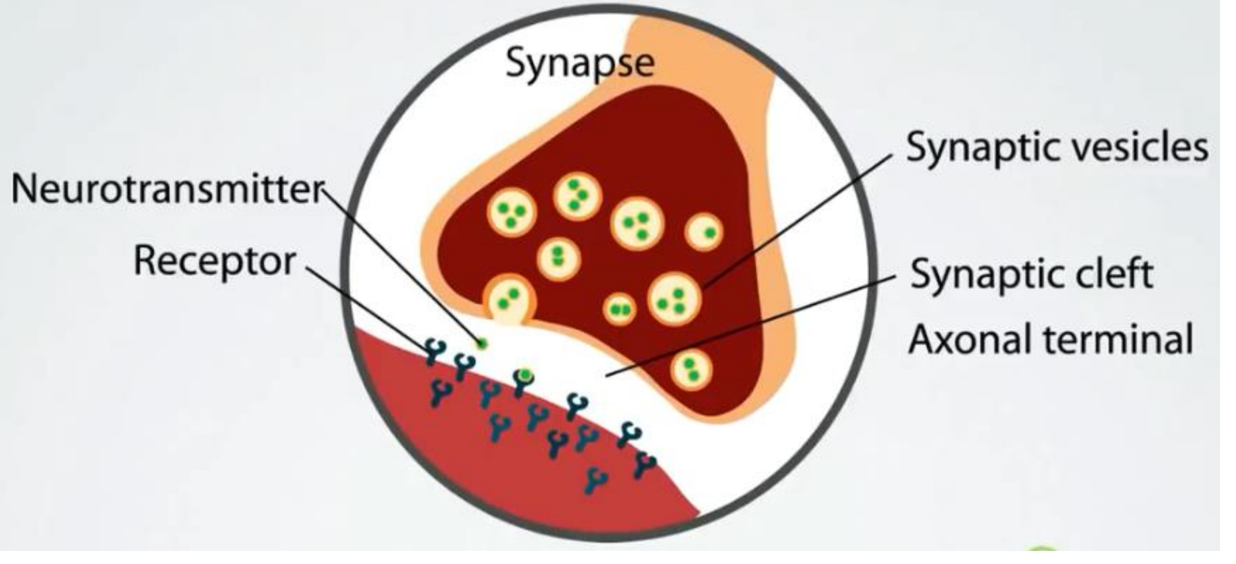
- How do neurons connect to form networks?
  - ➢ They use ***Synapses***



Interactive Biology

What is a Synapse?

- A ***Synapse*** is a connection or junction between two neurons



What is a Synapse?

A single cortical neuron can have up to 10,000 synapses on its dendrites and the cell body

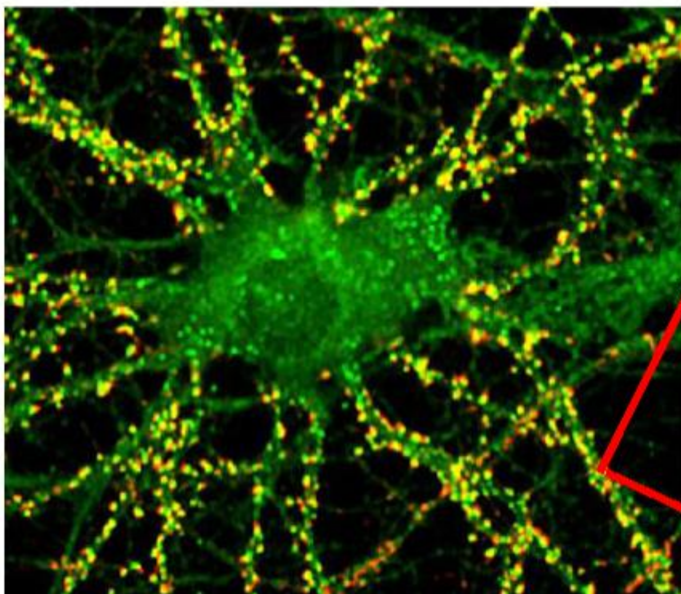
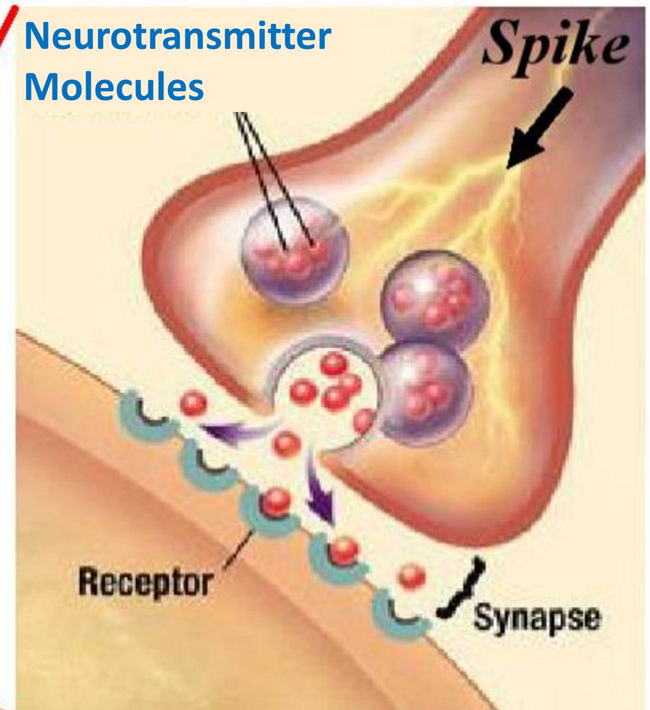


Image Credit: Kennedy lab, Caltech.
http://www.its.Caltech.edu/~mbkl



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What is a Synapse?

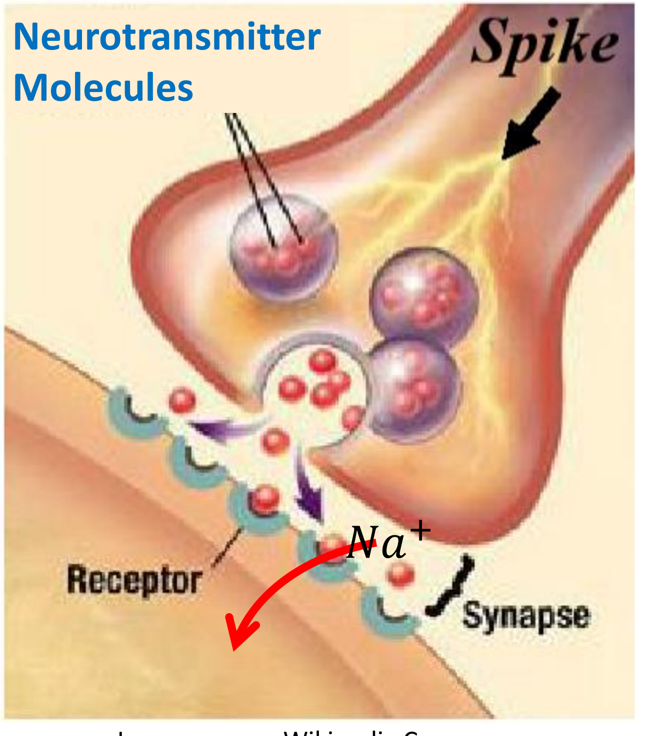
- A ***Synapse*** is a connection or junction between two neurons

⇨ Chemical synapses use *neurotransmitters*

Sequence of events:

- Electrical activity in axon
- → Chemical activity in the synapse
- → Electrical activity in the post-synaptic dendrite

➢ ***Let's see how this works***



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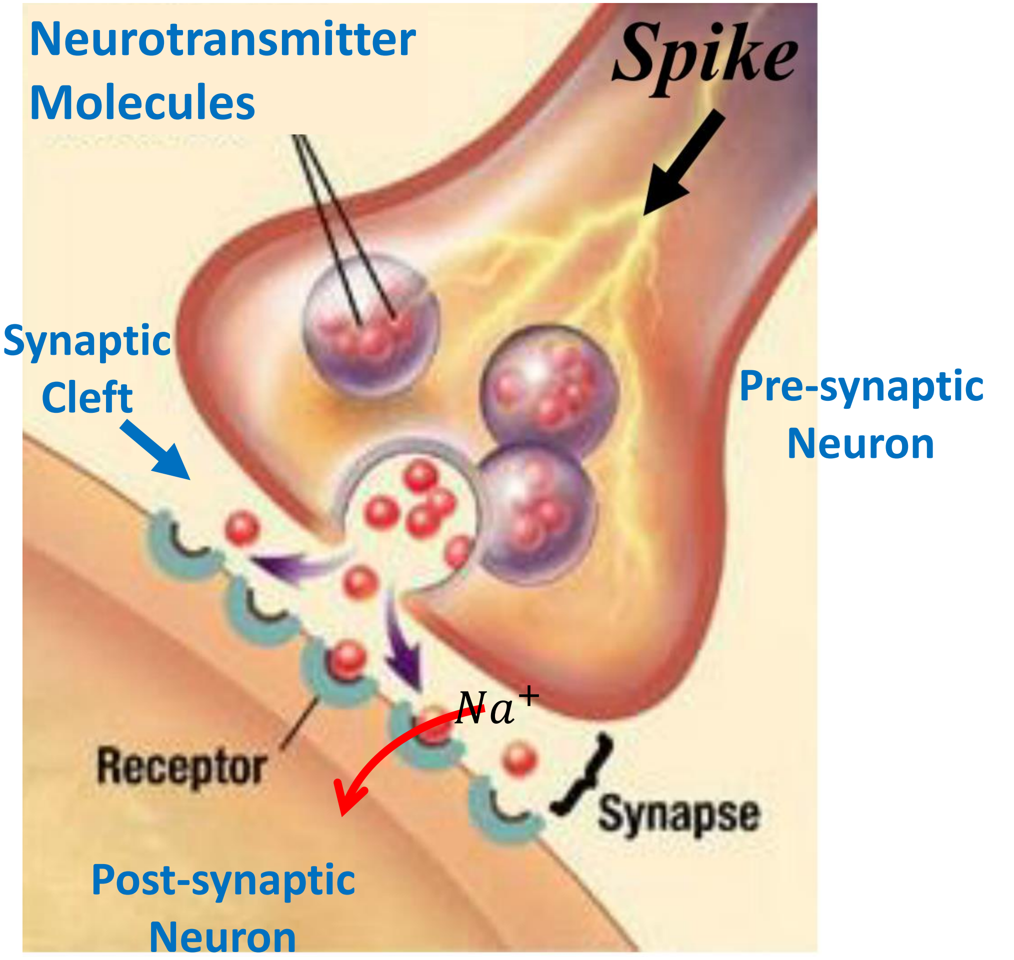
What is a Synapse?

