UNIVERSITY OF TECHNOLOGY
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CHEMNITZ

Neurocomputing

Neurons

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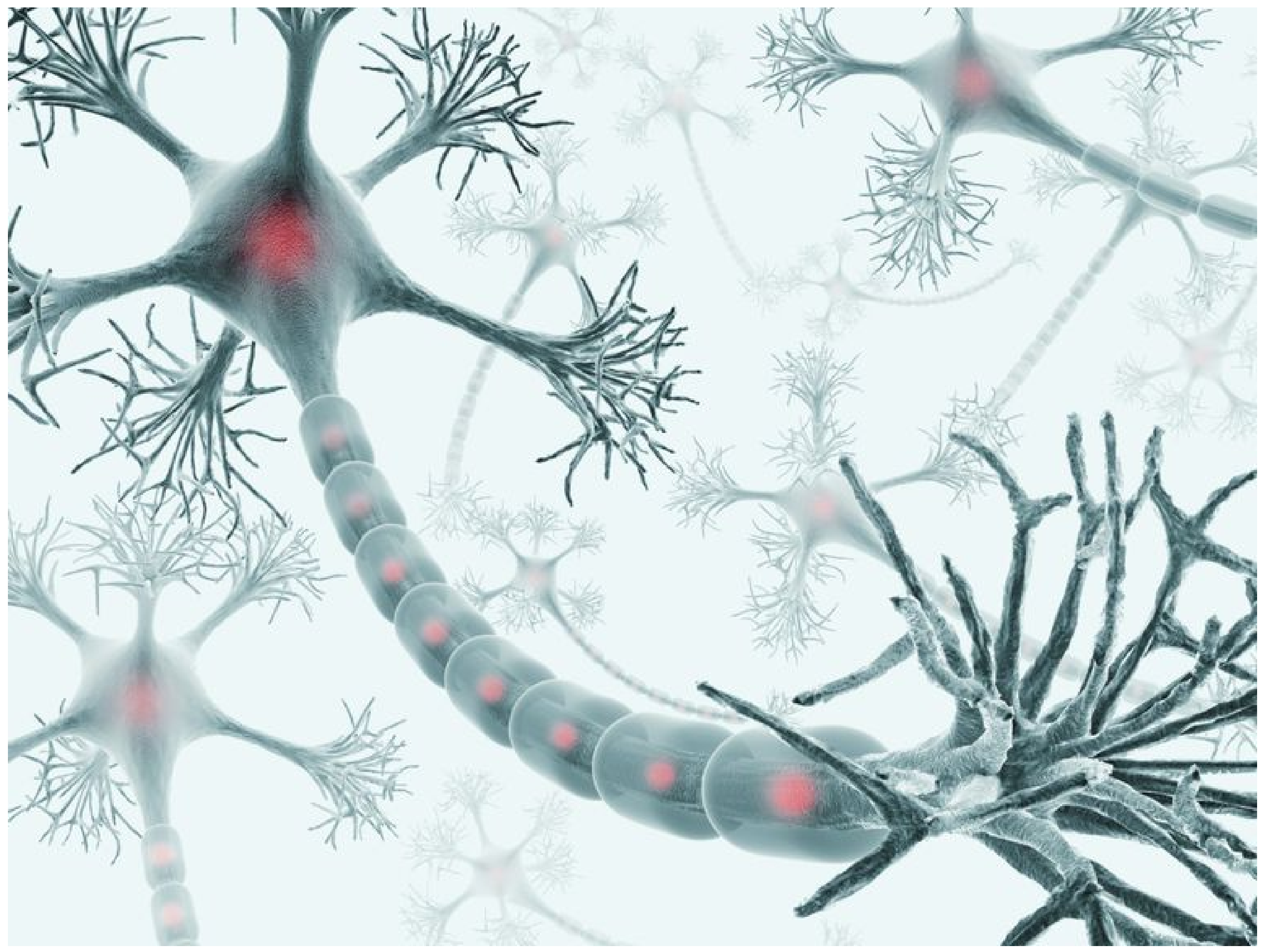
https://tu-chemnitz.de/informatik/KI/edu/neurocomputing

Biological neuron



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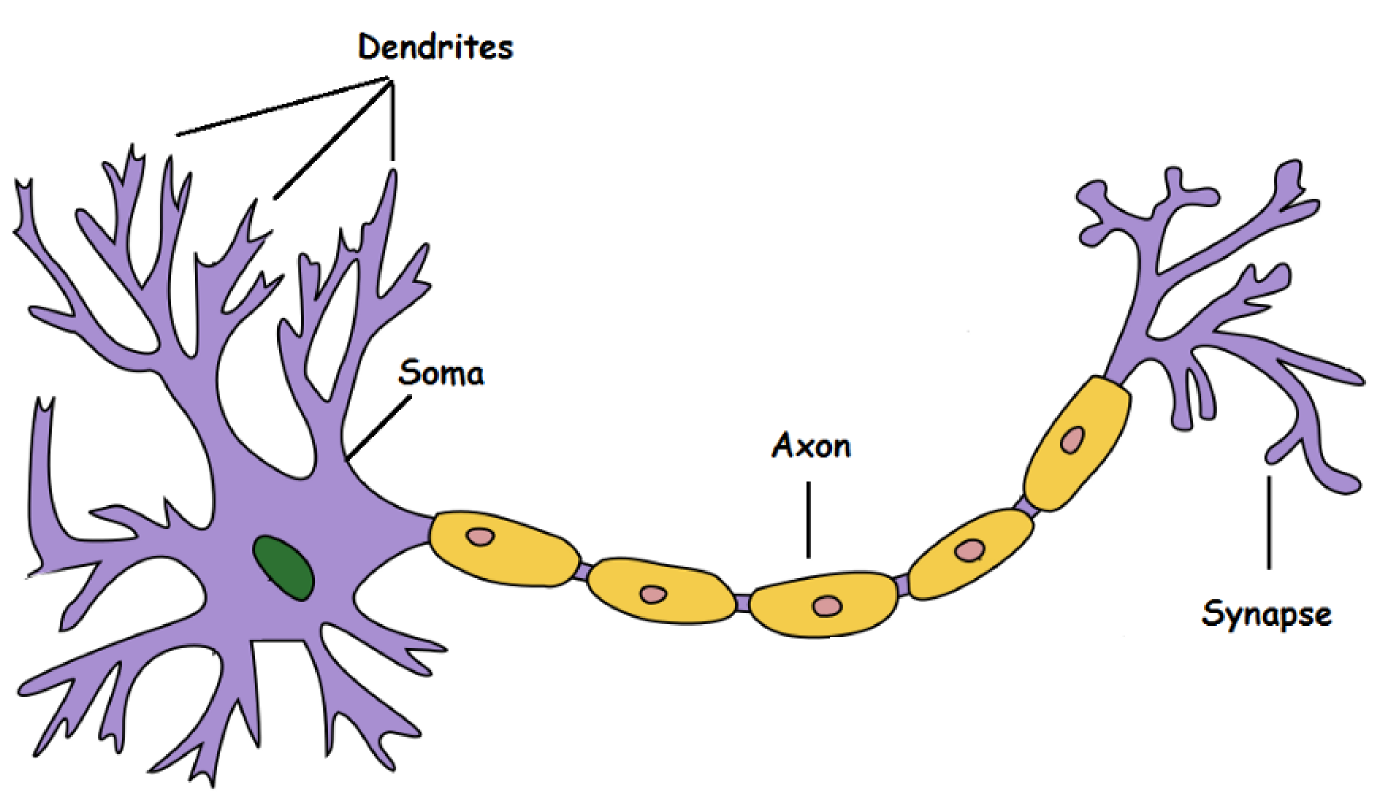
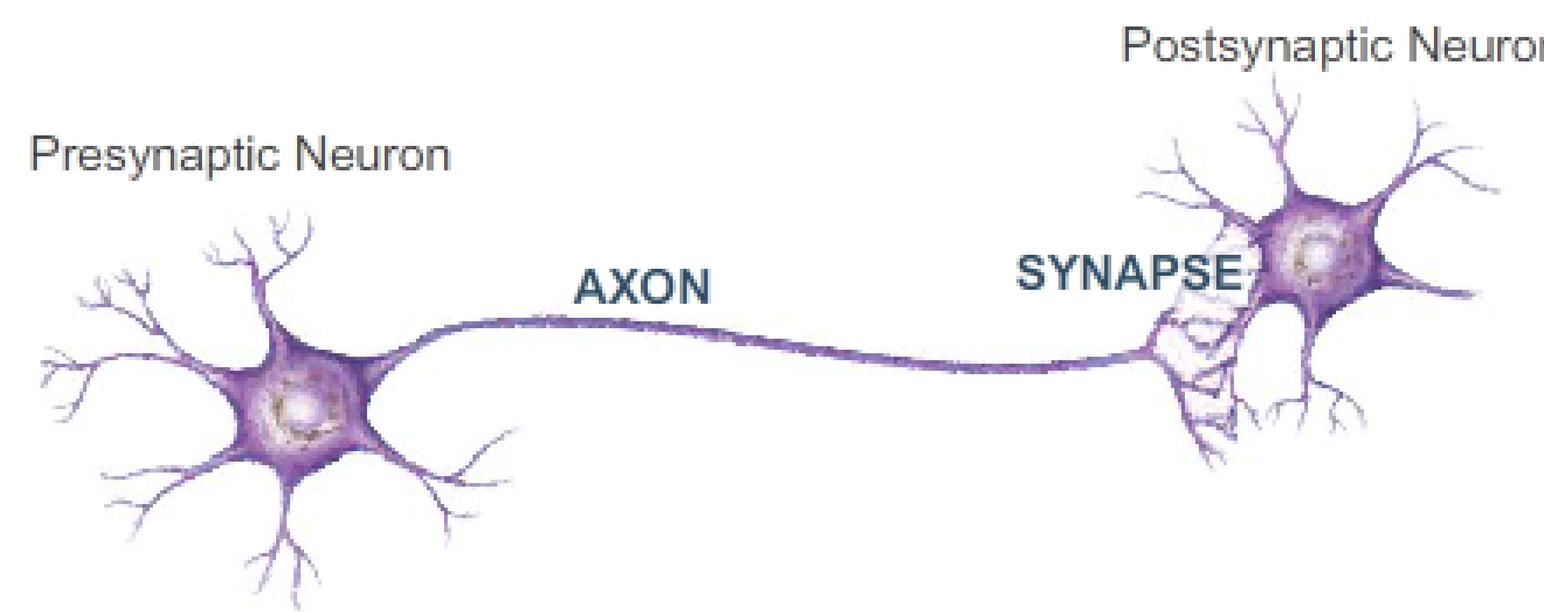


https://en.wikipedia.org/wiki/Neuron

- The human brain is composed of 100 billion **neurons**.
- A biological neuron is a cell, composed of a cell body (**soma**), multiple **dendrites** and an **axon**.
- The axon of a neuron can contact the dendrites of another through **synapses** to transmit information.
- There are hundreds of different types of neurons, each with different properties.