- Spikes from ***pre-synaptic*** neuron's axon cause ***neurotransmitters*** to be released into the ***synaptic cleft***
- Neurotransmitters bind with ***receptors*** on the ***post-synaptic*** neuron's membrane
- Ions (e.g. Na^+) flow through the channels controlled by the receptors
- This causes an ***increase*** (or a ***decrease***) in the membrane potential (depending on the type and direction of the ion flow)



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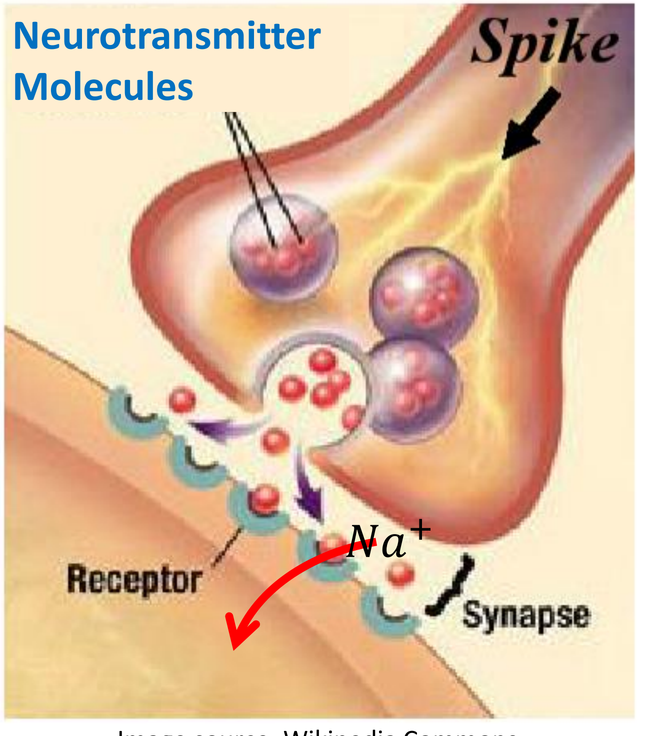
What is a Synapse?

In addition to transmission of information between the two neurons:

- This mechanism allows for **adjustment of the strength** between the spikes of the two neurons (in an adaptive way)

  (by controlling the number and activity of the receptors)

- **Chemical synapses are the basis of learning and memory**



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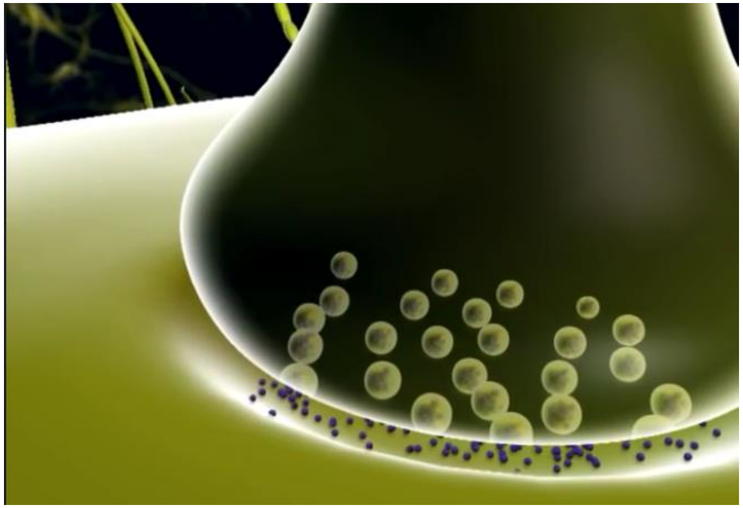
Types of Synapses

- ***Chemical synapses:***
  - Use neurotransmitters to communicate between two neurons
  - Are the most common type of synapse found in the brain



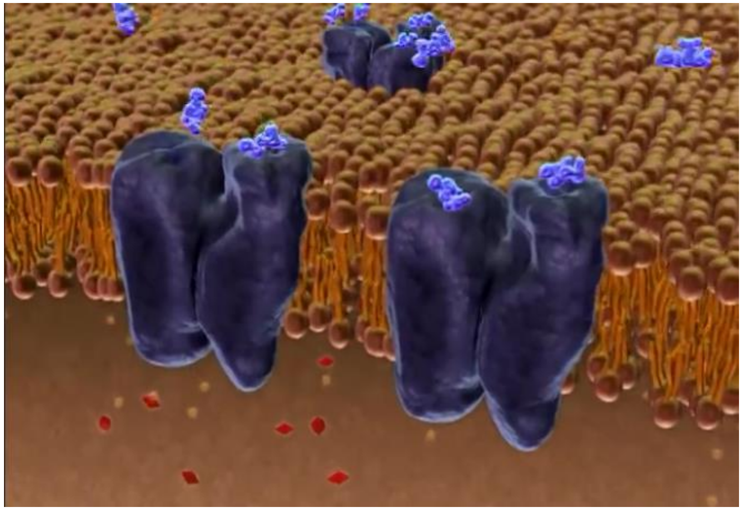


Image source: Pearson Education, Inc.

Types of Synapses

- There is also another type of synapse: ***electrical synapse***

➪ Electrical synapses use *gap junctions*
➪ Chemical synapses use *neurotransmitters*

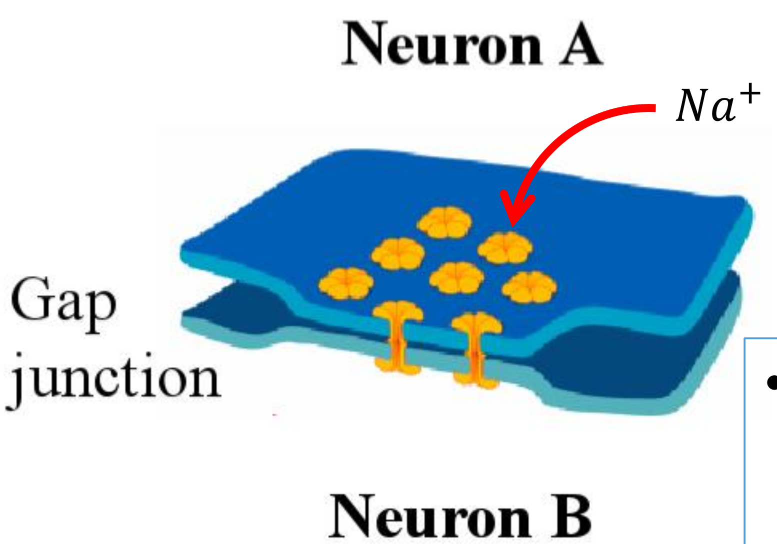


Image source: Wikipedia Commons

- Ionic channels connect the membranes of two neurons:
  - Higher concentration of ions on one side causes migration of some ions to the other side through the ***gap junctions***

- This type of synapse is used for fast connection between two neurons:
  - ***No delay*** caused by channel dynamics
  - The two neurons are ***synchronized***
  - ***No adaptation*** occurs

- Some motor neurons are of this type (fast transmission, no adaptation)

Synapses can be **Excitatory** or **Inhibitory**

Review

An **Excitatory** Synapse

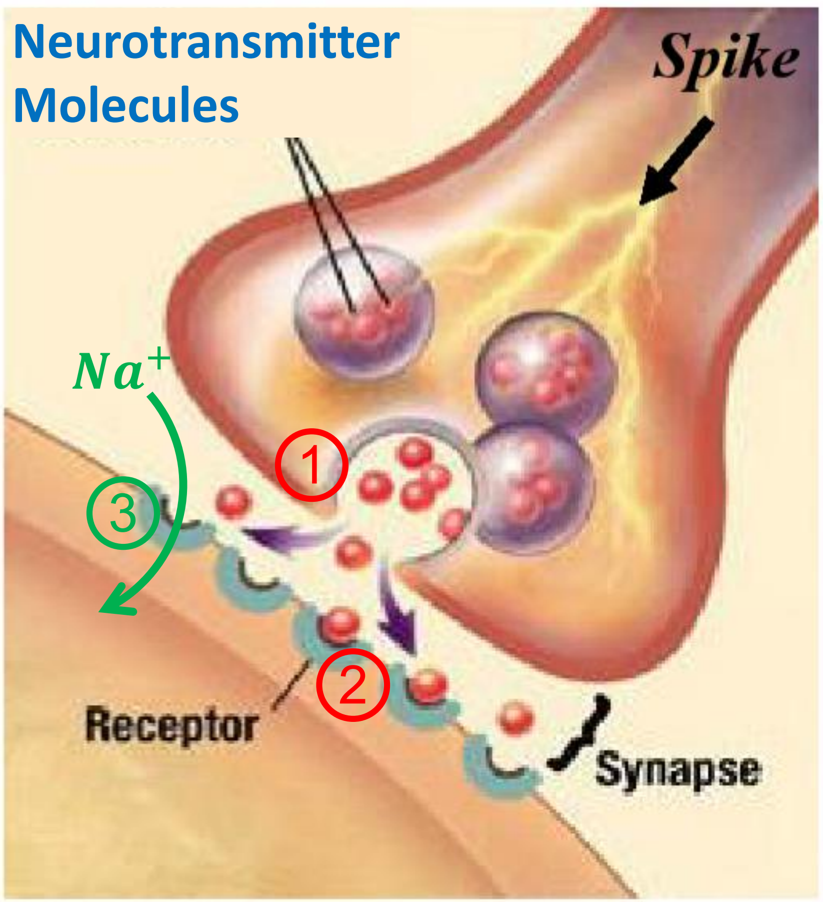


Image source: Wikipedia Commons

1. Input spike → Neurotransmitter release (e.g. Glutamate)

2. Neurotransmitter binds to ion channel receptor → Ion channel opens

3. Na+ influx → Depolarization

Called: EPSP (**Excitatory** Post-Synaptic Potential)

Synapses can be Excitatory or Inhibitory

Review

An **Inhibitory** Synapse

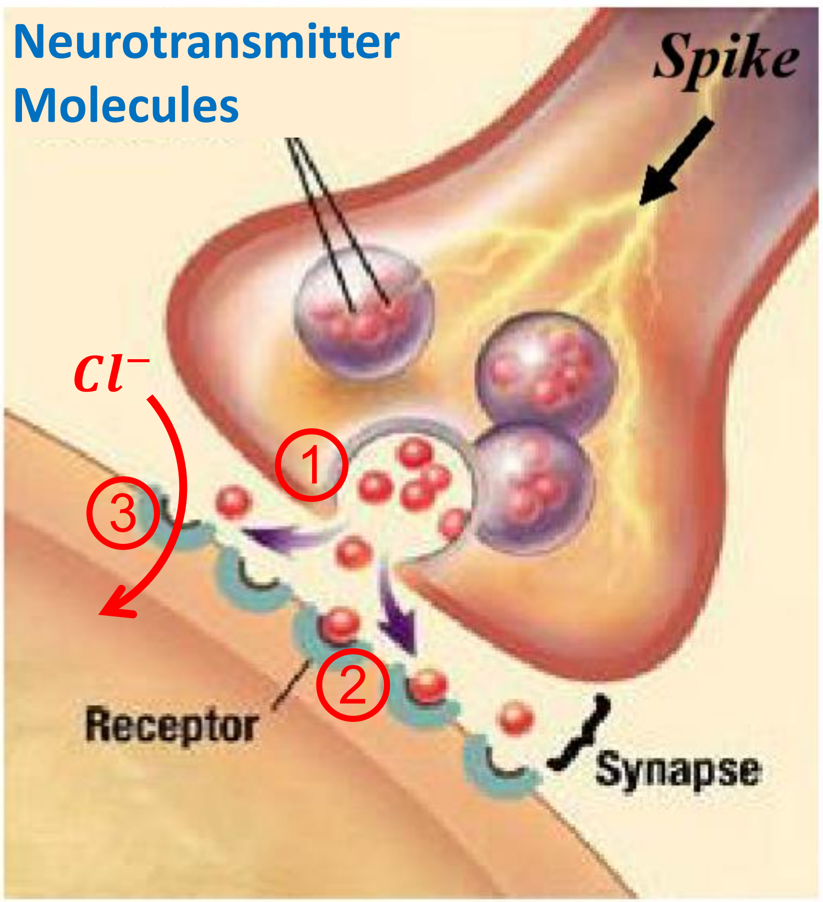


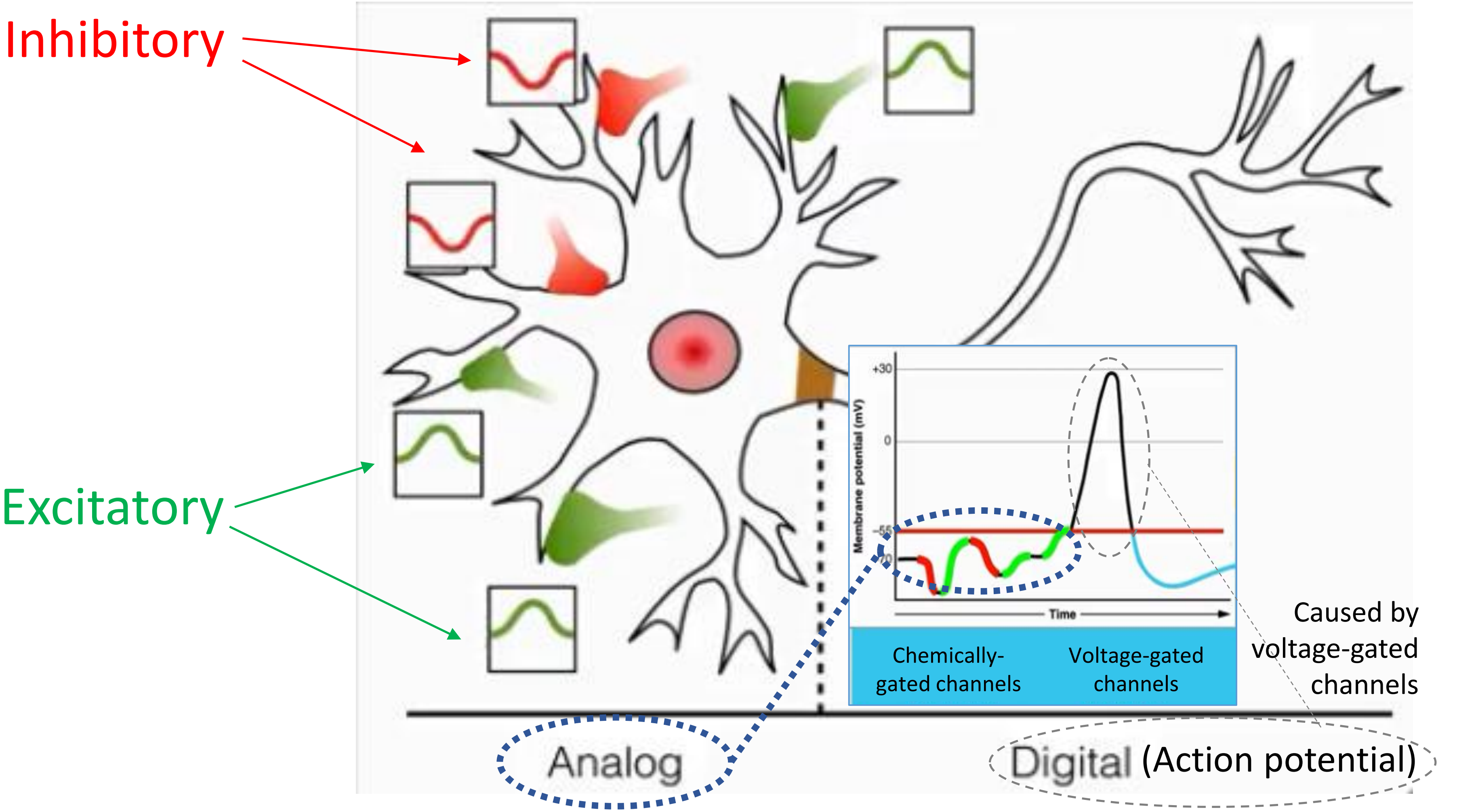
Image source: Wikipedia Commons

1. Input spike → Neurotransmitter release (e.g. GABA)
2. Neurotransmitter binds to ion channel receptor → Ion channel opens
3. K+ outflux or Cl- influx → Hyperpolarization

Called: IPSP (**Inhibitory** Post-Synaptic Potential)

Synapses can be **Excitatory** or **Inhibitory**

Review



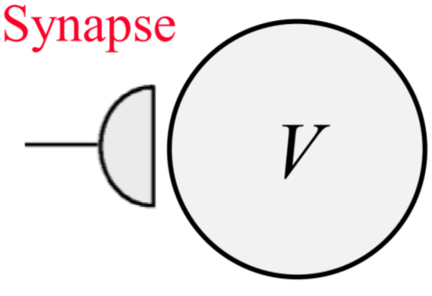
- ***We will now derive a mathematical formula for the operation of a neuron in its linear region***

Paul Andersen, BozemanScience.com

Modeling the Effects of a Synapse

Modeling the Effects of a Synapse

- We will now model the dynamics of a neuron in transferring its input current (ions entering through synapses) to voltage (a change in the membrane potential):
  - The membrane allows synaptic current I_s into the cell (with its time constant τ_s)
  - The voltage V has its own time constant τ_m
  - And follows the input current via a nonlinear function $F(I_s(t))$

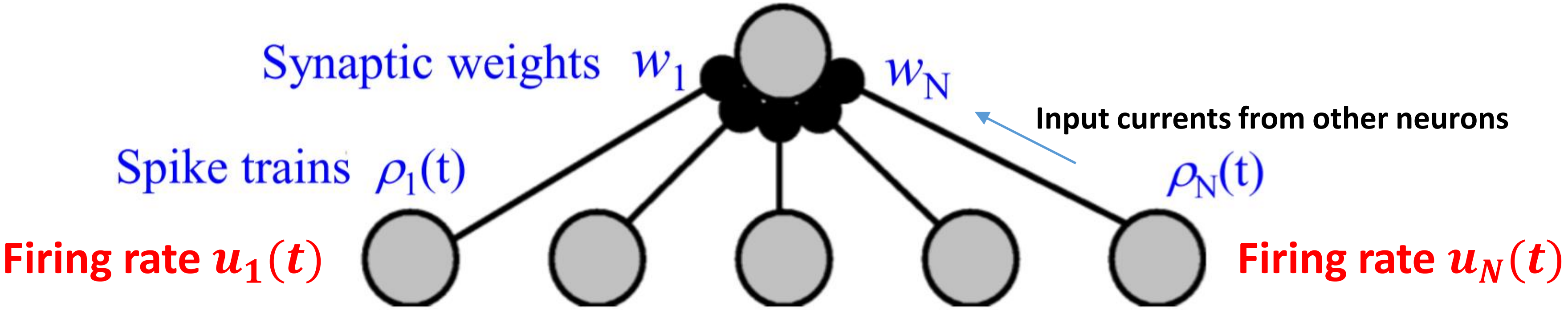


Modeling the Effects of a Synapse

- This approach allows us to add two important effects:

  1. Modeling of ***multiple input currents*** into a neuron (and expressing a neuron's output as weighted sum of its inputs)

  2. Moving from spiking model for a neuron to ***firing rate model*** (hence allowing to work with continuous functions and linear algebra in network-based analysis)

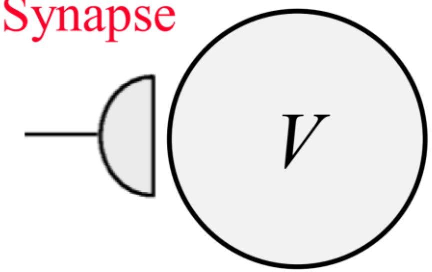


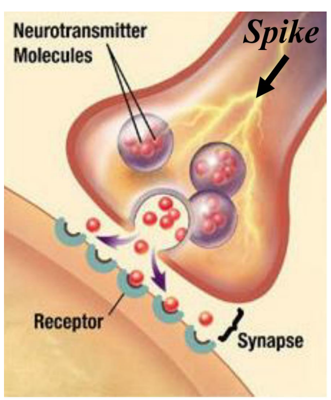
Modeling the Effects of a Synapse

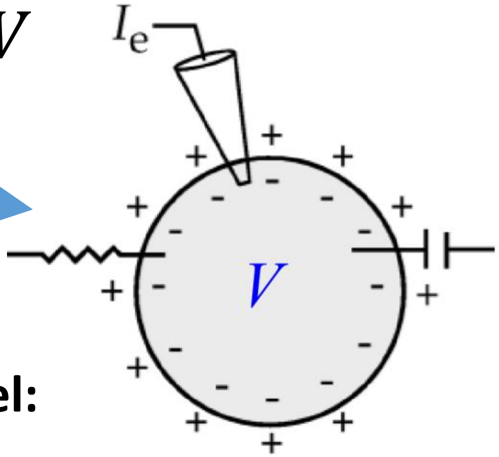
- We want to build a computational model of the effects of a synapse on the membrane potential V

Synapse

Membrane







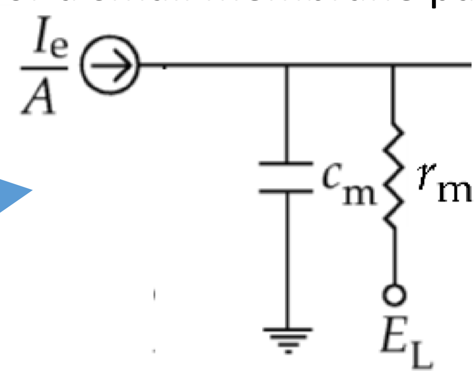
Starting again from the leakage model:

RC circuit model of the membrane

(using equivalent leakage values)

$$c_m \frac{dV}{dt} = -\frac{V - E_L}{r_m} + \frac{I_e}{A}$$

For a small membrane patch:



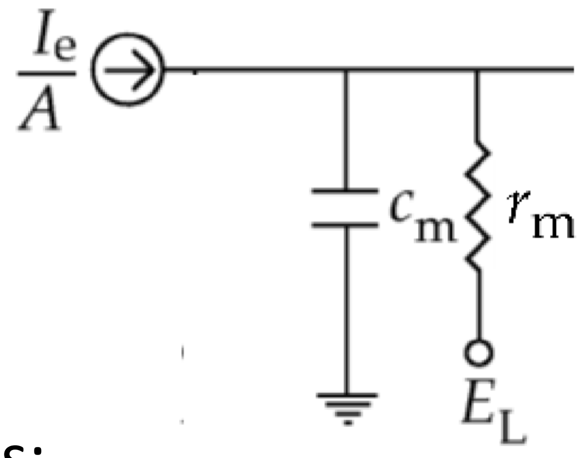
$E_L = -65\ mV$

We modeled voltage-gated channels earlier, here we will model the dynamics of synaptic channels

Modeling the Effects of a Synapse

- Circuit equation:

$$c_m \frac{dV}{dt} = -\frac{V - E_L}{r_m} + \frac{I_e}{A}$$



- Define membrane time constant as:

$\tau_m = r_m c_m = R_m C_m$ $\quad (R_m = \frac{r_m}{A}, C_m = c_m A)$

$c_m \approx 10\ \mathrm{nF/mm^2}$

$r_m \approx 1\ \mathrm{M\Omega\ mm^2}$

$C_m = c_m A$

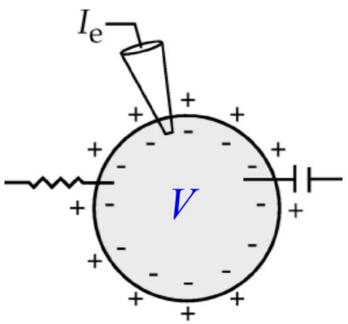
$R_m = r_m / A$

$$\Rightarrow \quad \boxed{\tau_m \frac{dV}{dt} = -(V - E_L) + I_e R_m}$$

- This equation describes how the membrane potential behaves as a function of time as some current is injected into the cell

Modeling the Effects of a Synapse

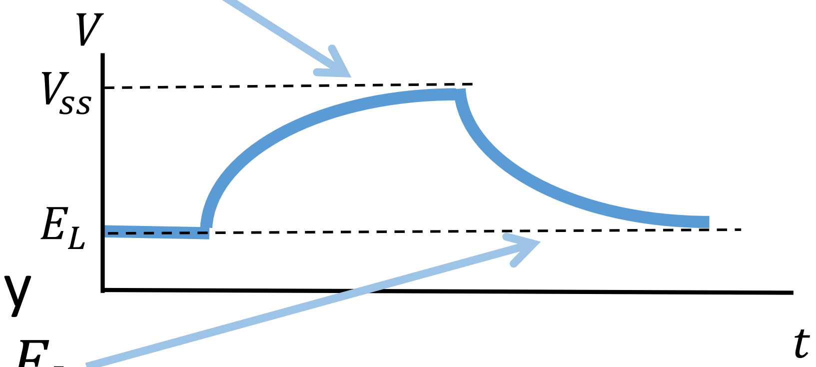
- What is this equation saying about the membrane potential? $\tau_m \frac{dV}{dt} = -(V - E_L) + I_e R_m$



1. If we inject a fixed current into this neuron, the voltage will rise and stabilize at the steady state value V_{ss}:

$$\frac{dV}{dt} = 0 \quad \rightarrow \quad V_{ss} = E_L + I_e R_m$$

2. If we turn off the input current there will be an exponential decay back to the equilibrium potential E_L

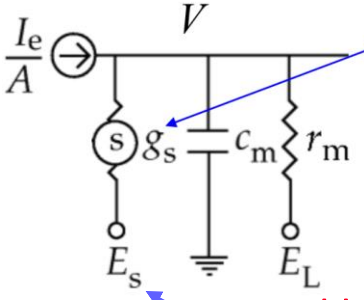


- The time constant τ_m determines the speed of convergence of the voltage to its final values

Modeling the Effects of a Synapse

- Let’s add the effect of the synaptic channels:

$$c_m \frac{dV}{dt} = -\underbrace{\frac{V - E_L}{r_m}}_{\text{Leakage current}} - \underbrace{g_s(V - E_s)}_{\text{Synaptic current}} + \frac{I_e}{A}$$



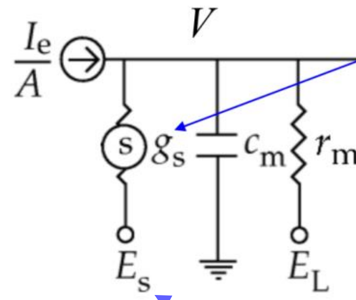
Synaptic conductance

Equilibrium potential of the synapse

Modeling the Effects of a Synapse

- Let's add the effect of the synaptic channels:

$$c_m \frac{dV}{dt} = -\underbrace{\frac{V - E_L}{r_m}}_{\text{Leakage current}} - \underbrace{g_s(V - E_s)}_{\text{Synaptic current}} + \frac{I_e}{A}$$



Synaptic conductance

Equilibrium potential of the synapse

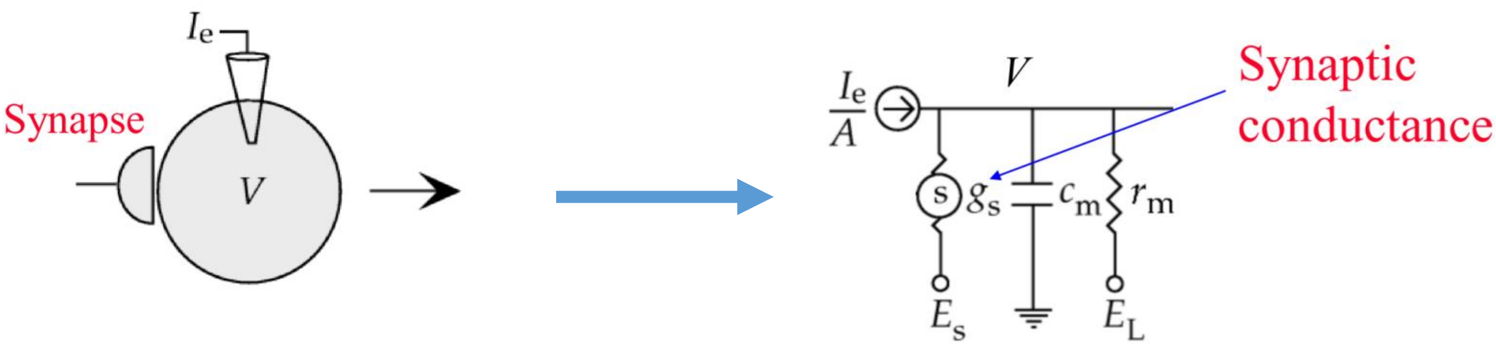
- At steady state ($\frac{dV}{dt} = 0$) (for a constant leakage current), membrane potential approaches E_s (i. e. $V \rightarrow E_s$) (and no current passes through g_s)

And at steady state:
$V_{ss} = E_L + I_e r_m = E_s$

- Both excitatory and inhibitory synapses can be modeled by this equation:
  - If the synapse is **excitatory**:
    $$V \rightarrow E_s = +50\ mV$$
  - If the synapse is **inhibitory**:
    $$V \rightarrow E_s = -80\ mV$$

Modeling the Effects of a Synapse – Summary

$$c_m \frac{dV}{dt} = -\frac{V - E_L}{r_m} - g_s(V - E_s) + \frac{I_e}{A}$$



- How do we model the effects of input spikes on the ***synaptic conductance*** g_s?

Modeling the Effects of a Synapse

- How do we model the effects of input spikes on the ***synaptic conductance*** g_s?

$$g_s = g_{s,max} P_{rel} P_s$$

- $g_{s,max}$: **Maximum conductance** associated with this particular synapse:
  - Related to **number of channels** on the post-synaptic neuron

- P_{rel}: Probability of **release of neurotransmitter**, given that there is an input spike:
  - Once there is an input spike, what is the probability that neurotransmitters are going to be released into the synaptic cleft?

- P_s: Probability of post-synaptic **channels being open** (or the fraction of channels opened at any point in time, minus the fraction of channels being closed)

Basic Synapse Model

- A simple model for how a synapse behaves:

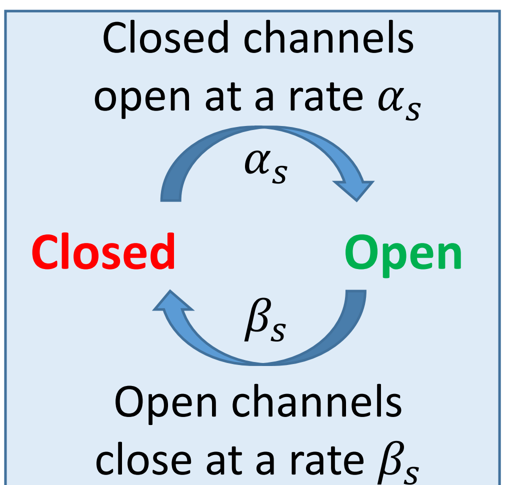
  1. Assume $P_{rel} = 1$
     - i.e. when there is a spike at the presynaptic neuron, it will **always cause the release of neurotransmitters** into the synaptic cleft

  2. Model the effect of a single spike input on P_s

     (i.e. the change in the fraction of channels that are open on the post-synaptic neuron):

     - Kinetic model of post-synaptic channels:

$$g_s = g_{s,max} P_{rel} P_s$$



Fraction of channels that are closed

Fraction of channels that are open

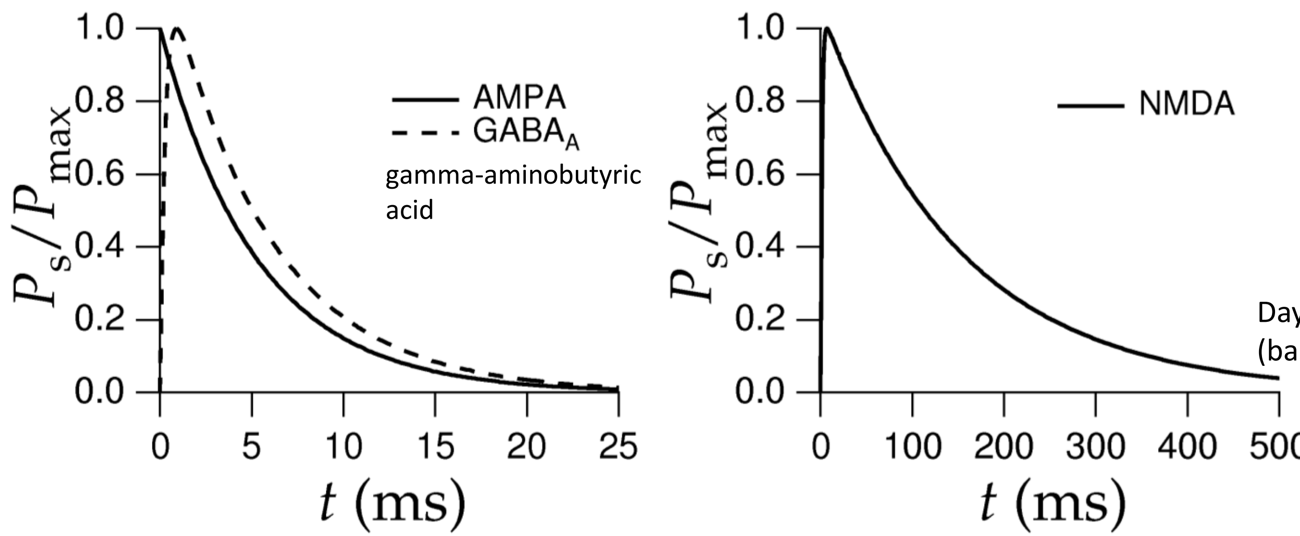
$$\frac{dP_s}{dt} = \alpha_s (1 - P_s) - \beta_s P_s$$

Channel opening rate

Channel closing rate

Basic Synapse Model

- What does P_s look like over time given a spike?