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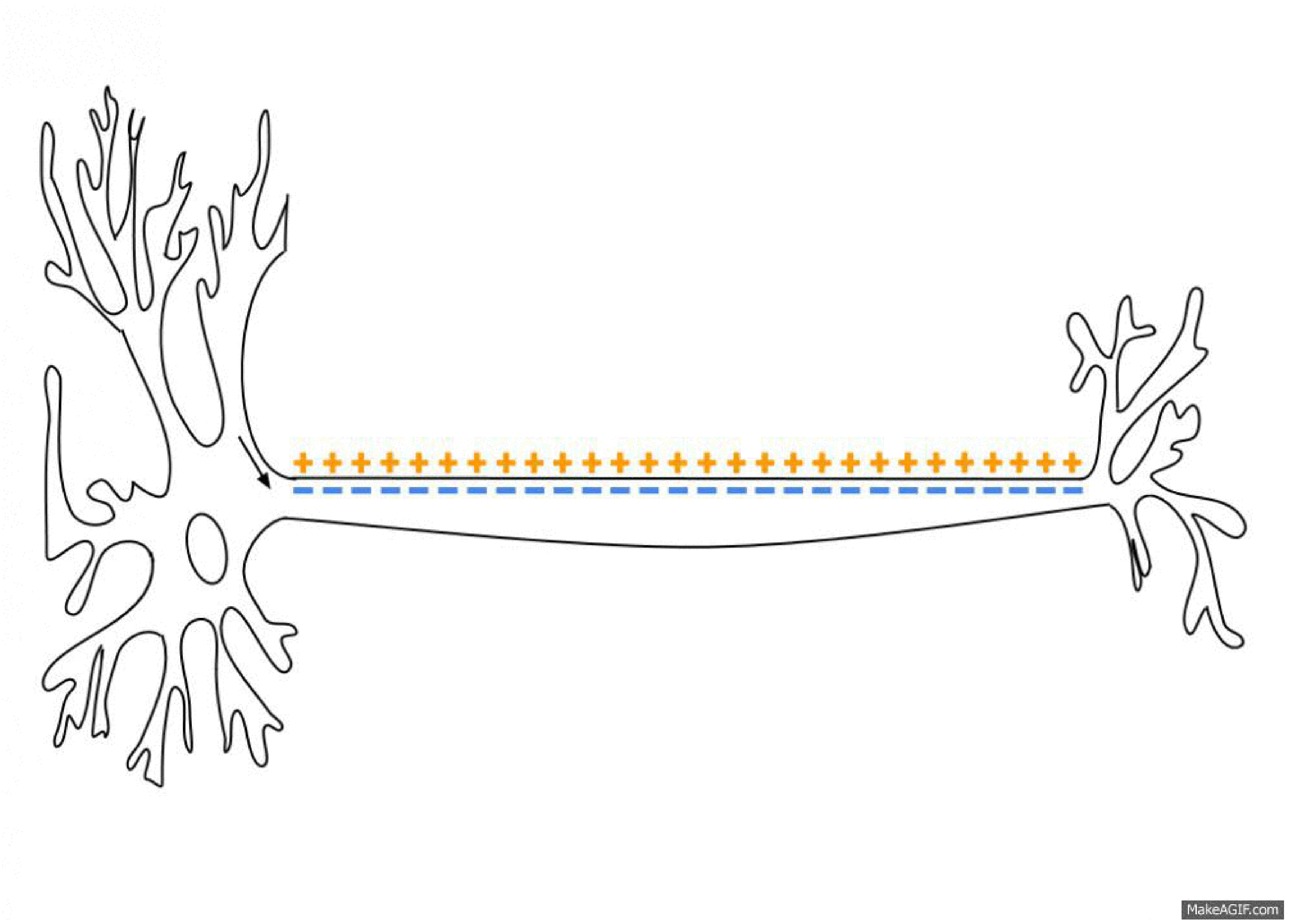
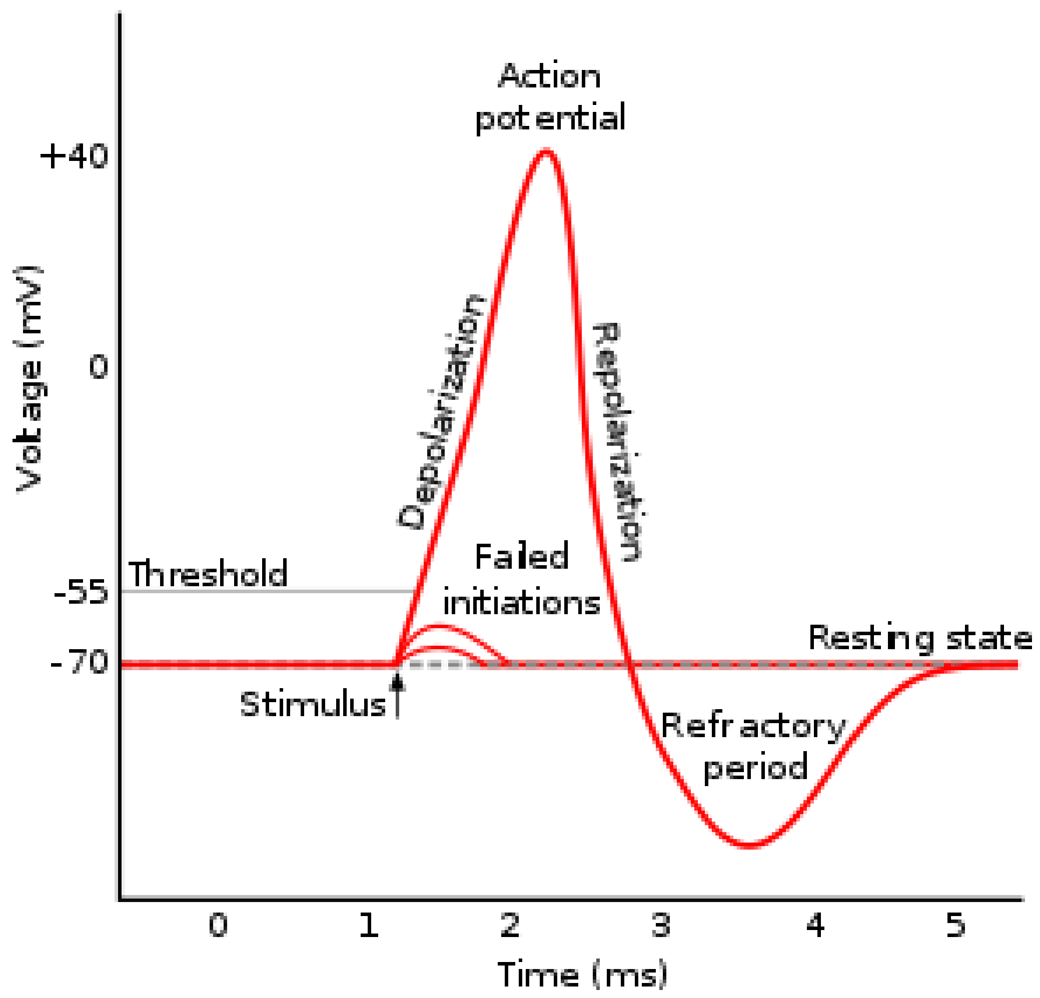
Biological neuron

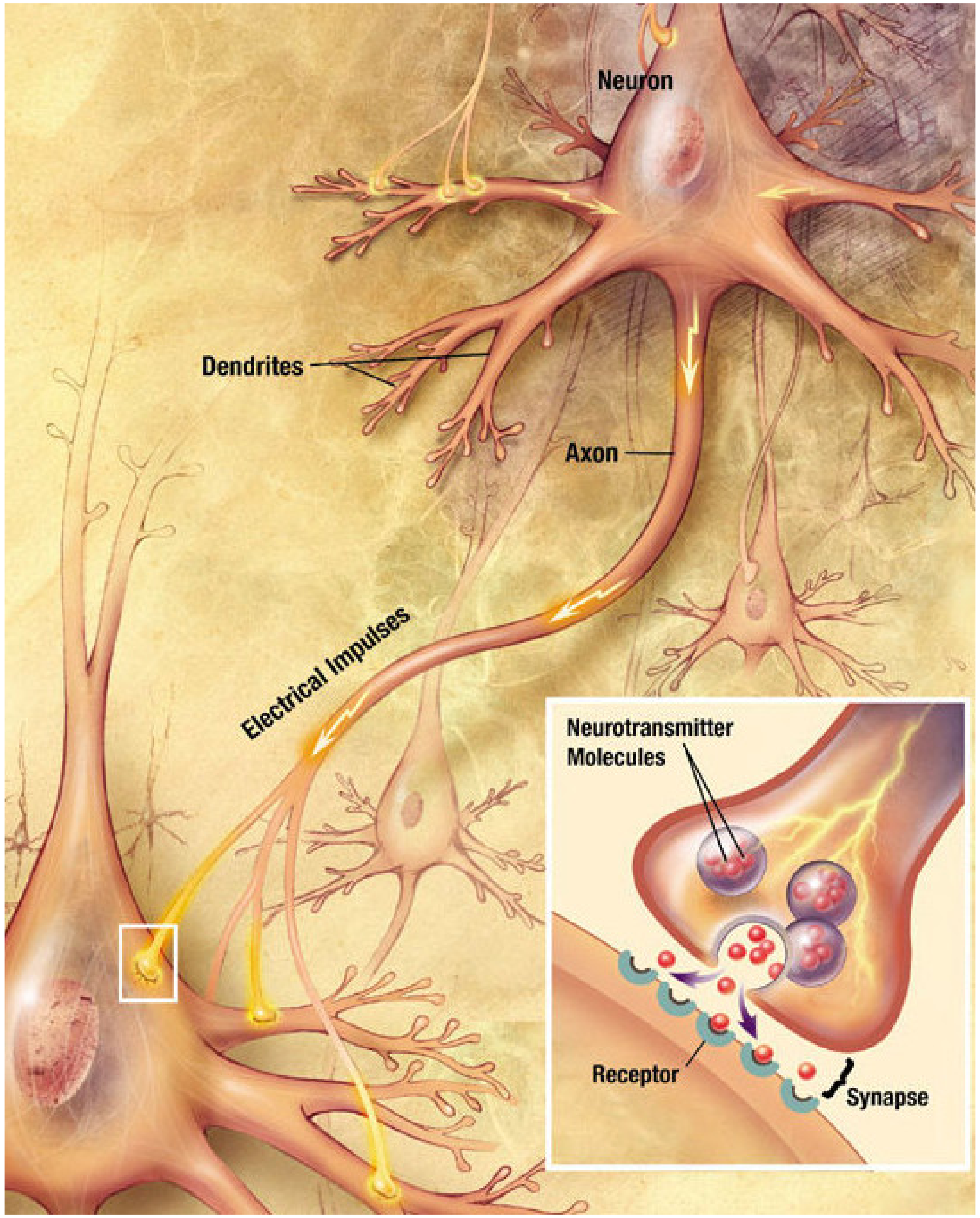




https://en.wikipedia.org/wiki/Action_potential

- Neurons are negatively charged: they have a resting potential at around -70 mV.
- When a neuron receives enough input currents, its **membrane potential** can exceed a threshold and the neuron emits an **action potential** (or **spike**) along its axon.
- A spike has a very small duration (1 or 2 ms) and its amplitude is rather constant.
- It is followed by a **refractory period** where the neuron is hyperpolarized, limiting the number of spikes per second to 200.

Biological neuron

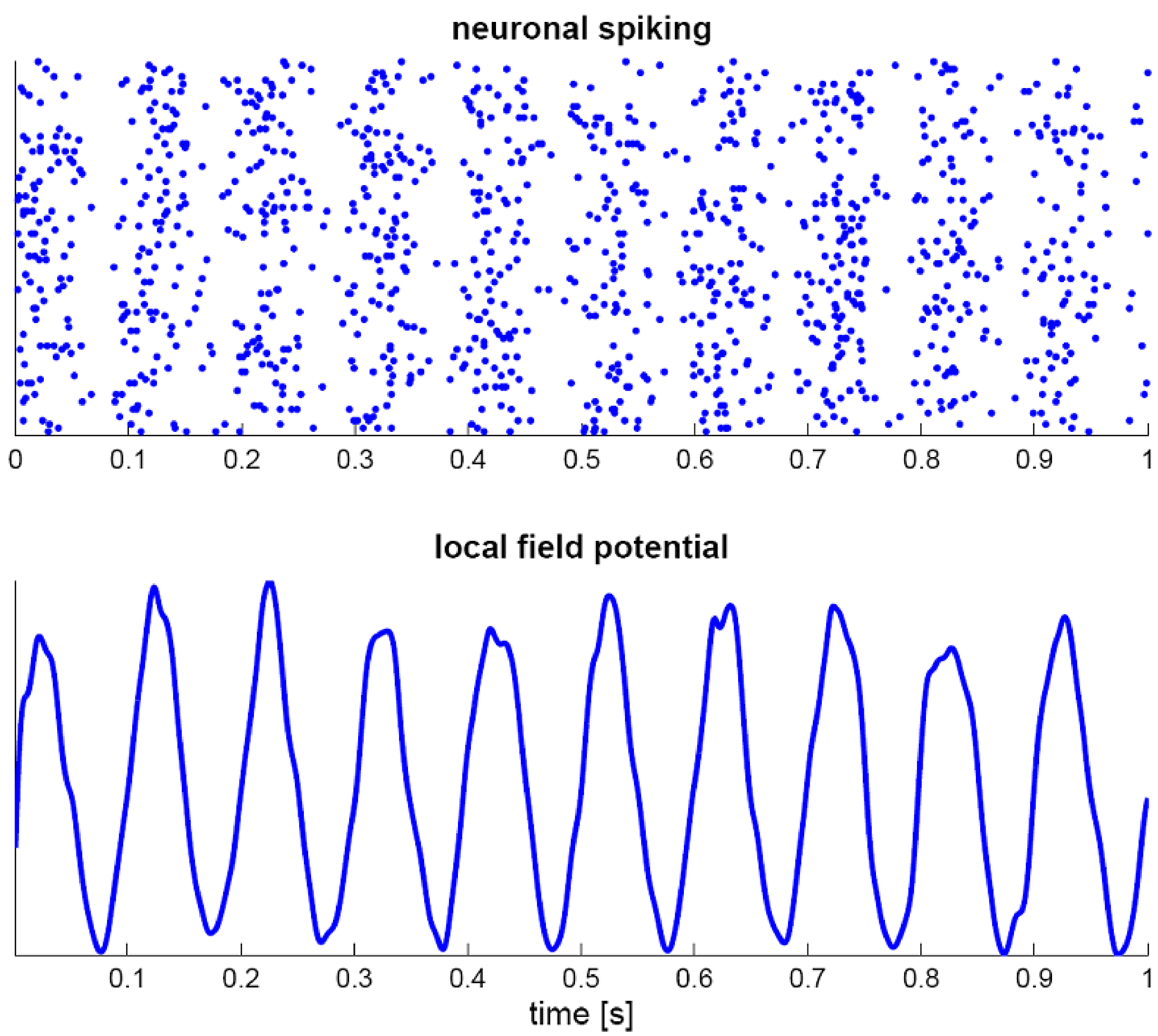


https://en.wikipedia.org/wiki/Neuron

- The action potential arrives at the synapses and releases **neurotransmitters** in the synaptic cleft:
  - glutamate (AMPA, NMDA)
  - GABA
  - dopamine
  - serotonin
  - nicotin
  - etc...
- Neurotransmitters can enter the receiving neuron through **receptors** and change its potential: the neuron may emit a spike too.
- Synaptic currents change the membrane potential of the post.synaptic neuron.
- The change depends on the strength of the synapse called the **synaptic efficiency** or **weight**.
- Some synapses are stronger than others, and have a larger influence on the post-synaptic cell.

Biological neuron

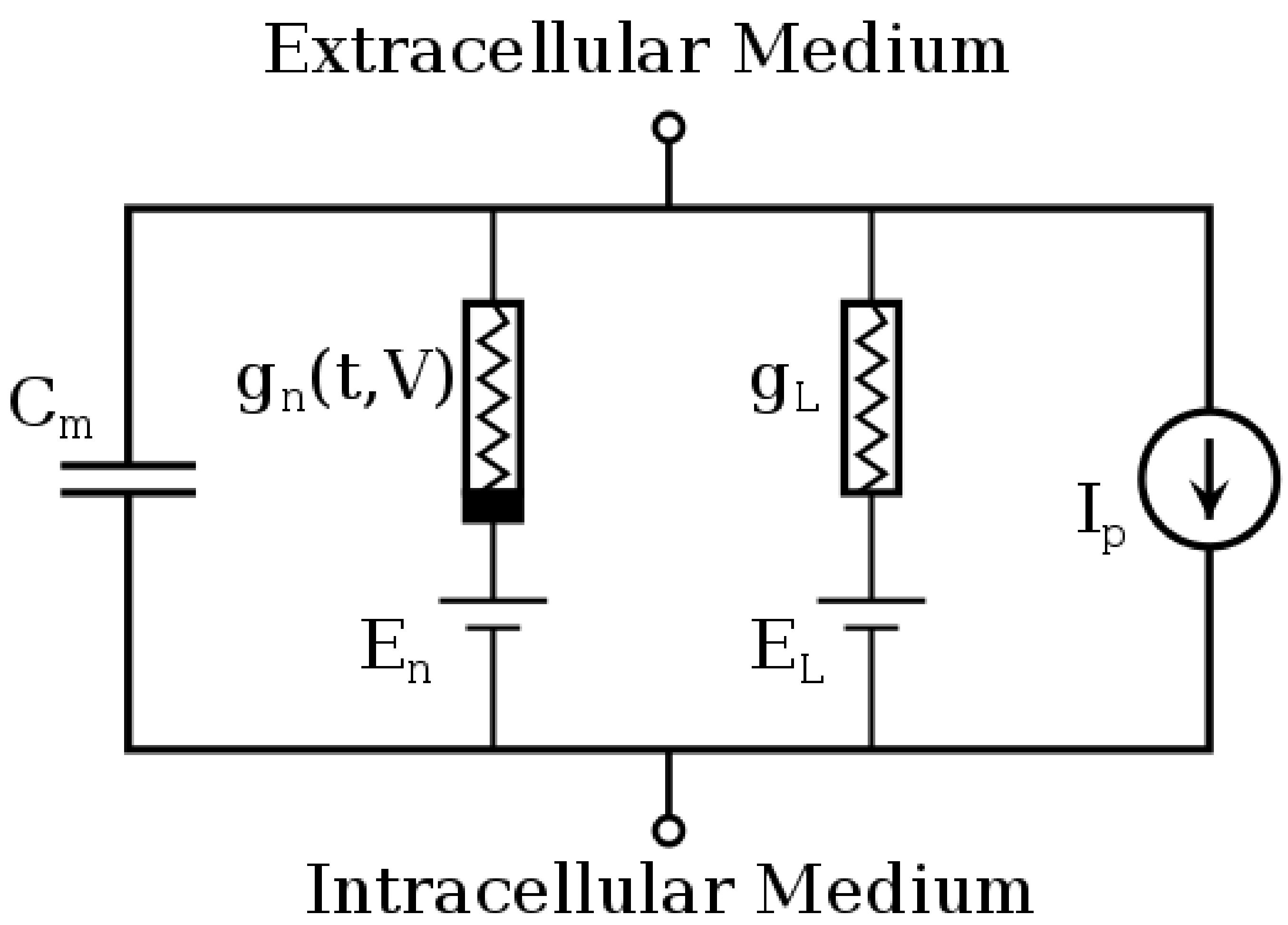
Information is transmitted through spike trains



Source: https://en.wikipedia.org/wiki/Neural_oscillation

- The two important dimensions of the information exchanged by neurons are:
  - The instantaneous **frequency** or **firing rate**: number of spikes per second (Hz).
  - The precise **timing** of the spikes.
- The shape of the spike (amplitude, duration) does not matter much.
- Spikes are binary signals (0 or 1) at precise moments of time.
- Some neuron models called **rate-coded models** only represent the firing rate of a neuron and ignore spike timing.
- Other models called **spiking models** represent explicitly the spiking behavior.

The Hodgkin-Huxley neuron (Hodgkin and Huxley, 1952)



- Alan Hodgkin and Andrew Huxley (Nobel prize 1963) were the first to propose a detailed mathematical model of the giant squid neuron.
- The membrane potential V of the neuron is governed by an electrical circuit, including sodium and potassium channels.
- The membrane has a **capacitance** C that models the dynamics of the membrane (time constant).
- The **conductance** g_L allows the membrane potential to relax back to its resting potential E_L in the absence of external currents.
- For electrical engineers: it is a simple RC network…
- External currents (synaptic inputs) perturb the membrane potential and can bring the neuron to fire an action potential.

https://en.wikipedia.org/wiki/Hodgkin%E2%80%93Huxley_model

The Hodgkin-Huxley neuron (Hodgkin and Huxley, 1952)

- Their model include:
  - An ordinary differential equation (ODE) for the membrane potential v.
  - Three ODEs for n, m and h representing potassium channel activation, sodium channel activation, and sodium channel inactivation.
  - Several parameters determined experimentally.
- Not only did they design experiments to find the parameters, but they designed the equations themselves.

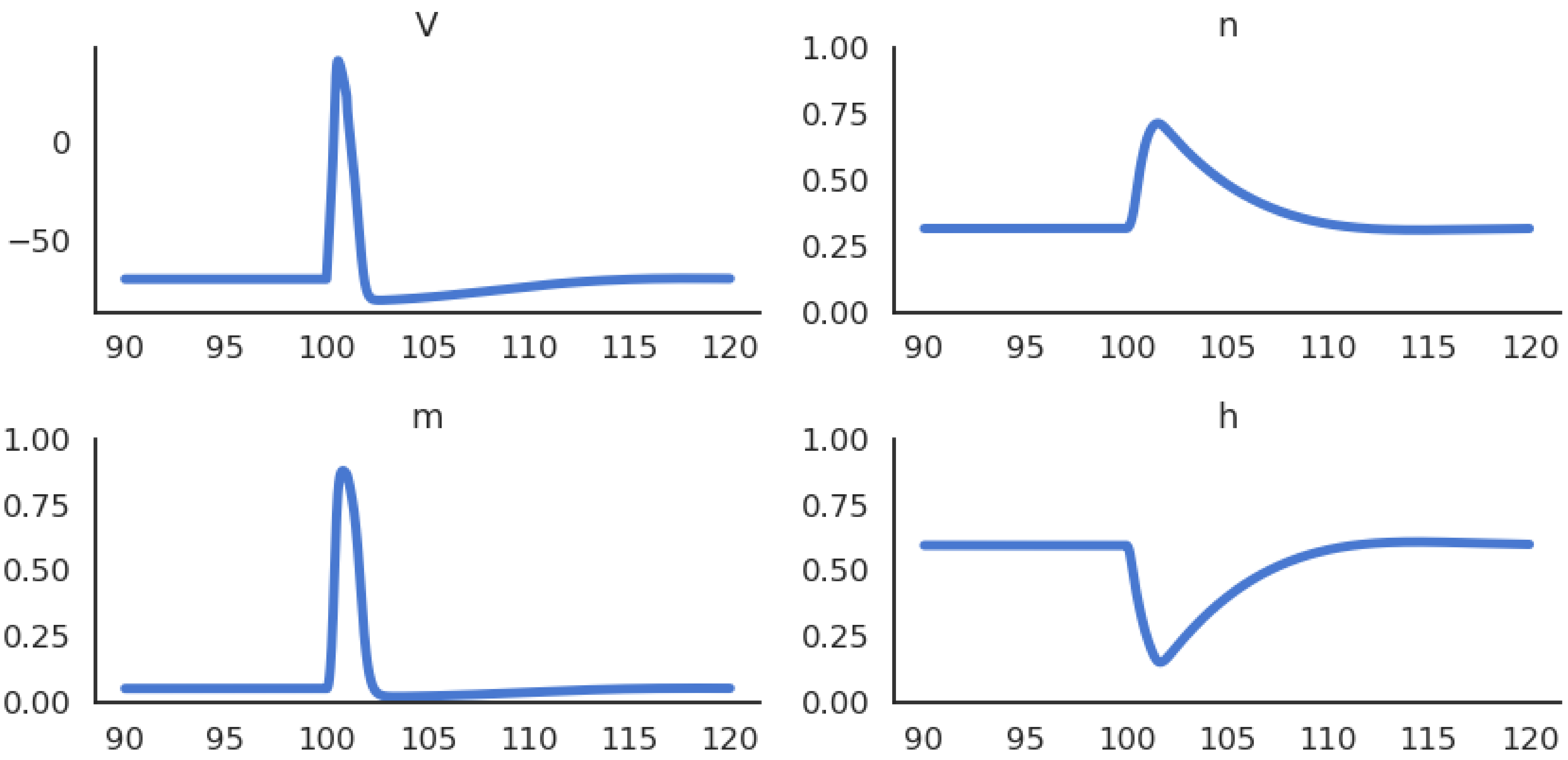
$$
\begin{aligned}
a_n &= 0.01\,(v+60)/(1.0-\exp(-0.1\,(v+60))) \\
a_m &= 0.1\,(v+45)/(1.0-\exp(-0.1\,(v+45))) \\
a_h &= 0.07\,\exp(-0.05\,(v+70)) \\
b_n &= 0.125\,\exp(-0.0125\,(v+70)) \\
b_m &= 4\,\exp(-(v+70)/80) \\
b_h &= 1/(1+\exp(-0.1\,(v+40)))
\end{aligned}
$$

$$
\begin{aligned}
\frac{dn}{dt} &= a_n\,(1-n) - b_n\,n \\
\frac{dm}{dt} &= a_m\,(1-m) - b_m\,m \\
\frac{dh}{dt} &= a_h\,(1-h) - b_h\,h
\end{aligned}
$$

$$
\begin{aligned}
C\,\frac{dv}{dt} = g_L\,(V_L-v) + g_K\,n^4\,(V_K-v) \\
+ g_{\mathrm{Na}}\,m^3\,h\,(V_{\mathrm{Na}}-v) + I
\end{aligned}
$$

The Hodgkin-Huxley neuron (Hodgkin and Huxley, 1952)

- These equations allow to describe very precisely how an action potential is created from external currents.

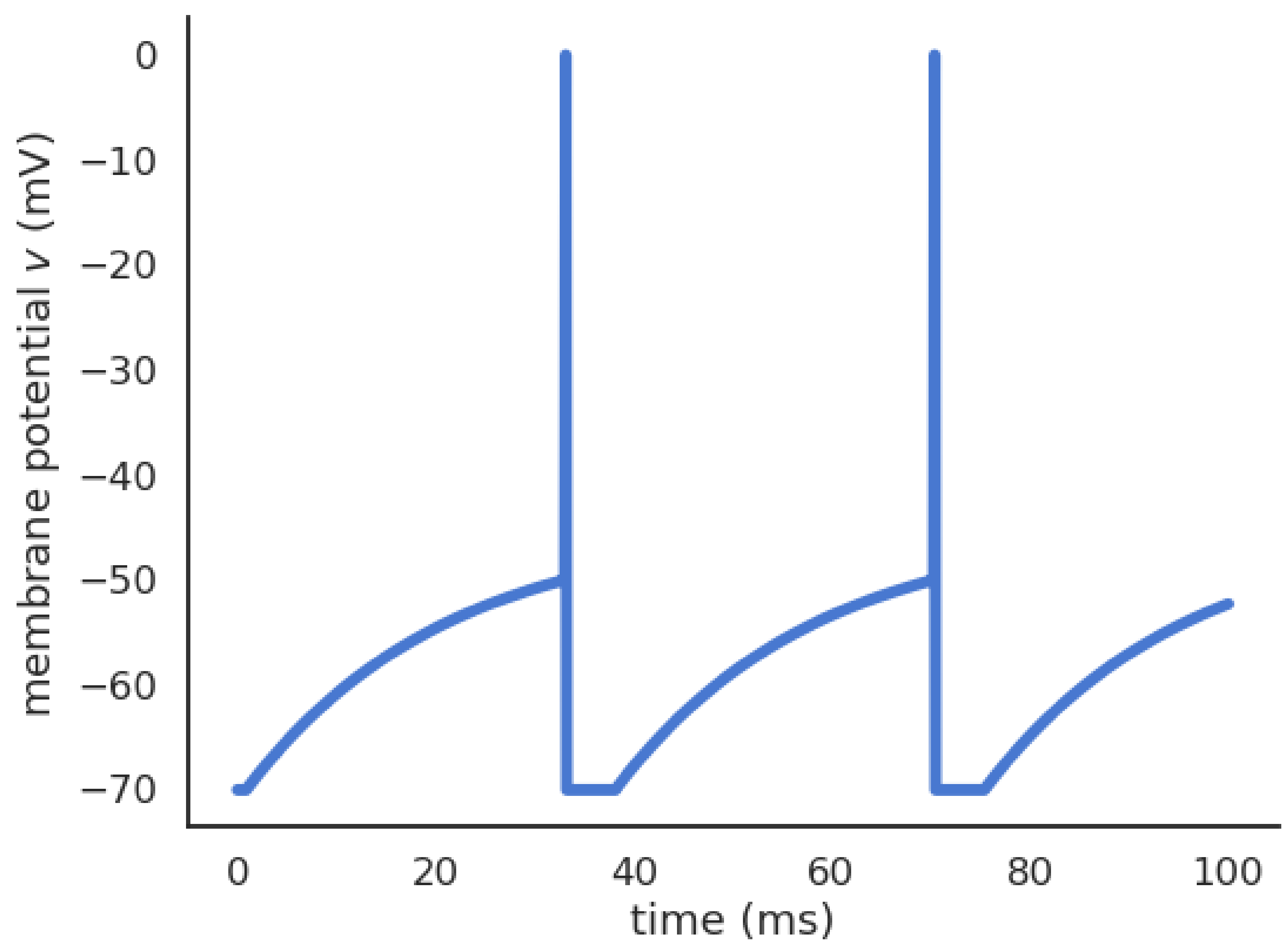


The leaky integrate-and-fire neuron (Lapicque, 1907)

- As action potentials are stereotypical, it is a waste of computational resources to model their generation precisely.
- What actually matters are the **sub-threshold dynamics**, i.e. what happens before the spike is emitted.
- The **leaky integrate-and-fire** (LIF) neuron integrates its input current and emits a spike if the membrane potential exceeds a threshold.

$$C \, \frac{dv}{dt} = - g_L \, (v - V_L) + I$$

$$\text{if } v > V_T \text{ emit a spike and reset.}$$



Different spiking neuron models are possible

- Izhikevich quadratic IF (Izhikevich, 2001).