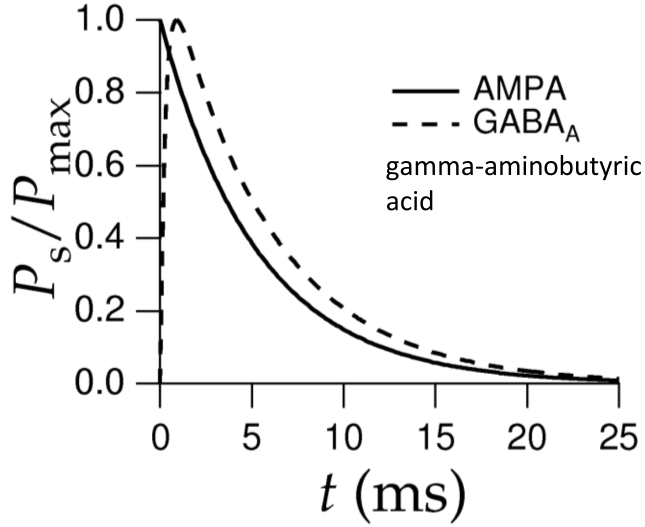
Dayan & Abbott Book
(based on biological data)

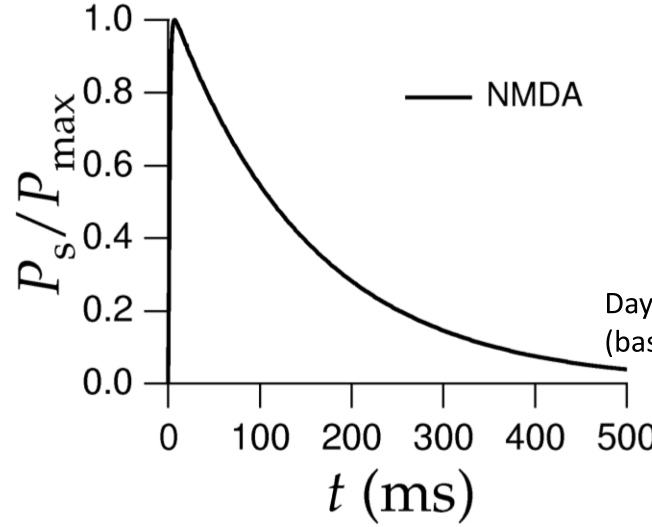
- ***Exponential function*** yields reasonable fit for some synapses (e.g. AMPA synapse)

$$K(t) = e^{-\frac{t}{\tau_s}}$$

Basic Synapse Model

- What does P_s look like over time given a spike?





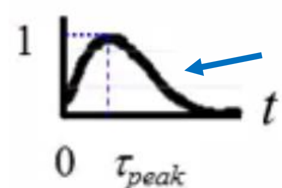
Dayan & Abbott Book
(based on biological data)

- ***Exponential function*** yields reasonable fit for some synapses (e.g. AMPA synapse)

$$K(t) = e^{-\frac{t}{\tau_s}}$$

- Others (e.g. NMDA, GABA$_A$ synapses) can be fitted using ***Alpha function***

$$\alpha(t) = \frac{t}{\tau_{peak}} e^{1-\frac{t}{\tau_{peak}}}$$

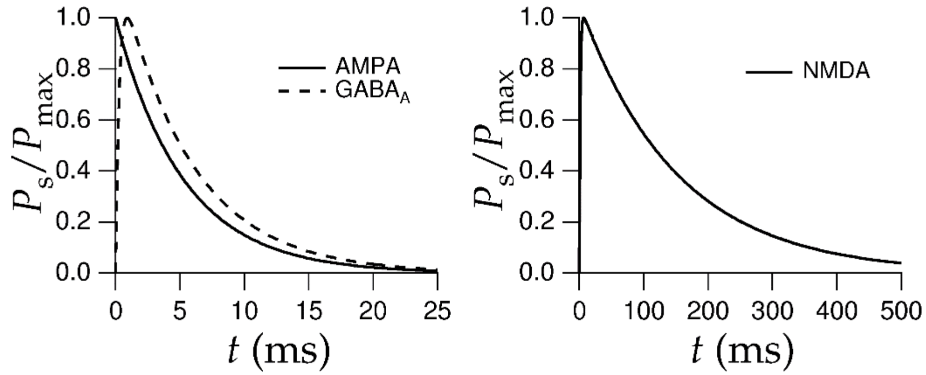


Decays with a time constant τ_{peak}

(Different mathematical forms are used to model these functions, see Dayan & Abbott Book)

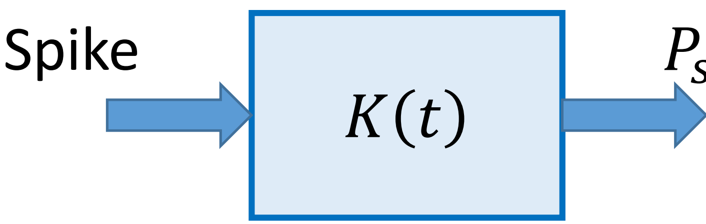
Basic Synapse Model

- What does P_s look like over time given a spike?



Dayan & Abbott Book (based on biological data)

For AMPA channel
we can model:



$$P_s(t) = K(t)$$

$$\boxed{K(t) = e^{-\frac{t}{\tau_s}}}$$

impulse response

Linear Filter Model of a Synapse

Linear Filter Model of a Synapse –
Delta Function (Review)

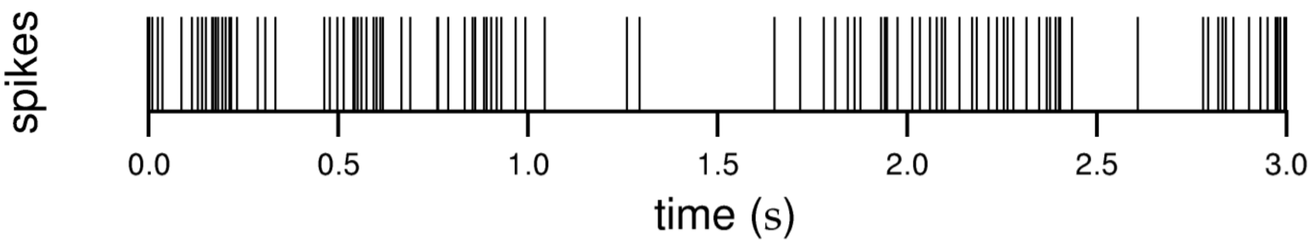
Practice in HW

- What if there are more than one spikes?
- Let's model the effect of a train of spikes on P_s
  (P_s : Probability of post-synaptic channels opening)

- Write the input spike train as:

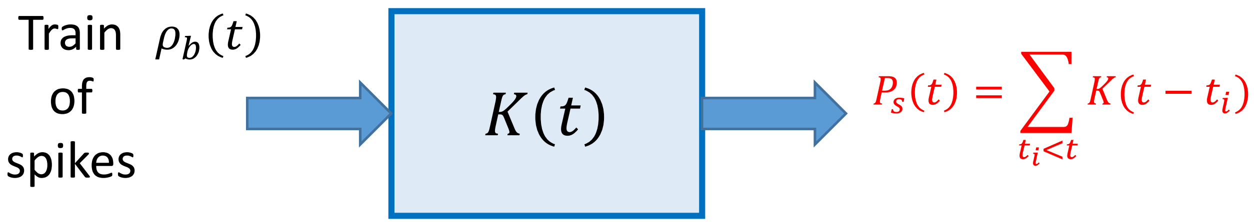
$$\rho_b(t) = \sum_i \delta(t - t_i)$$

where t_i are the input spike times

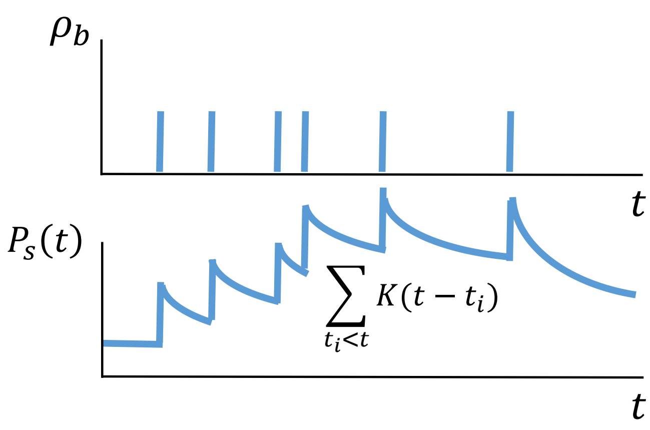


Linear Filter Model of a Synapse – Delta Function (Review)

Practice in HW



- Assuming $K(t)$ as the exponential function: $K(t) = e^{-\frac{t}{\tau_s}}$



Linear Filter Model of a Synapse –
Delta Function (Review)

Practice in HW

- We know that any function $h(t)$ can be written as:

$$h(t) = \int_{-\infty}^{\infty} h(\tau)\, \delta(t - \tau)\, d\tau$$

(Sifting property)

- We can use simple math to write:

(see derivation details on next page – *simple exercise*)

$$\boxed{\sum_{t_i<t} h(t - t_i) = \int_{-\infty}^{t} h(t - \tau)\rho(\tau)d\tau}$$

$$\rho(t) = \sum_i \delta(t - t_i)$$

Linear Filter Model of a Synapse –
Delta Function (Review)

Practice in HW

- We know that any function $h(t)$ can be written as:

$$h(t) = \int_{-\infty}^{\infty} h(\tau)\, \delta(t-\tau)\, d\tau$$

- We can also write:

$$\sum_{t_i<t} h(t-t_i) = \sum_{t_i<t} \int_{-\infty}^{\infty} h(\tau)\, \delta(t-t_i-\tau)\, d\tau$$

$$= \int_{-\infty}^{\infty} h(\tau) \left(\sum_{t_i<t} \delta(t-t_i-\tau) \right) d\tau$$

$$= \int_{0}^{\infty} h(\tau)\rho(t-\tau)d\tau$$

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

$$\boxed{\sum_{t_i<t} h(t-t_i) = \int_{-\infty}^{t} h(t-\tau)\rho(\tau)d\tau}$$

$\delta(t-t_i-\tau)$

Nonzero for:

$\tau = t - t_i$

$\sum_{t_i<t} \delta(t-t_i-\tau)$

All spikes for:

$\tau = t - t_i > 0$

$$\rho(t) = \sum_i \delta(t-t_i)$$

$$\rho(t-\tau) = \sum_i \delta(t-t_i-\tau)$$

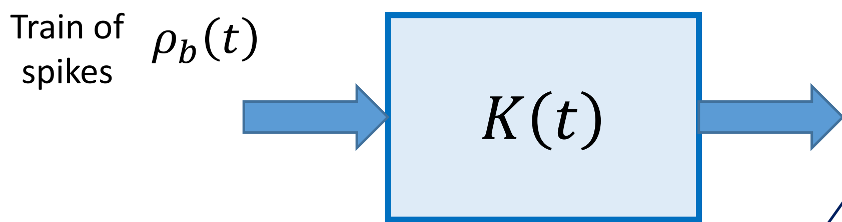
For $\tau = t - t_i > 0 \rightarrow$

$$\rho(t-\tau)_{\tau>0} = \sum_{t_i<t} \delta(t-t_i-\tau)$$

Linear Filter Model of a Synapse

Practice in HW

- We can use the ***linear filter*** model (with an impulse response $K(t)$) to derive the effect of the synapse on a train of input spikes:



$$P_s(t) = \sum_{t_i<t} K(t-t_i) = \int_{-\infty}^{t} K(t-\tau)\rho_b(\tau)d\tau$$

- Using $g_s(t) = g_{s,max} P_{rel} P_s(t)$ (with assumption $P_{rel} = 1$) yields for input from a neighbour b ($b = 1, \dots, N$):

$$g_b(t) = g_{sb,max} \sum_{t_i<t} K(t-t_i) = g_{sb,max} \int_{-\infty}^{t} K(t-\tau)\rho_b(\tau)d\tau$$

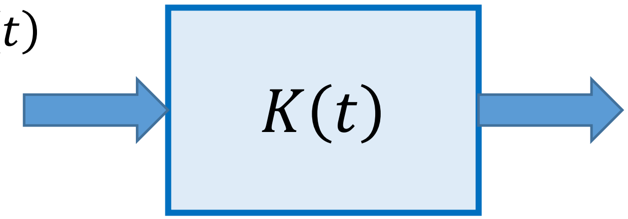
Synaptic conductance
(for neighbor b)

- This is the conductance g_b of one of the inputs to a neuron

Linear Filter Model of a Synapse

Practice in HW

Train of spikes $\rho_b(t)$



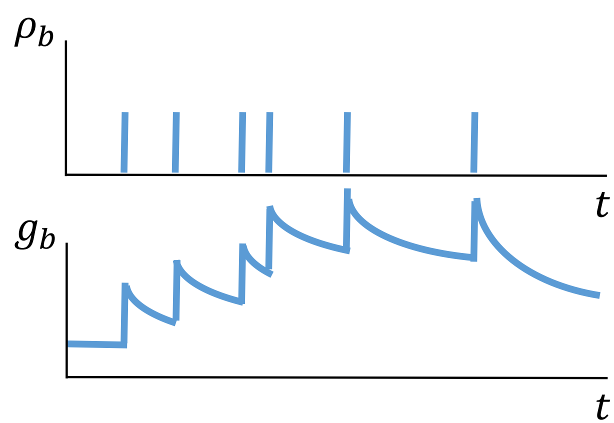
$$\color{red}{P_s(t)} = \sum_{t_i<t} K(t-t_i) = \int_{-\infty}^{t} K(t-\tau)\rho_b(\tau)d\tau$$

$$g_b(t) = g_{sb,max} \sum_{t_i<t} K(t-t_i) = g_{sb,max} \int_{-\infty}^{t} K(t-\tau)\rho_b(\tau)d\tau$$

Synaptic conductance

(for neighbor b)

- Assuming $K(t)$ as the exponential function: $$K(t) = e^{-\frac{t}{\tau_s}}$$



➢ ***We will use this formula to derive the total input current to a neuron from multiple neighbors***

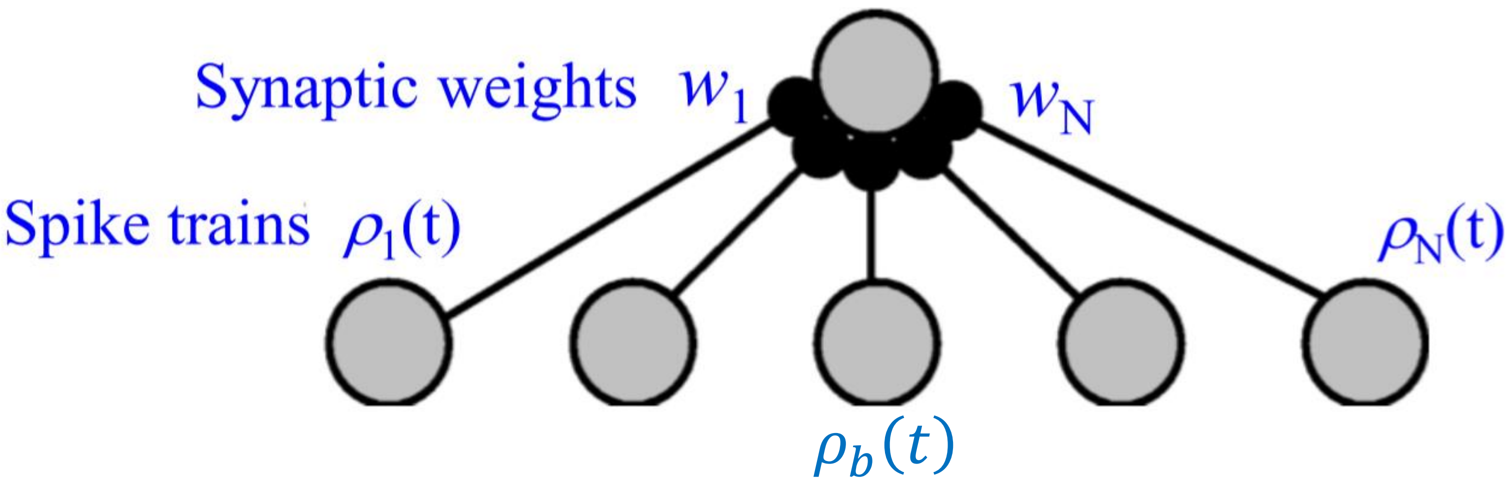
Outline

- Modeling synaptic inputs
  - Excitatory and inhibitory synapses
  - Modeling the effects of a synapse
  - Linear filter model of a synapse
- From spiking to firing-rate-based network
  - Multiple synapses
  - Firing-rate-based network
- Feedforward networks
  - Linear feedforward networks
  - Large networks: Continuous model
  - Mexican hat model
- Recurrent networks
  - Network stability
  - Application: Memory
  - Nonlinear recurrent networks
  - Excitatory–inhibitory networks
  - Phase plane stability analysis
  - Oscillations in olfactory system

Multiple Synapses

From Single Synapse to Multiple Synapses

- A neuron receives inputs from N other neurons
- Spike trains $\rho_1(t), \ldots, \rho_N(t)$ arrive at each of the input synapses



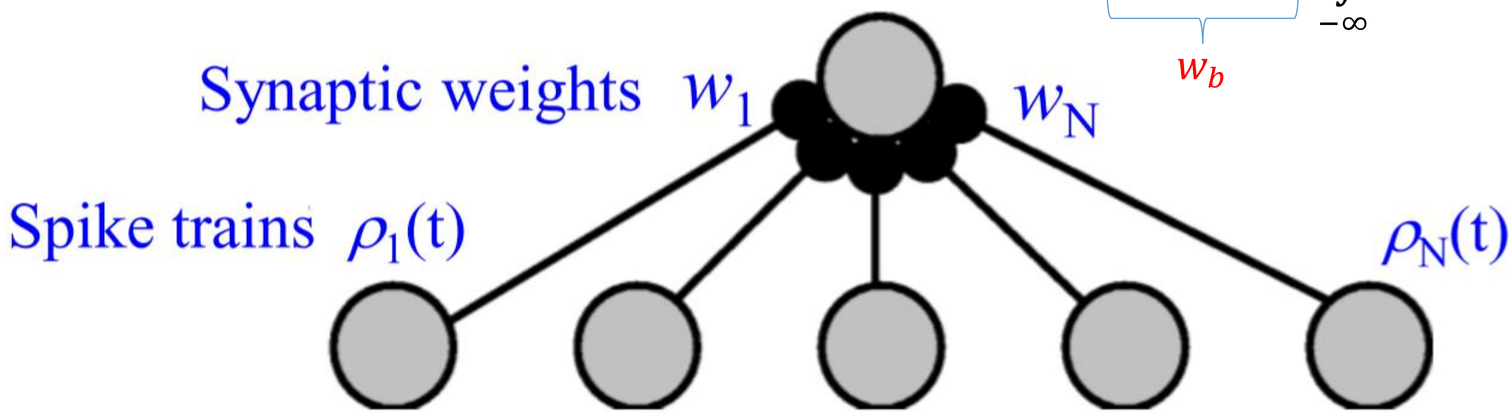
- Input from a neighbour b ($b = 1, \ldots, N$):

$$I_b(t) \propto \underbrace{g_b(t)}_{\text{Synaptic conductance}} = g_{sb,max} P_{rel} \int_{-\infty}^{t} K(t-\tau)\rho_b(\tau)d\tau$$

From Single Synapse to Multiple Synapses

- Each synapse has a weight $w_1, \dots, w_N$
- Replace $g_{sb,max}P_{rel}$ with w_b in synaptic conductance:

$$g_b(t) = \underbrace{g_{sb,max}P_{rel}}_{w_b} \int_{-\infty}^{t} K(t-\tau)\rho_b(\tau)d\tau$$



- Total synaptic current:

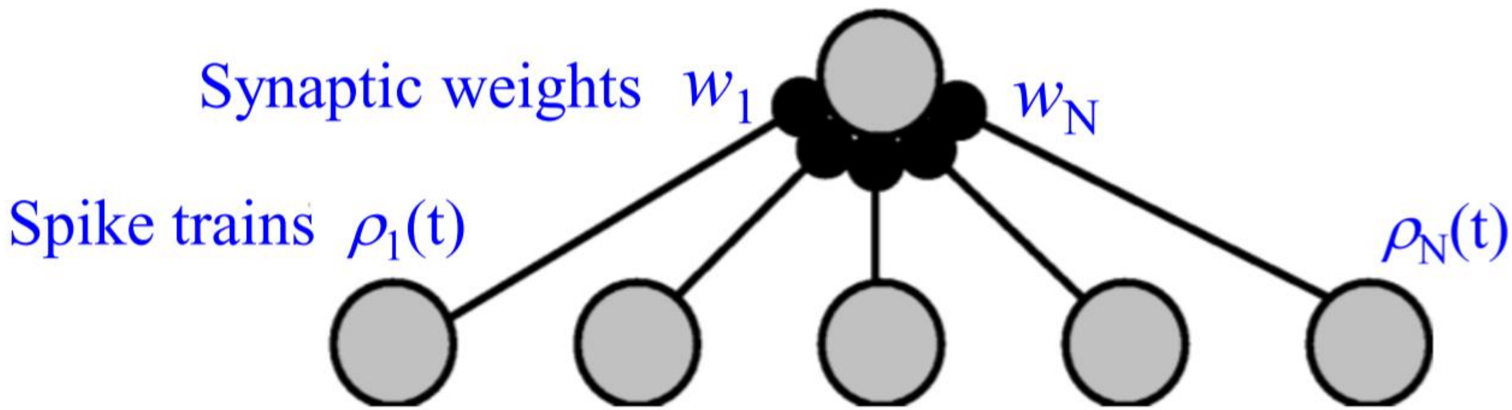
(assuming no nonlinear interactions between synapses)

$$I_s(t) = \sum_{b=1}^{N} I_b(t) \propto \sum_{b=1}^{N} w_b \int_{-\infty}^{t} K(t-\tau)\rho_b(\tau)d\tau$$

From Single Synapse to Multiple Synapses

- Total synaptic current:

$$I_s(t) = \sum_{b=1}^{N} I_b(t) \propto \sum_{b=1}^{N} w_b \int_{-\infty}^{t} K(t-\tau)\rho_b(\tau)d\tau$$



$$g_{sb,max}P_{rel} \rightarrow w_b$$

- The total **conductance** of the synapse determines the **weight** between the two neurons across the synapse
- The synaptic weight (number of channels, their conductance, P_{rel}) is ***adapted*** during the learning and memory formation functions

Modeling Network of Neurons – Spiking versus Firing Rate

- **<u>Option 1</u>:** Model networks using ***spiking*** neurons
  - **Advantages:**
    - Model computation and learning based on:
      - **Spike timing** (can use individual spike times in analysis)
      - Spike correlations / synchrony between individual neurons
  - **Disadvantages:**
    - Solving differential equations can be **computationally expensive** or impossible for large networks

Modeling Network of Neurons – Spiking versus Firing Rate

- **<u>Option 2</u>:** Use neurons with ***firing-rate*** outputs
  - Output of neurons is not 0 or 1 or a spike, but a real-valued output denoting the firing-rate of the neuron
  - **Advantages:**
    - Greater **efficiency**, **scales well** to large networks
  - **Disadvantages:**
    - Not able to model phenomena based on **spike timing** or synchrony

Question:

- How are these two approaches related?

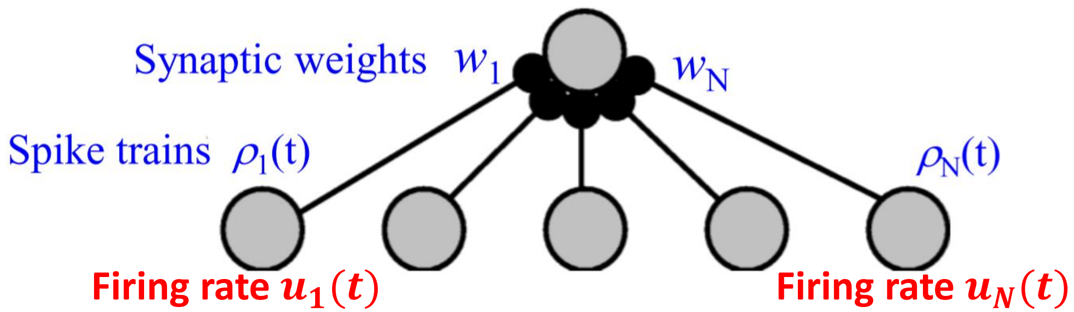
➢ ***We will now transform the input current formula into a form based on using firing rates***

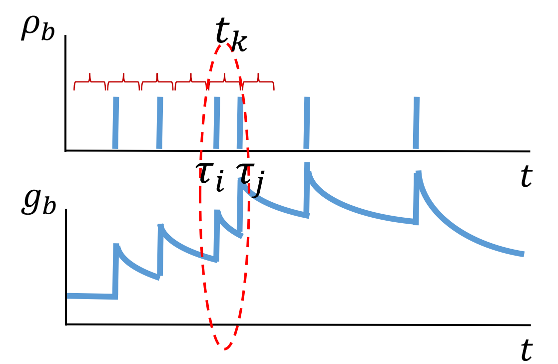
From Single Synapse to Multiple Synapses

- Total synaptic current:

$$I_s(t) = \sum_{b=1}^{N} I_b(t) \propto \sum_{b=1}^{N} w_b \int_{-\infty}^{t} K(t-\tau)\rho_b(\tau)d\tau$$

Spike train $\rho_b(t)$





$K(t-\tau_i) + K(t-\tau_j) \approx 2K(t-t_k)$

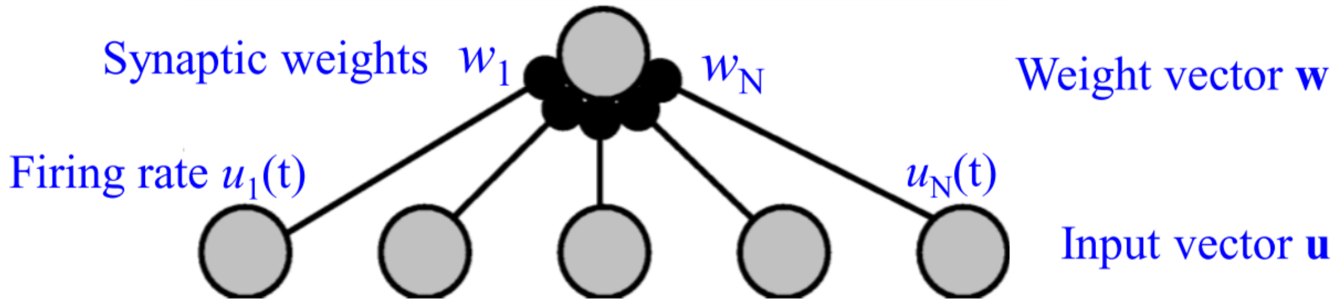
- Replace spike train with firing rate:

$$\approx \sum_{b=1}^{N} w_b \int_{-\infty}^{t} K(t-\tau)u_b(\tau)d\tau$$

Firing rate $u_b(t)$

- Instantaneous firing rates involve low-pass filtering of the spike train
  (In fact, they are time-averaged replacements for ensemble averages in a population of similar neurons)

Simplifying the Input Current Equation



- Let's remove the integral from the equation for $I_s(t)$

$$I_s(t) = \sum_{b=1}^{N} w_b \int_{-\infty}^{t} K(t-\tau)u_b(\tau)d\tau$$

- Suppose synaptic filter K is exponential: $K(t) = \frac{1}{\tau_s} e^{-\frac{t}{\tau_s}}$
- Differentiating the equation for $I_s(t)$ w.r.t. time t yields:

Weighted linear sum of inputs

$$\tau_s \frac{dI_s}{dt} = -I_s + \sum_b w_b u_b = -I_s + \boldsymbol{w.u}$$

Same time constant from $K(t)$ describes the dynamics of $I_s(t)$

➢ ***We will derive this equation on next page***

Simplifying the Input Current Equation

$$I_s(t) = \sum_{b=1}^{N} w_b \int_{-\infty}^{t} K(t-\tau) u_b(\tau) d\tau$$

$$\boxed{K(t) = \frac{1}{\tau_s} e^{-\frac{t}{\tau_s}}}$$

$$= \frac{1}{\tau_s} \sum_{b=1}^{N} w_b \, e^{-\frac{t}{\tau_s}} \int_{-\infty}^{t} e^{+\frac{\tau}{\tau_s}} u_b(\tau) d\tau$$

- Differentiating the equation for $I_s(t)$:

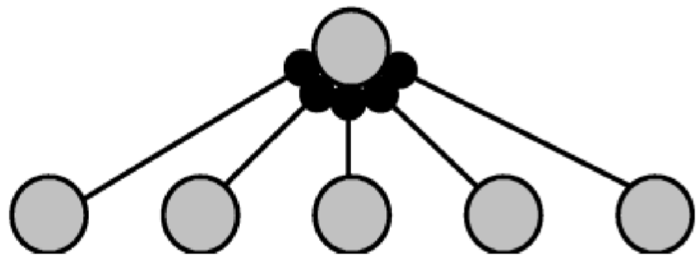
$$\frac{dI_s(t)}{dt} = \frac{1}{\tau_s}\left[\sum_{b=1}^{N} w_b \left(-\frac{1}{\tau_s}\right) e^{-\frac{t}{\tau_s}} \int_{-\infty}^{t} e^{+\frac{\tau}{\tau_s}} u_b(\tau) d\tau + \sum_{b=1}^{N} w_b \, e^{-\frac{t}{\tau_s}} e^{+\frac{t}{\tau_s}} u_b(t)\right]$$

$$= \frac{1}{\tau_s}\left[\underbrace{-\sum_{b=1}^{N} w_b \int_{-\infty}^{t} \underbrace{\frac{1}{\tau_s} e^{-\frac{(t-\tau)}{\tau_s}}}_{K(t-\tau)} u_b(\tau) d\tau}_{-I_s(t)} + \sum_{b=1}^{N} w_b \, u_b(t)\right]$$

$$\Rightarrow \boxed{\tau_s \frac{dI_s}{dt} = -I_s + \boldsymbol{w}.\boldsymbol{u}}$$

Firing-Rate-based Network

General Firing-Rate-based Network



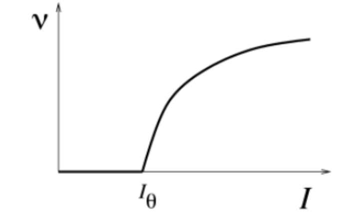
- Dynamics of input current I_s:

$$\boxed{\tau_s \frac{dI_s}{dt} = -I_s + \boldsymbol{w}.\boldsymbol{u}}$$

- Output firing rate v:
  - It does not follow the input current instantaneously
  - But has dynamics similar to the membrane potential's dynamics:

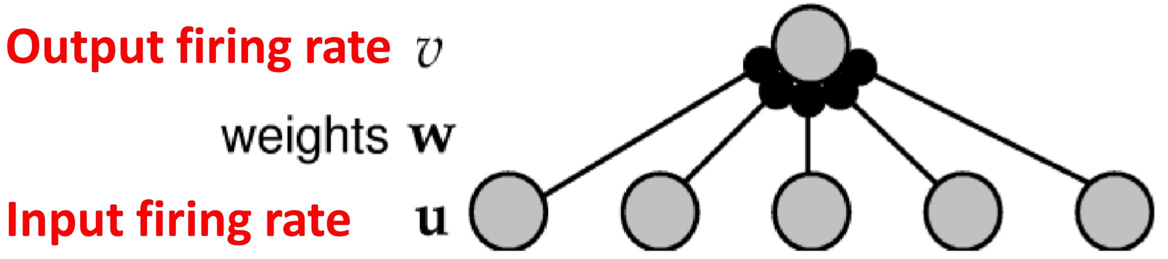
$$\boxed{\tau_r \frac{dv}{dt} = -v + F\big(I_s(t)\big)}$$

Nonlinear function



Wulfram Gerstner "Neuronal Dynamics"

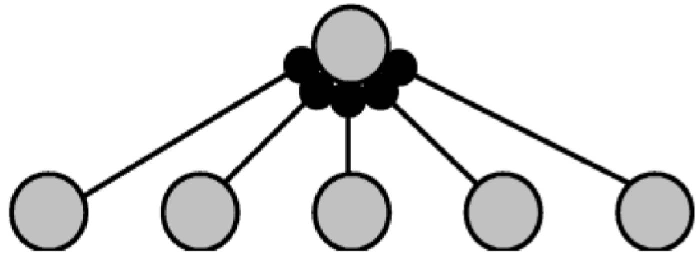
General Firing-Rate-based Network



$$\tau_r \frac{dv}{dt} = -v + F\big(I_s(t)\big), \qquad \tau_s \frac{dI_s}{dt} = -I_s + \boldsymbol{w}.\boldsymbol{u}$$

- Relation between τ_r and τ_s determines how the output firing rate follows the input firing rates
  - Assume $\tau_s \ll \tau_r$ or $\tau_r \ll \tau_s$

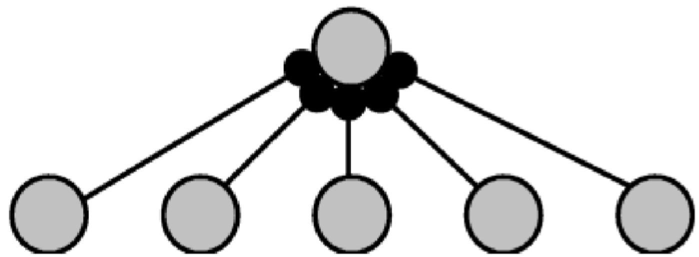
General Firing-Rate-based Network



$$\tau_r \frac{dv}{dt} = -v + F\big(I_s(t)\big), \qquad \tau_s \frac{dI_s}{dt} = -I_s + \boldsymbol{w}.\boldsymbol{u}$$

- If $\tau_r \ll \tau_s$:
  - The output dynamics is fast (or synapses are slow), so the output quickly reaches its steady-state value:
  $$v = F\big(I_s(t)\big)$$
  - The synaptic inputs take longer to converge:
  $$\tau_s \frac{dI_s}{dt} = -I_s + \boldsymbol{w}.\boldsymbol{u}$$

General Firing-Rate-based Network

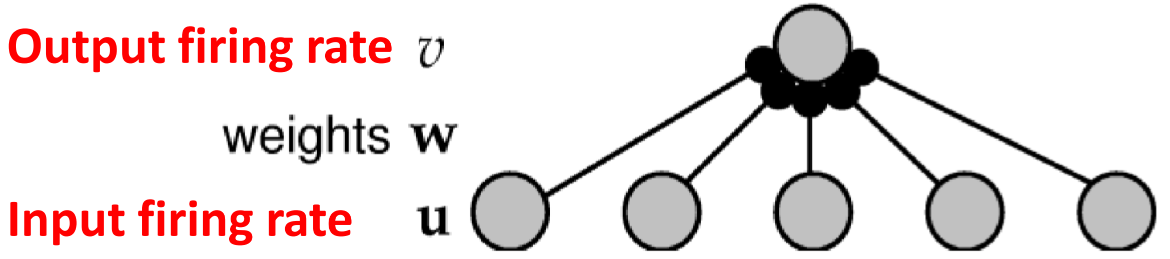


$$\tau_r \frac{dv}{dt} = -v + F\big(I_s(t)\big), \qquad \tau_s \frac{dI_s}{dt} = -I_s + \boldsymbol{w}.\boldsymbol{u}$$

- If $\tau_s \ll \tau_r$:
  - The synaptic input converges quickly to its steady-state value:
    $$I_s = \boldsymbol{w}.\boldsymbol{u}$$
  - As opposed to the network dynamics, which take longer to converge:
    - The equation for the output firing rate:
      $$\tau_r \frac{dv}{dt} = -v + F(\boldsymbol{w}.\boldsymbol{u})$$

➢ ***We will use this approximation in our upcoming network models***

General Firing-Rate-based Network

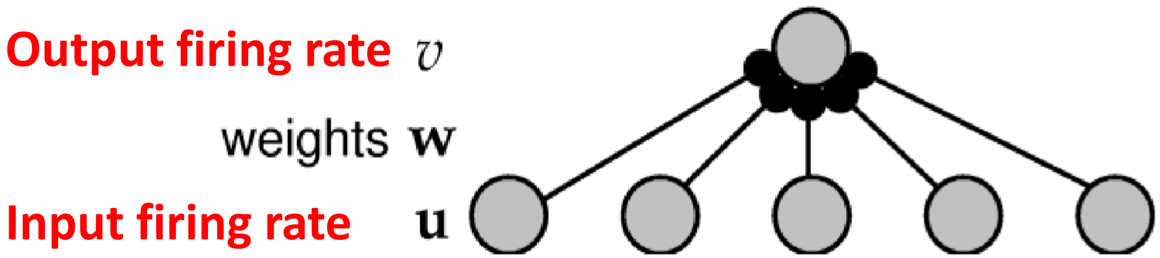


$$\tau_r \frac{dv}{dt} = -v + F\big(I_s(t)\big), \qquad \tau_s \frac{dI_s}{dt} = -I_s + \boldsymbol{w}.\boldsymbol{u}$$

- For general values of τ_s and τ_r:
  - In the case of **static inputs** (i.e. the inputs do not change for a long time):
  - The steady-state output is reached at a time $\gg \tau_s, \tau_r$
  - By setting: $\frac{dI_s}{dt} = 0, \frac{dv}{dt} = 0$ in the dynamics equations:

$$I_s = \boldsymbol{w}.\boldsymbol{u} \quad \rightarrow v_{ss} = F(I_s) = F(\boldsymbol{w}.\boldsymbol{u})$$

General Firing-Rate-based Network



- The steady-state output (setting: $\frac{dI_s}{dt} = 0, \frac{dv}{dt} = 0$):

$$I_s = \boldsymbol{w}.\boldsymbol{u} \quad \rightarrow \boxed{v_{ss} = F(I_s) = F(\boldsymbol{w}.\boldsymbol{u})}$$

➢ *This equation should look familiar to those who work with* ***artificial neural networks****!*

➢ *There, the function F is usually a threshold or a sigmoid function*

➢ *Note that this is a simplification of the rich dynamics of* ***real neural networks***

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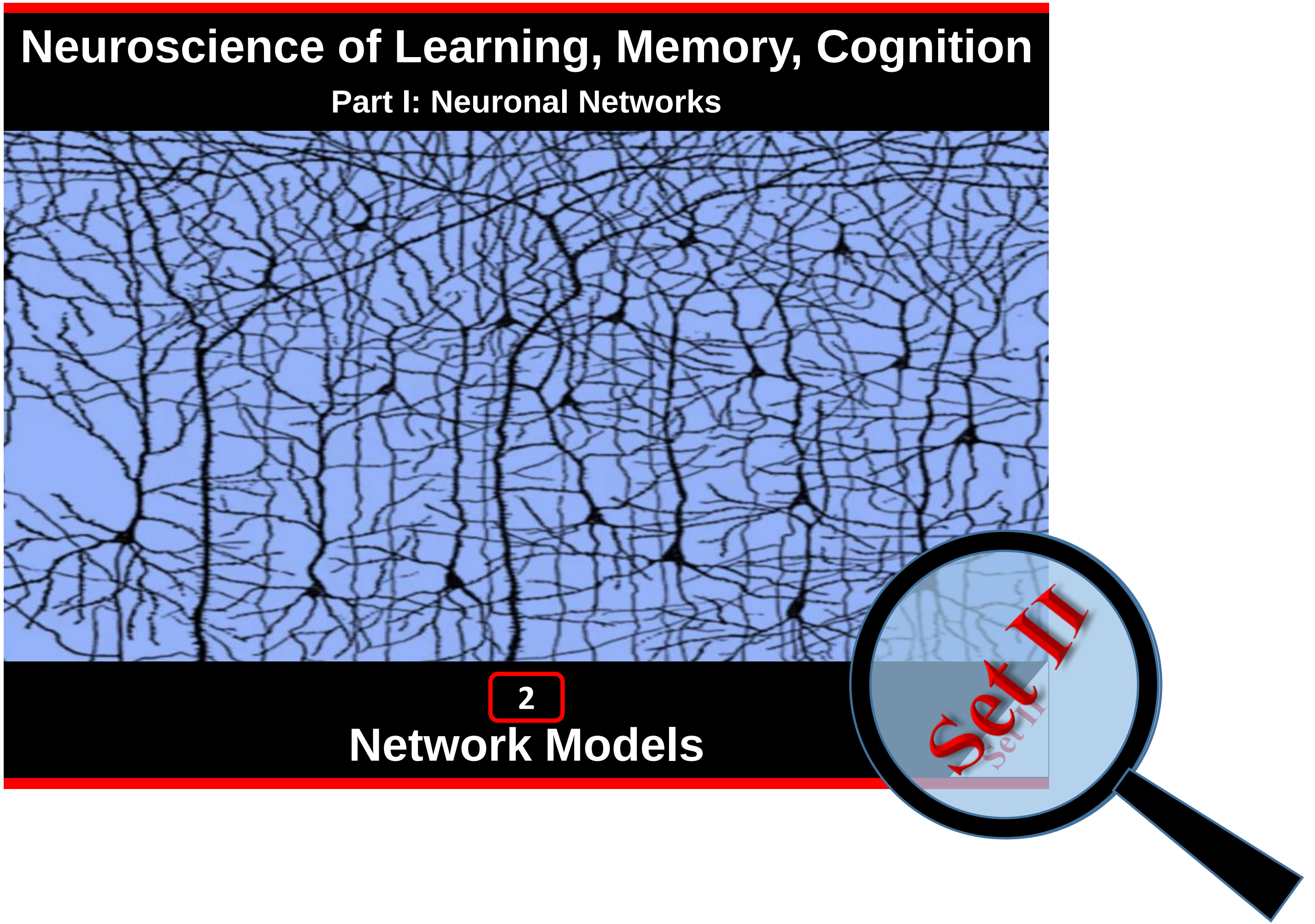
Next



Neuroscience of Learning, Memory, Cognition
Part I: Neuronal Networks
2
Network Models
Set II