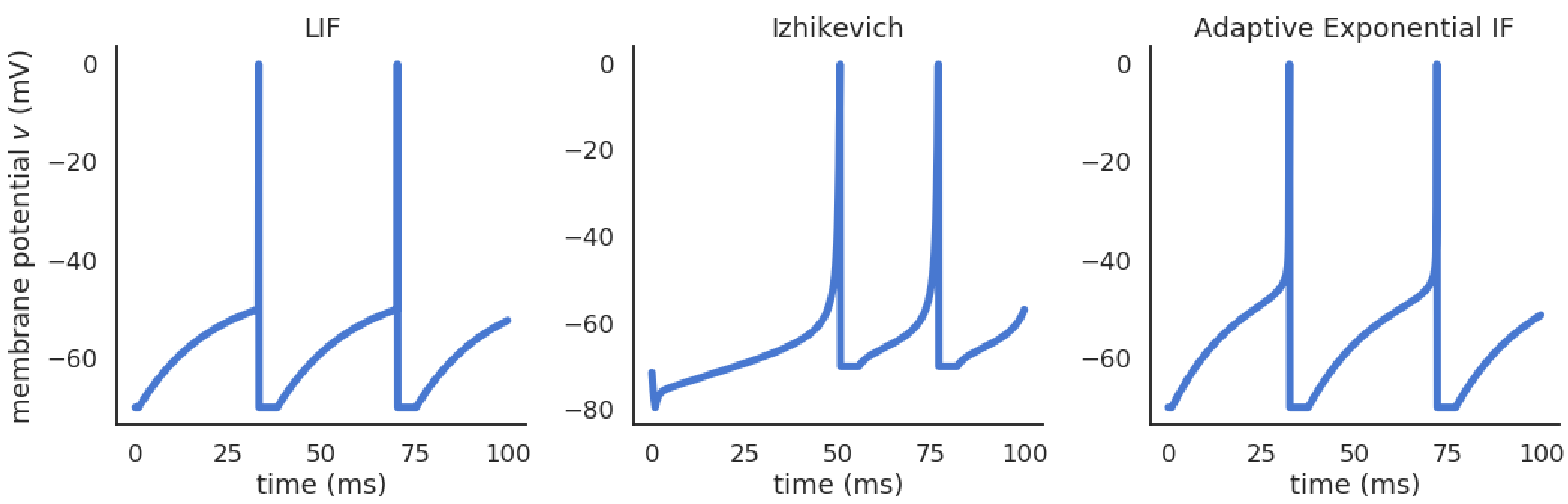
$$\frac{dv}{dt} = 0.04\, v^2 + 5\, v + 140 - u + I$$

$$\frac{du}{dt} = a\, (b\, v - u)$$

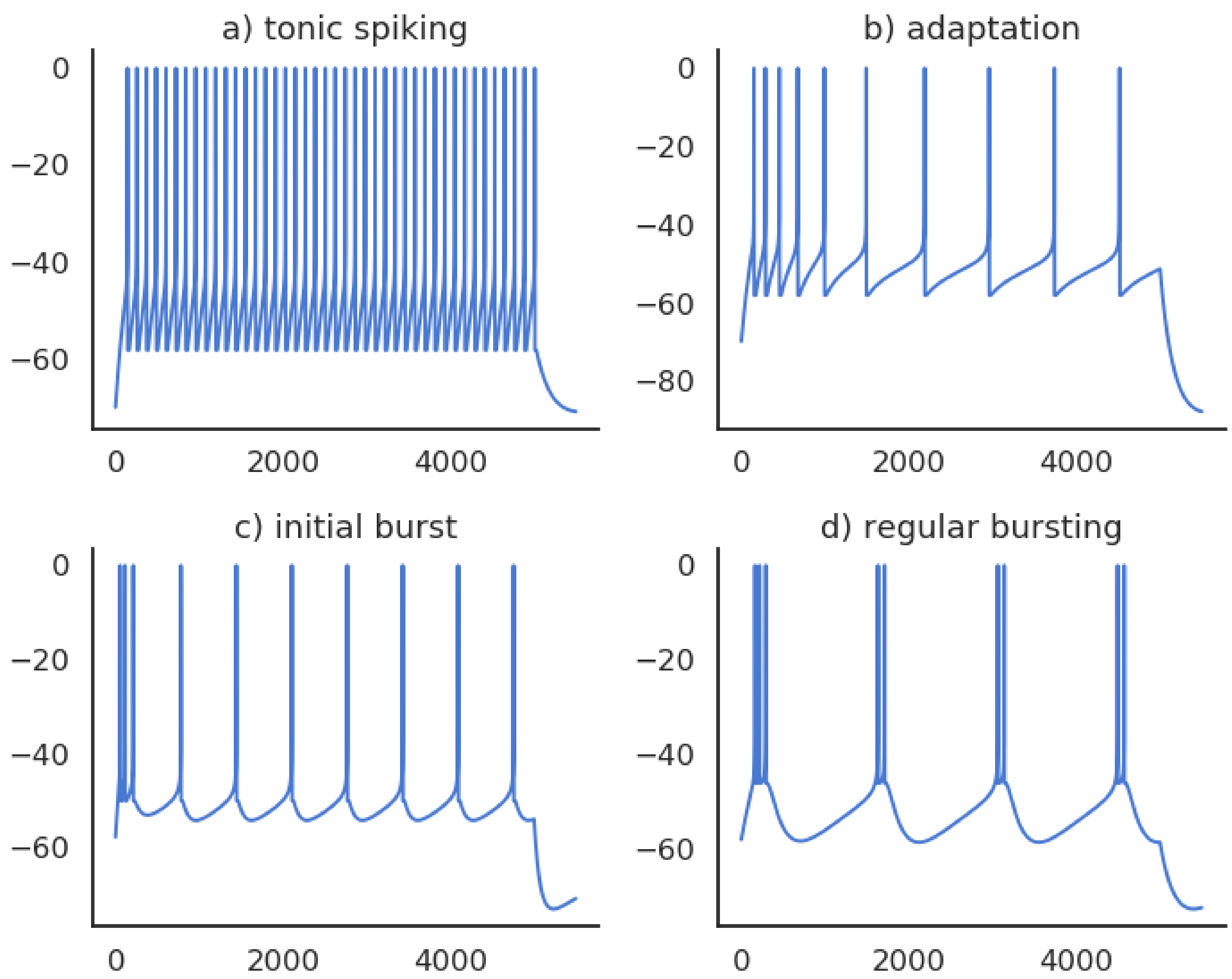
- Adaptive exponential IF (AdEx, Brette and Gerstner, 2005).

$$C \, \frac{dv}{dt} = -g_L \, (v - E_L) + g_L \, \Delta_T \, \exp(\frac{v - v_T}{\Delta_T}) + I - w$$

$$\tau_w \, \frac{dw}{dt} = a \, (v - E_L) - w$$



Realistic neuron models can reproduce a variety of dynamics

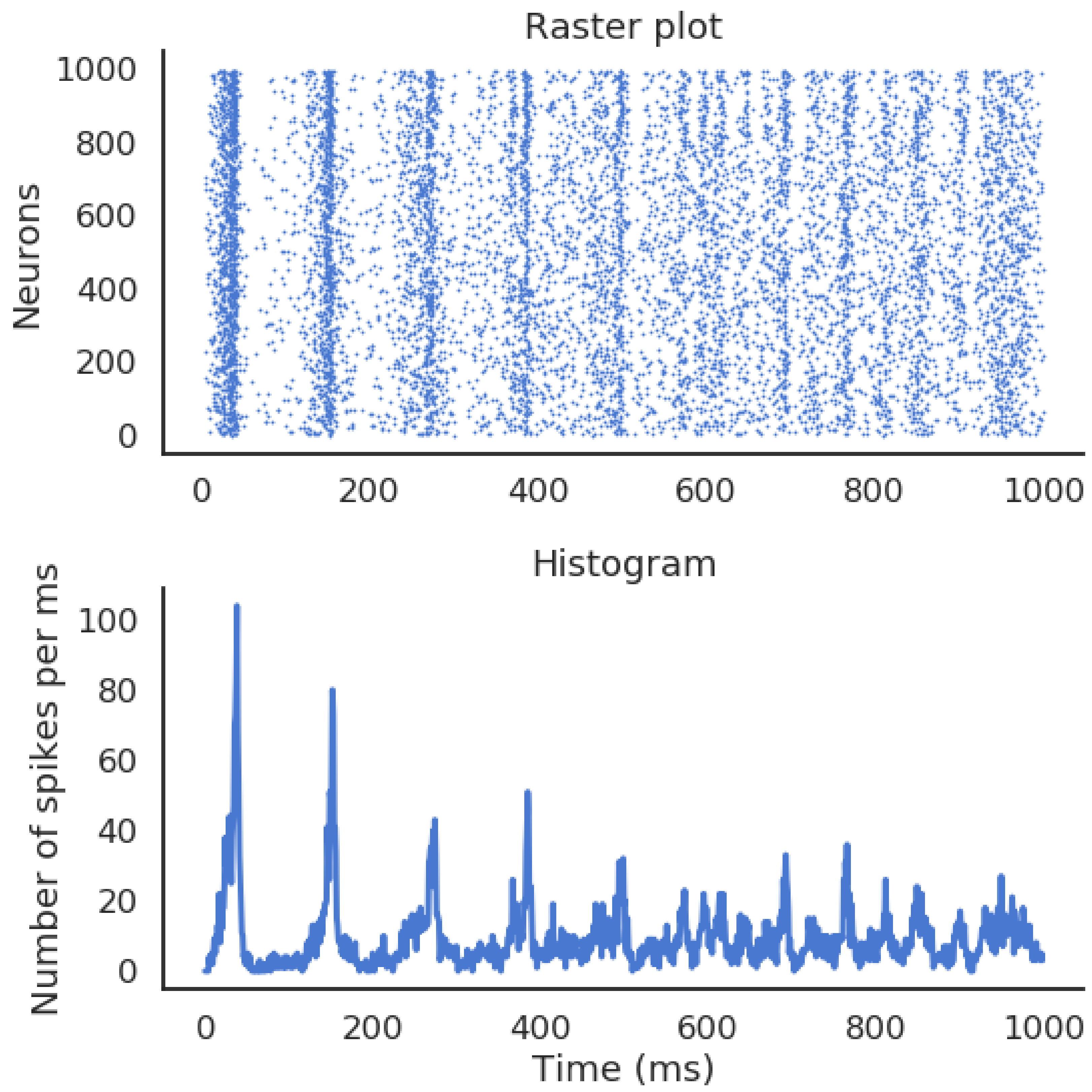


Biological neurons do not all respond the same to an input current.

- Some fire regularly.
- Some slow down with time.
- Some emit bursts of spikes.

Modern spiking neuron models allow to recreate these dynamics by changing a few parameters.

Populations of spiking neurons

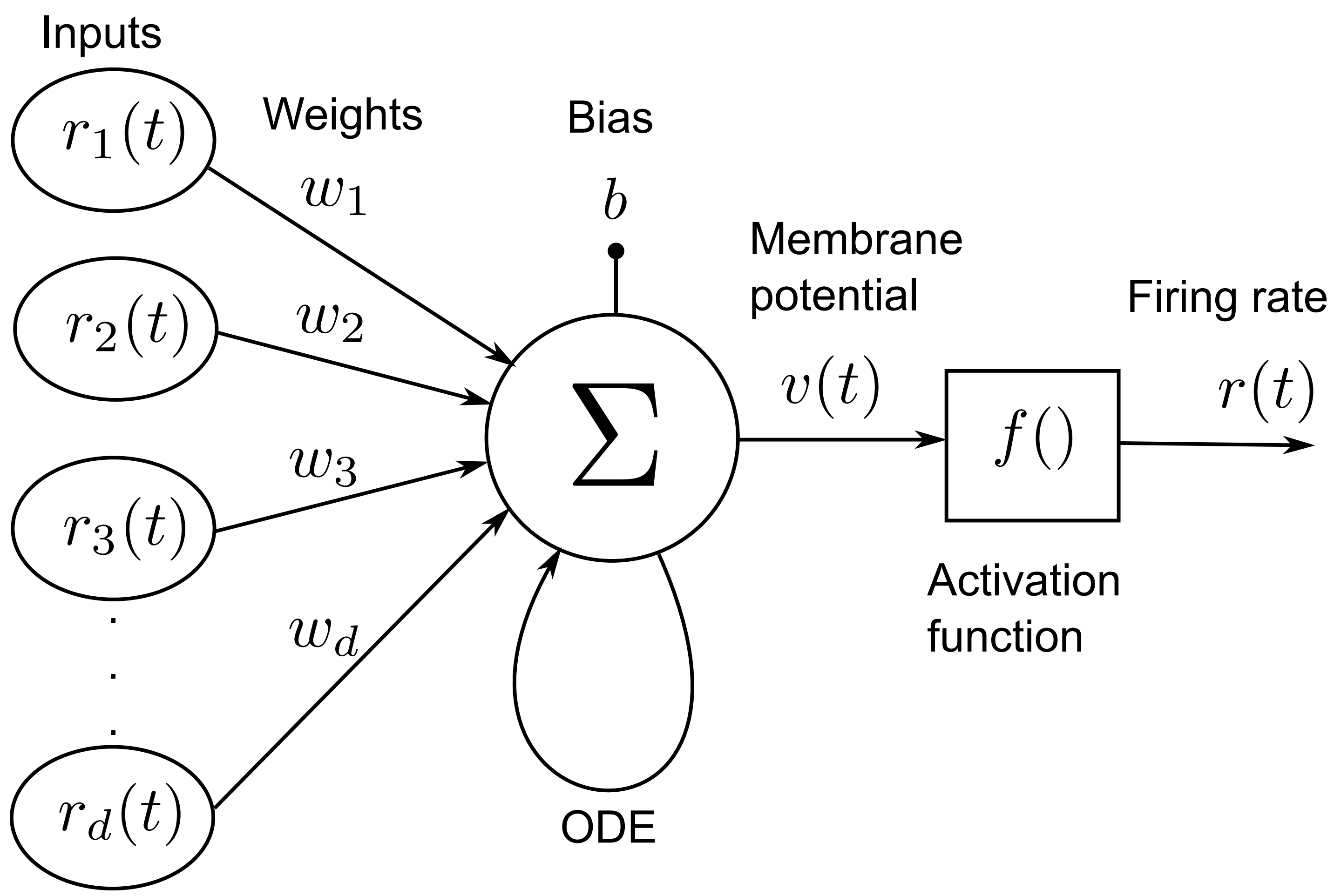


- Interconnected networks of spiking neurons tend to fire synchronously (redundancy).
- What if the important information was not the precise spike timings, but the **firing rate** of a small population?
- The instantaneous firing rate is defined in Hz (number of spikes per second).
- It can be estimated by an histogram of the spikes emitted by a network of similar neurons, or by repeating the same experiment multiple times for a single neuron.
- One can also build neural models that directly model the **firing rate** of (a population of) neuron(s): the **rate-coded** neuron.

Izhikevich, E.M. (2003). Simple Model of Spiking Neurons, IEEE Transaction on Neural Networks, 14:6

The rate-coded neuron

- A rate-coded neuron is represented by two time-dependent variables:
    - The **“membrane potential”** $v(t)$ which evolves over time using an ODE.
    - The **firing rate** $r(t)$ which transforms the membrane potential into a single continuous value using a **transfer function** or **activation function**.



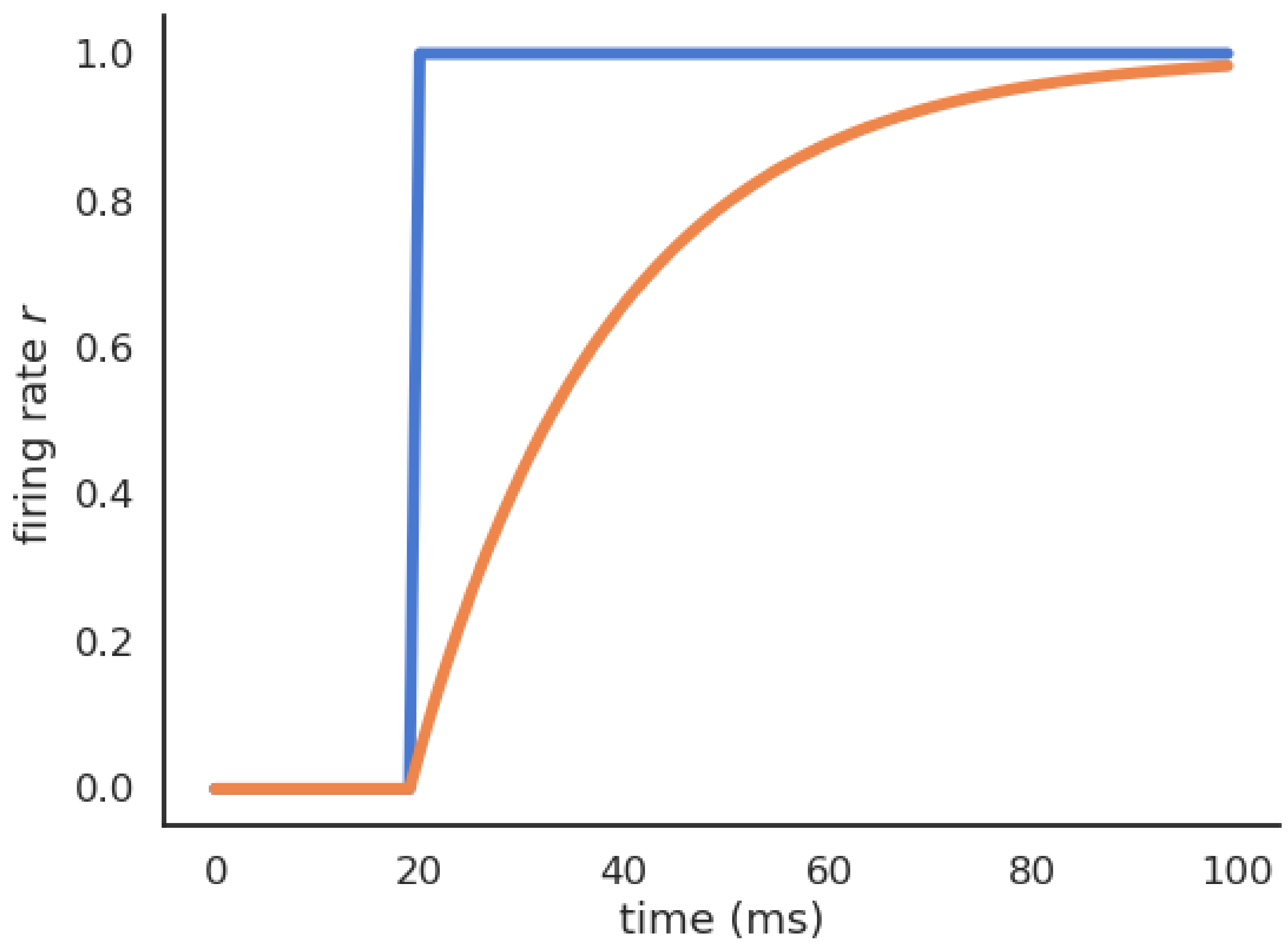
Rate-coded neuron

$$\tau \frac{dv(t)}{dt} + v(t) = \sum_{i=1}^d w_{i,j} \, r_i(t) + b$$

$$r(t) = f(v(t))$$

- The membrane potential uses a weighted sum of inputs (the firing rates $r_i(t)$ of other neurons) by multiplying each rate with a **weight** w_i and adds a constant value b (the **bias**). The activation function can be any non-linear function, usually making sure that the firing rate is positive.

The rate-coded neuron



- Let's consider a simple rate-coded neuron taking a step signal $I(t)$ as input:

$$\tau \frac{dv(t)}{dt} + v(t) = I(t)$$

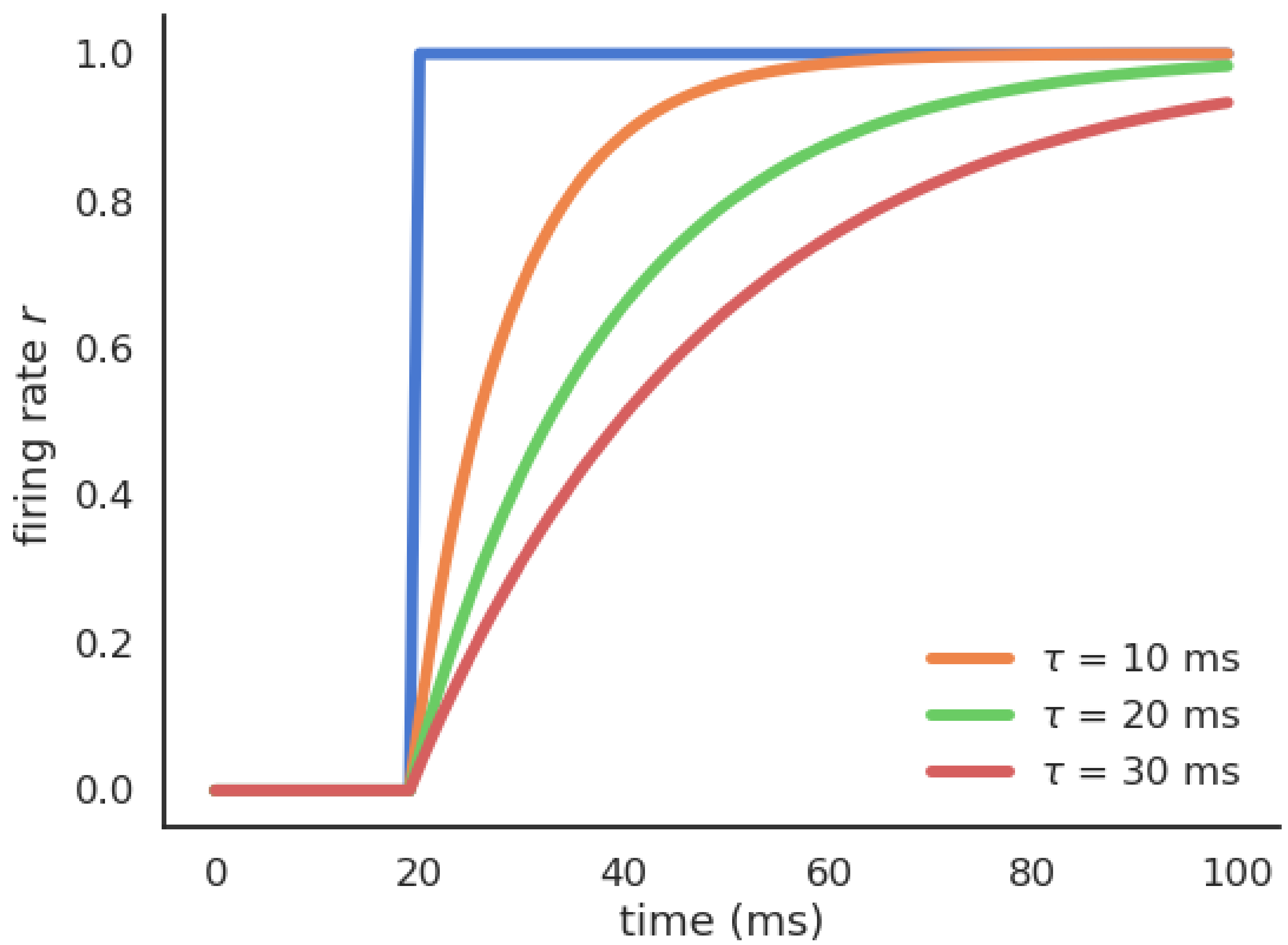
$$r(t) = (v(t))^+$$

- The "speed" of $v(t)$ is given by its temporal derivative:

$$\frac{dv(t)}{dt} = \frac{I(t) - v(t)}{\tau}$$

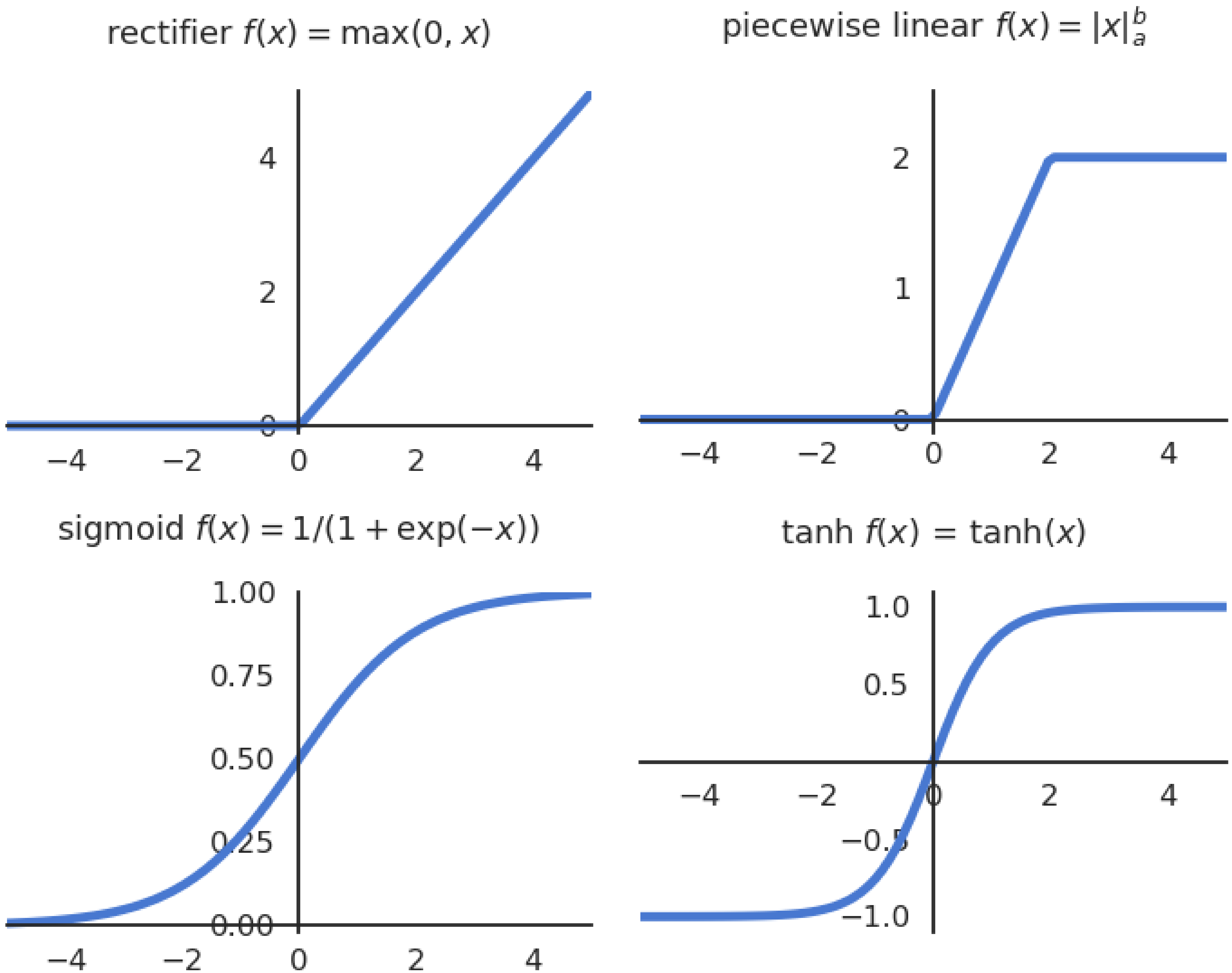
- When $v(t)$ is quite different from $I(t)$, the membrane potential "accelerates" to reduce the difference.
- When $v(t)$ is similar to $I(t)$, the membrane potential stays constant.

The rate-coded neuron



- The membrane potential follows an exponential function which tries to “match” its input with a speed determined by the **time constant** τ.
- The time constant τ determines how fast the rate-coded neuron matches its inputs.
- Biological neurons have time constants between 5 and 30 ms depending on the cell type.

Activation functions

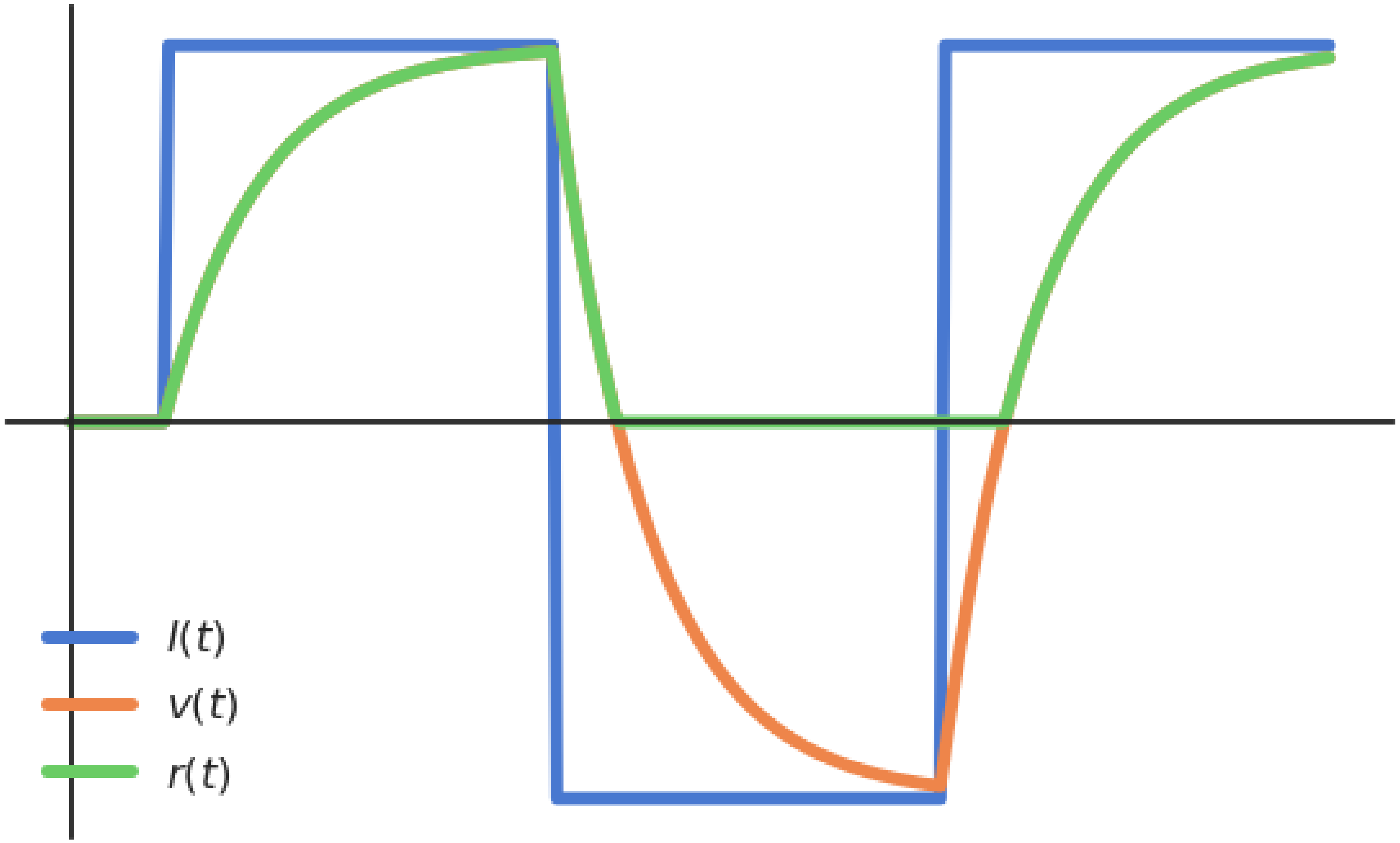


Rectifier activation function

- When using the rectifier activation function

$$f(x) = \max(0, x)$$

the membrane potential $v(t)$ can take any value, but the firing rate $r(t)$ is only positive.

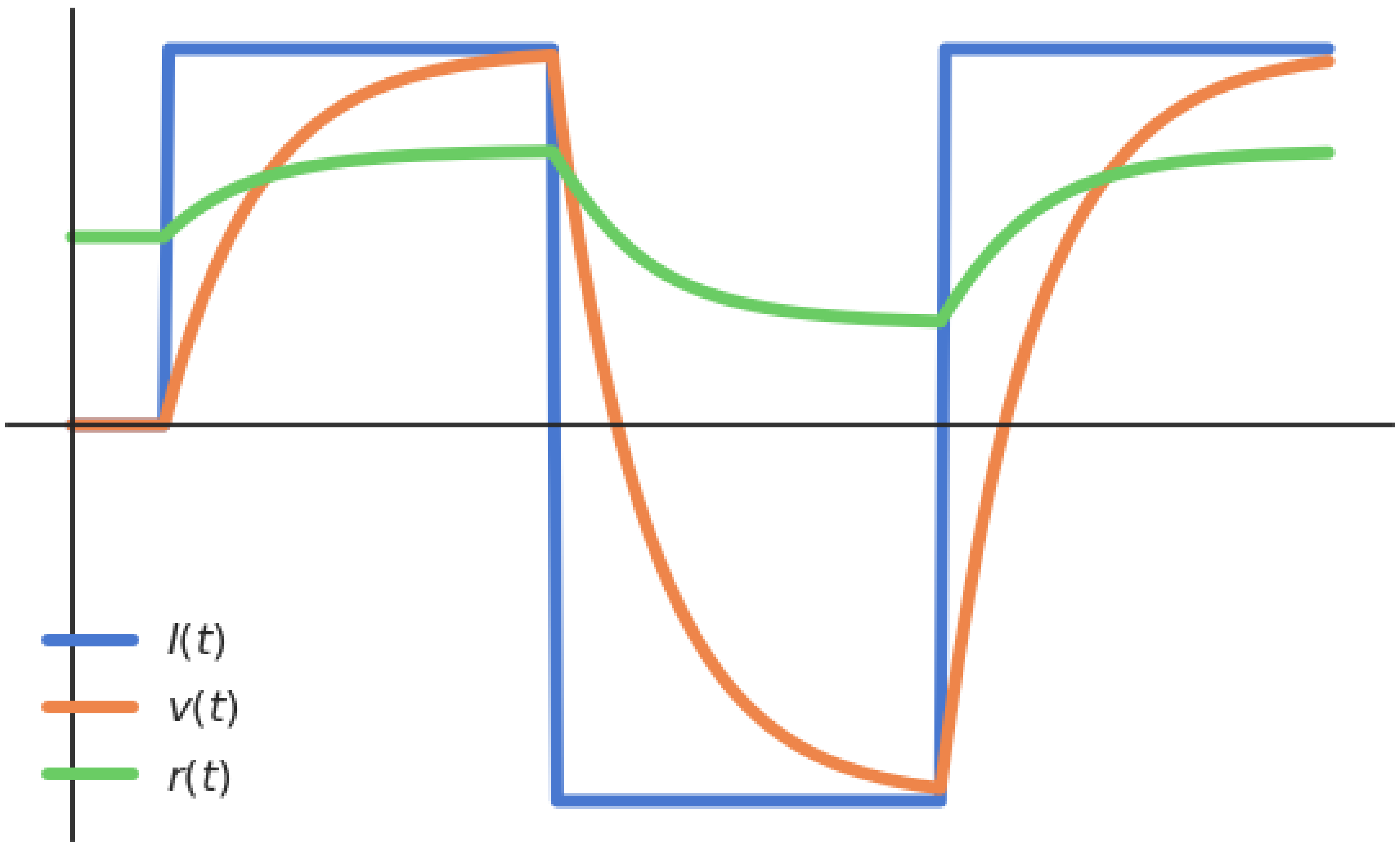


Logistic activation function

- When using the logistic (or sigmoid) activation function

$$f(x) = \frac{1}{1 + \exp(-x)}$$

the firing rate $r(t)$ is bounded between 0 and 1, but responds for negative membrane potentials.

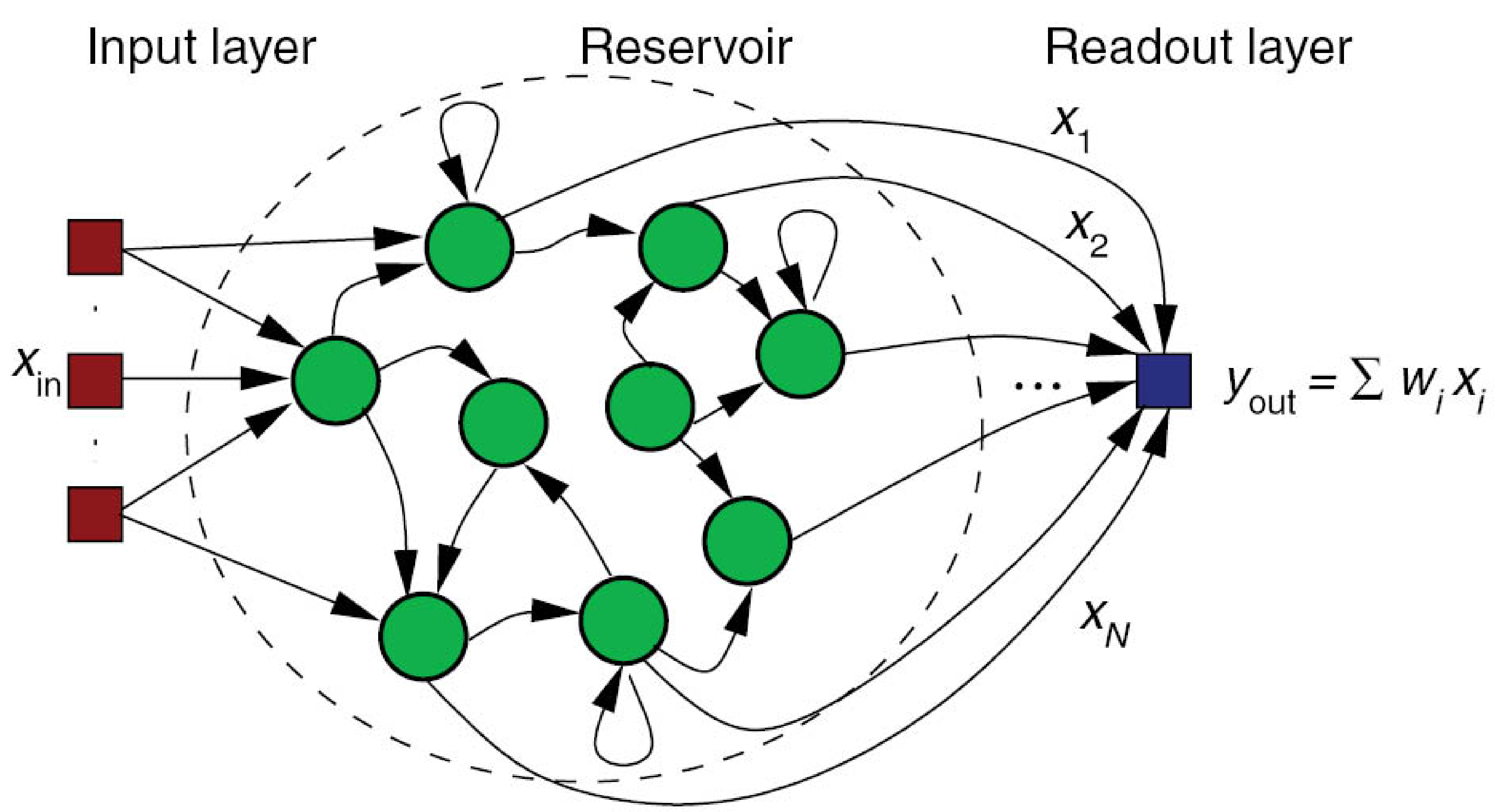


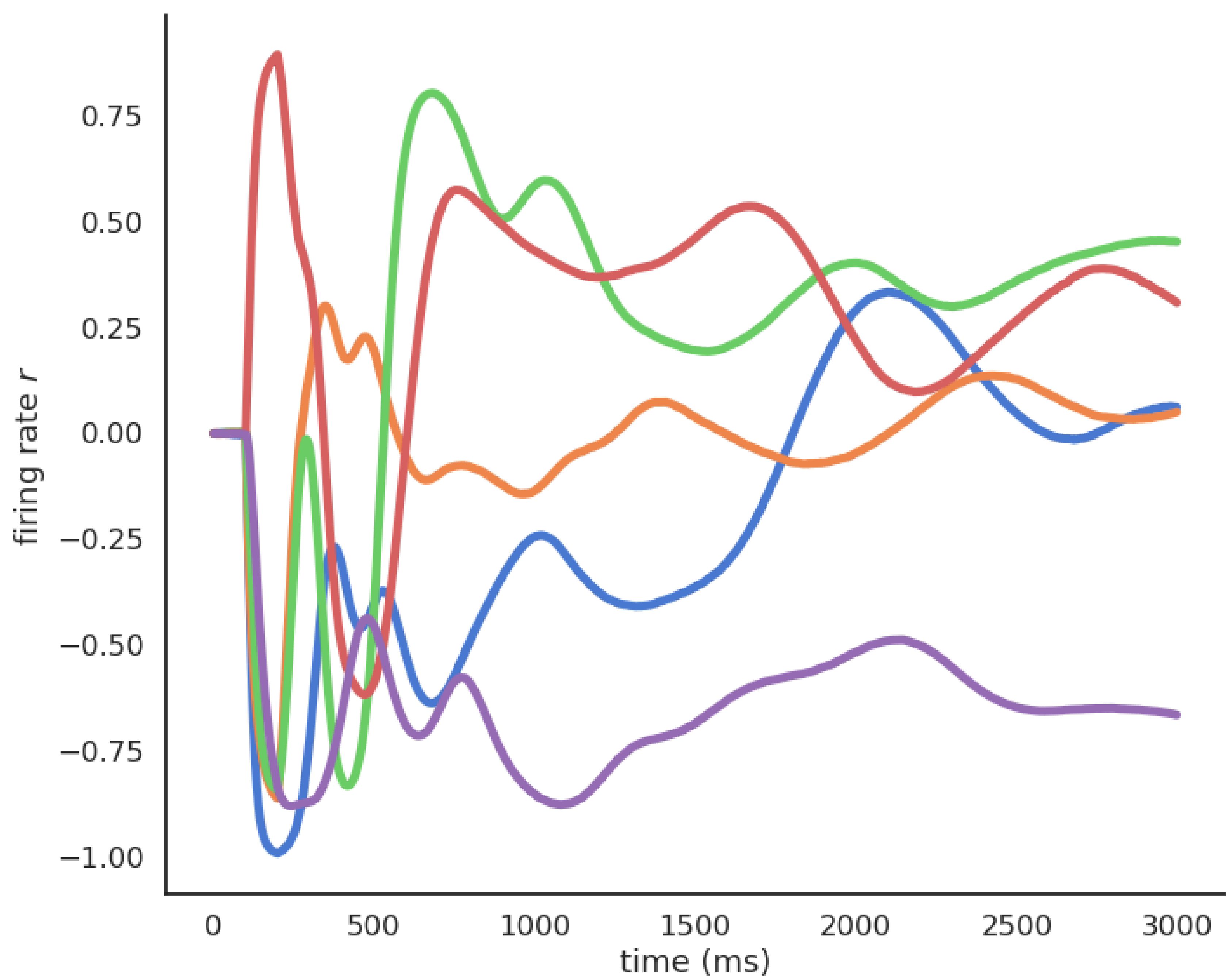
Networks of rate-coded neurons

- Networks of interconnected rate-coded neurons can exhibit very complex dynamics (e.g. **reservoir computing**).

$$\tau \frac{dv(t)}{dt} + v(t) = \sum_{\text{input}} w^{\text{I}} \, I(t) + g \, \sum_{\text{rec}} w^{\text{R}} \, r(t) + \xi(t)$$

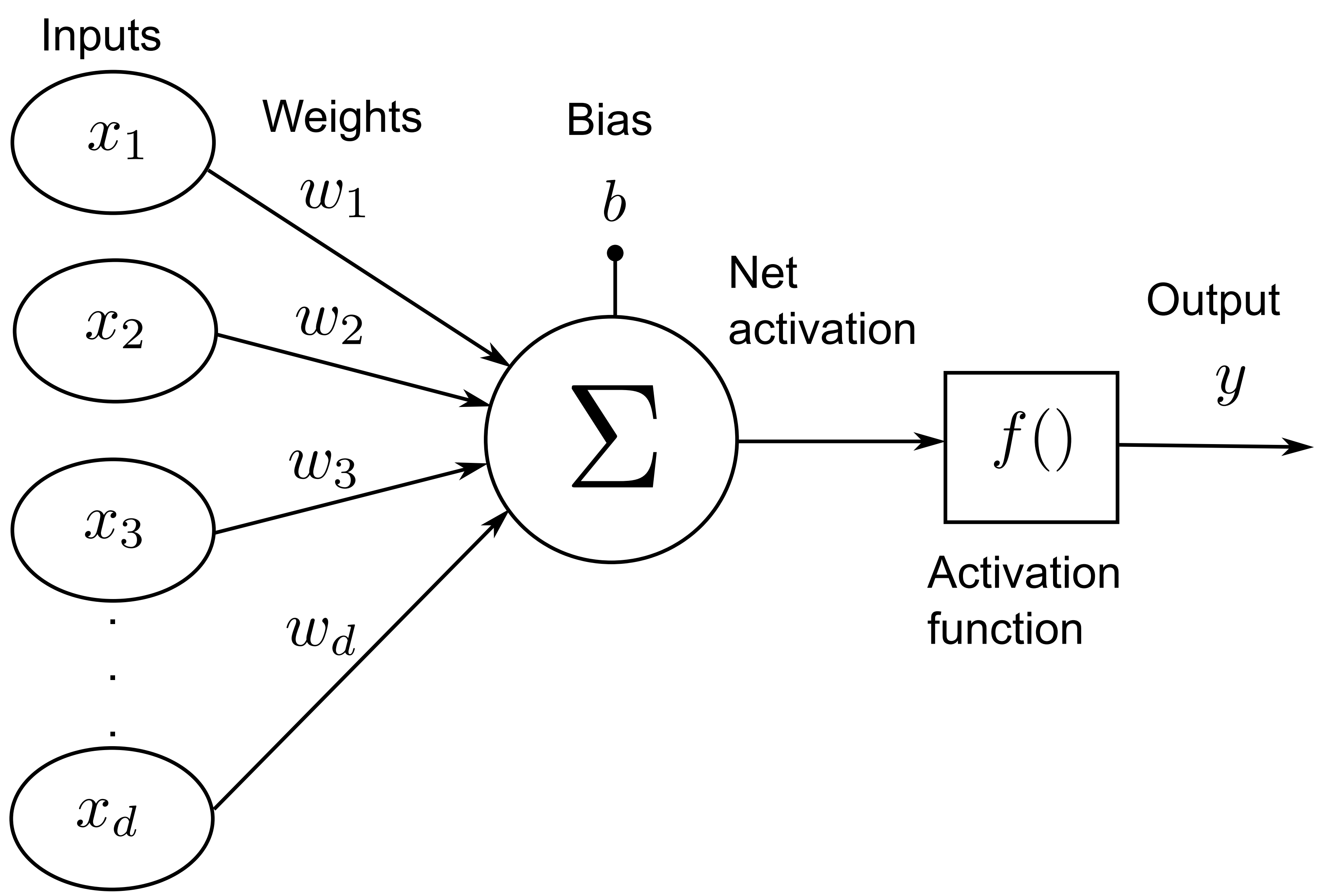
$$r(t) = \tanh(v(t))$$





The McCulloch & Pitts neuron (McCulloch and Pitts, 1943)

- By omitting the dynamics of the rate-coded neuron, one obtains the very simple **artificial neuron**:



Artificial neuron

$$y = f(\sum_{i=1}^d w_i \, x_i + b)$$

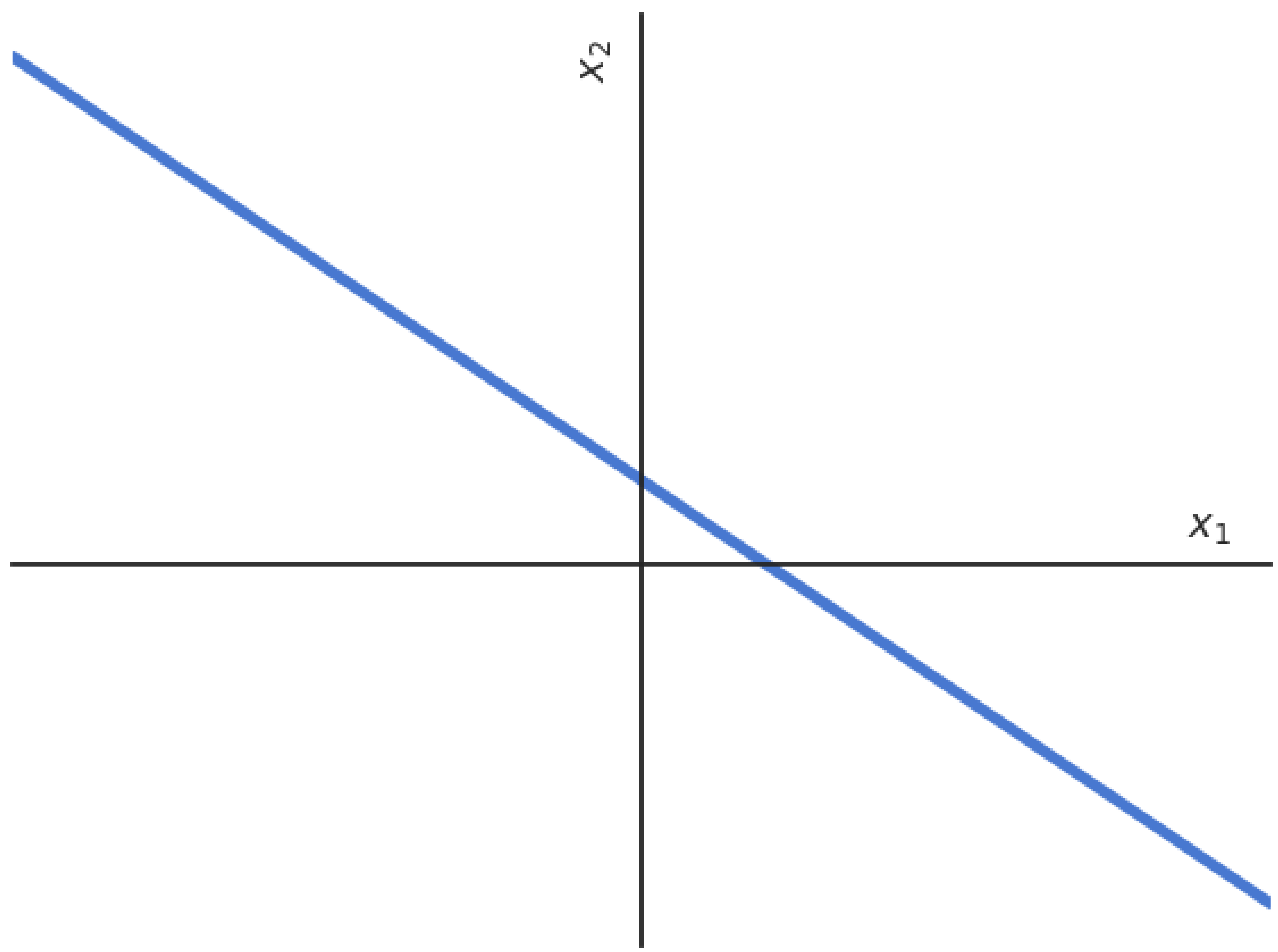
- An artificial neuron sums its inputs $x_1, \dots, x_d$ by multiplying them with weights $w_1, \dots, w_d$, adds a bias b and transforms the result into an output y using an activation function f.
- The output y directly reflects the input, without temporal integration.

- The **weighted sum of inputs + bias** $\sum_{i=1}^d w_i \, x_i + b$ is called the **net activation**.
- This overly simplified neuron model is the basic unit of the **artificial neural networks** (ANN) used in machine learning / deep learning.

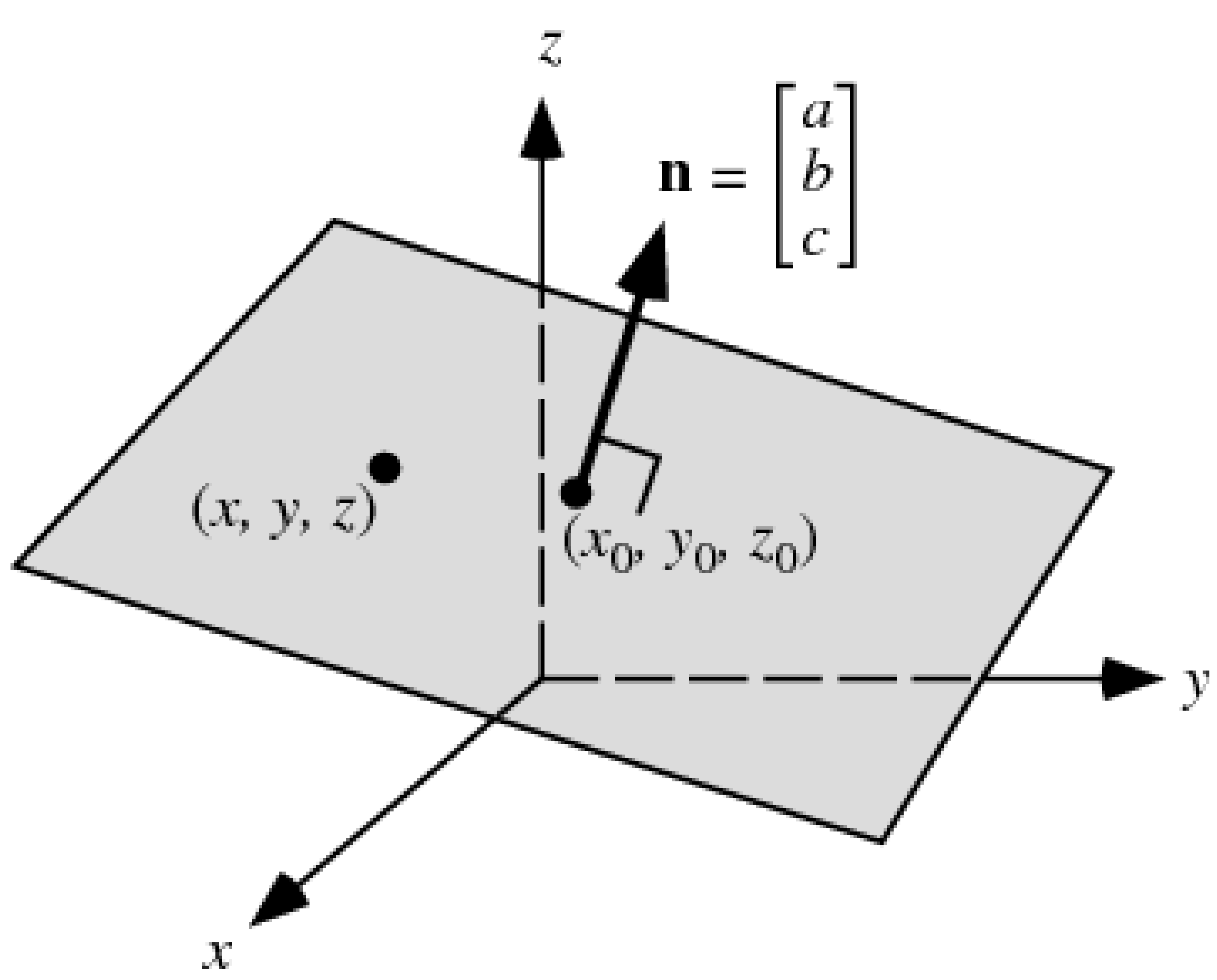
Artificial neurons and hyperplanes

- Let's consider an artificial neuron with only two inputs x_1 and x_2.
- The net activation $w_1 \, x_1 + w_2 \, x_2 + b$ is the equation of a line in the space (x_1, x_2).

$$w_1 \, x_1 + w_2 \, x_2 + b = 0 \Leftrightarrow x_2 = - \frac{w_1}{w_2} \, x_1 - \frac{b}{w_2}$$



Artificial neurons and hyperplanes



https://newvitruvian.com/explore/vector-planes/#gal_post_7186_nonzero-vector.gif

- The net activation is a line in 2D, a plane in 3D, etc.
- Generally, the net activation describes an **hyperplane** in the input space with d dimensions $(x_1, x_2, \ldots, x_d)$.
- An hyperplane has one dimension less than the space.

- We can write the net activation using a **weight vector** $\mathbf{w}$ and a **bias** b:

$$\sum_{i=1}^{d} w_i \, x_i + b = \langle \mathbf{w} \cdot \mathbf{x} \rangle + b$$

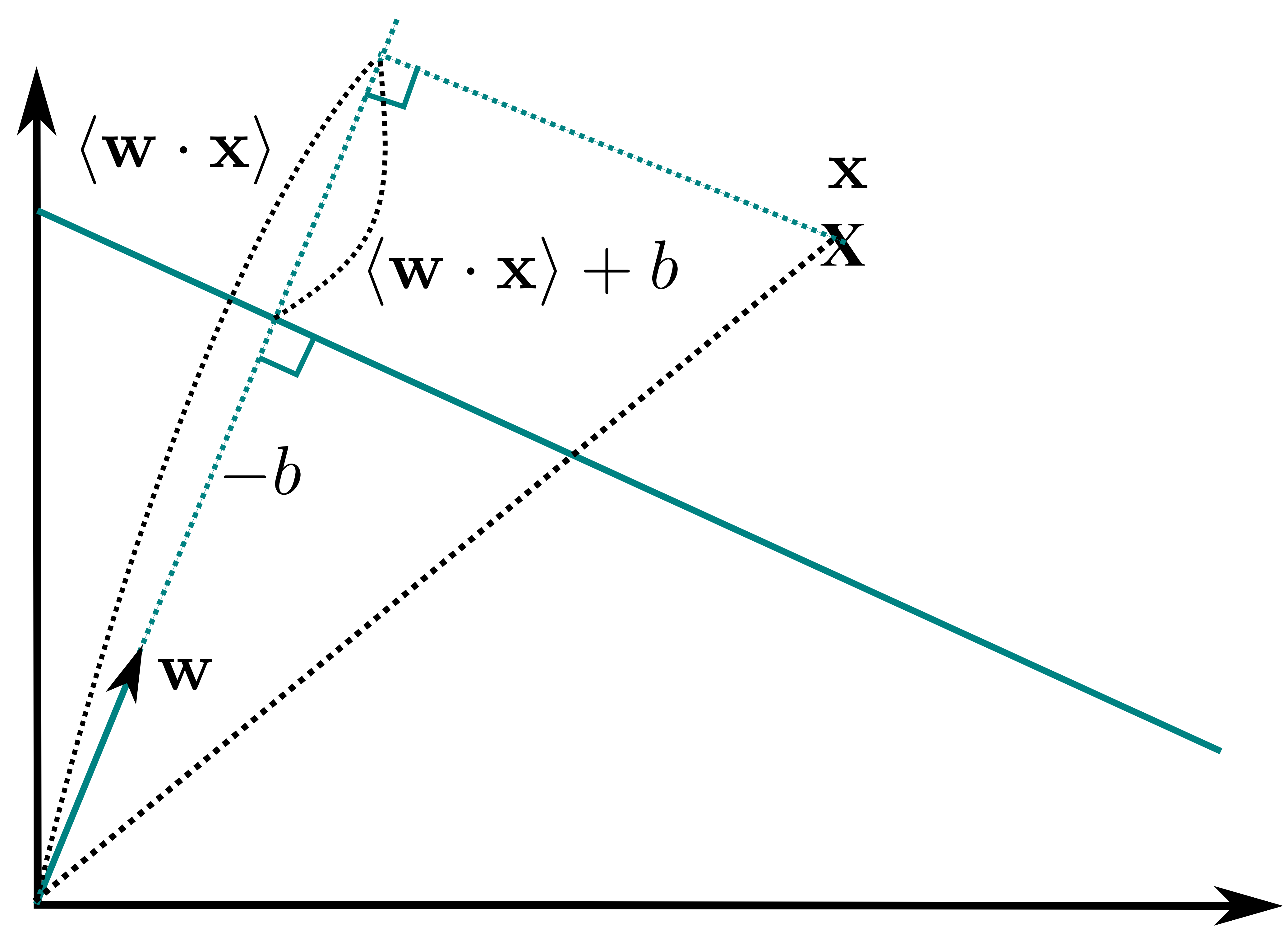
with:

$$\mathbf{w} = \begin{bmatrix} w_1 \\ w_2 \\ \ldots \\ w_d \end{bmatrix} \qquad \mathbf{x} = \begin{bmatrix} x_1 \\ x_2 \\ \ldots \\ x_d \end{bmatrix}$$

- $\langle \cdot \rangle$ is the **dot product** (aka inner product, scalar product) between the **input vector** $\mathbf{x}$ and the weight vector $\mathbf{w}$.
- The weight vector is orthogonal to the hyperplane $(\mathbf{w}, b)$ and defines its orientation. b is the “signed distance” between the hyperplane and the origin.

Artificial neurons and hyperplanes

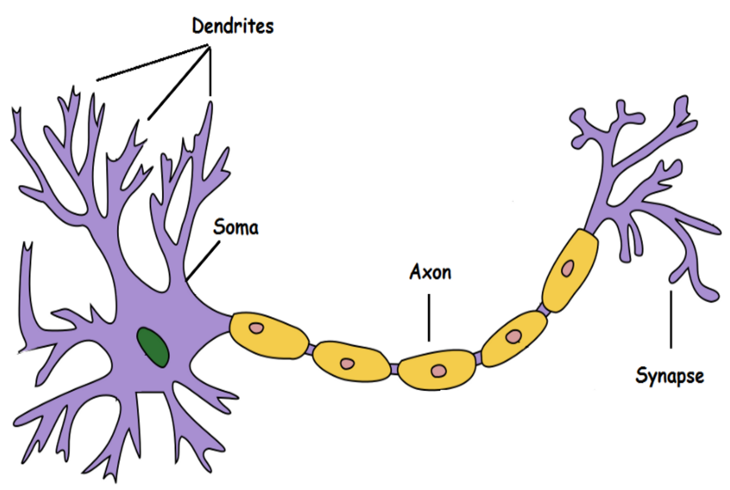
- The hyperplane separates the input space into two parts:
  - $\langle \mathbf{w} \cdot \mathbf{x} \rangle + b > 0$ for all points $\mathbf{x}$ **above** the hyperplane.
  - $\langle \mathbf{w} \cdot \mathbf{x} \rangle + b < 0$ for all points $\mathbf{x}$ **below** the hyperplane.
- By looking at the **sign** of the net activation, we can separate the input space into two classes.

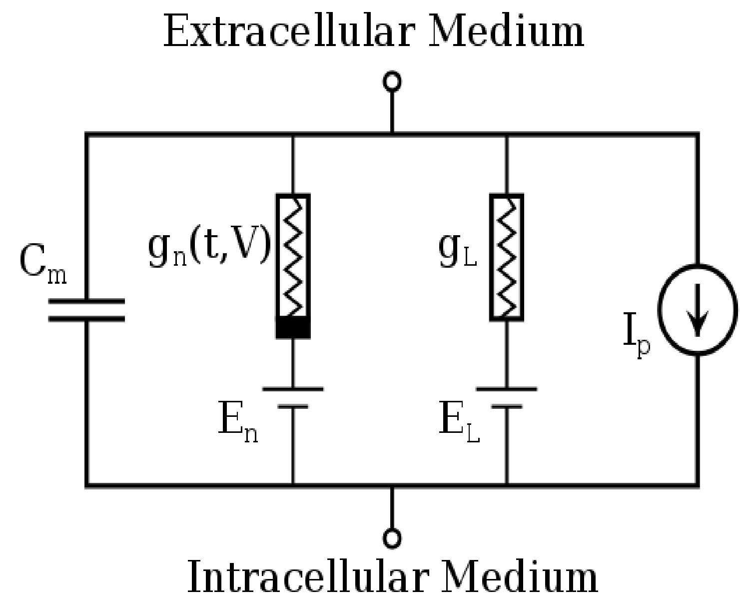


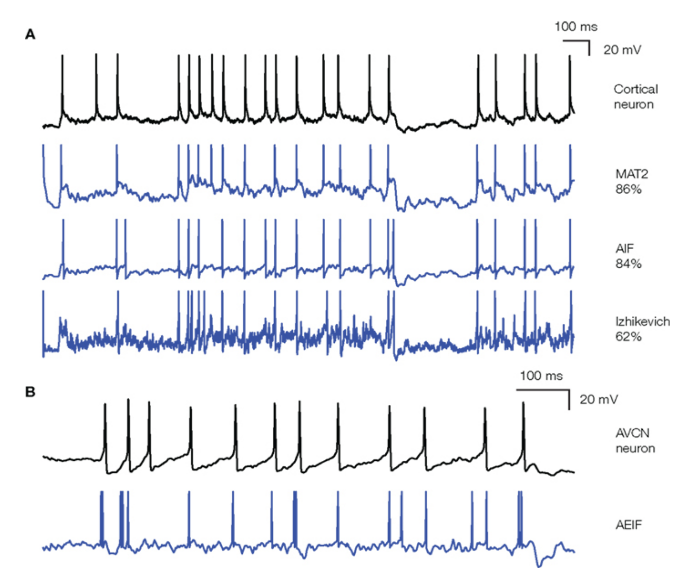
Overview of neuron models

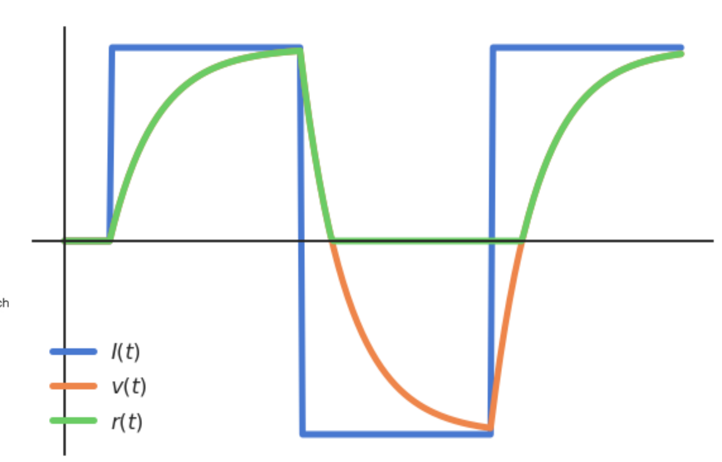
Biological plausibility

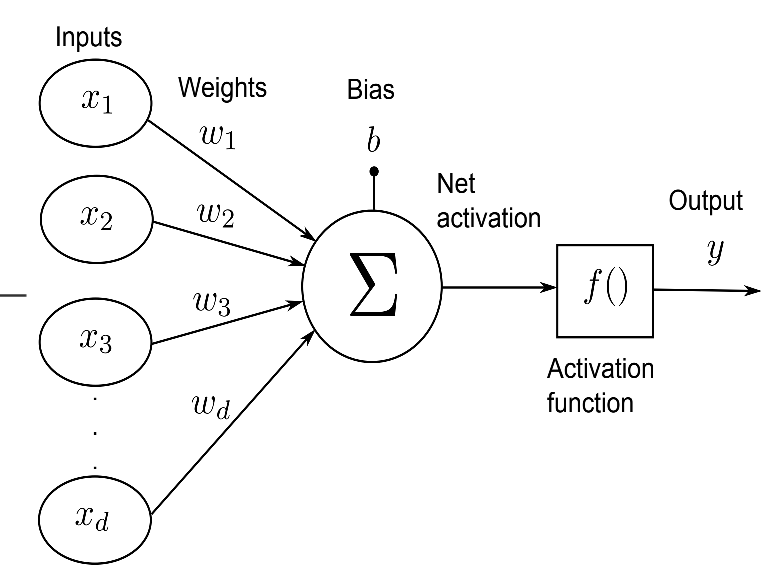
Biological neuron | Hodgkin-Huxley | Spiking neuron | Rate-coded neuron | Artificial neuron







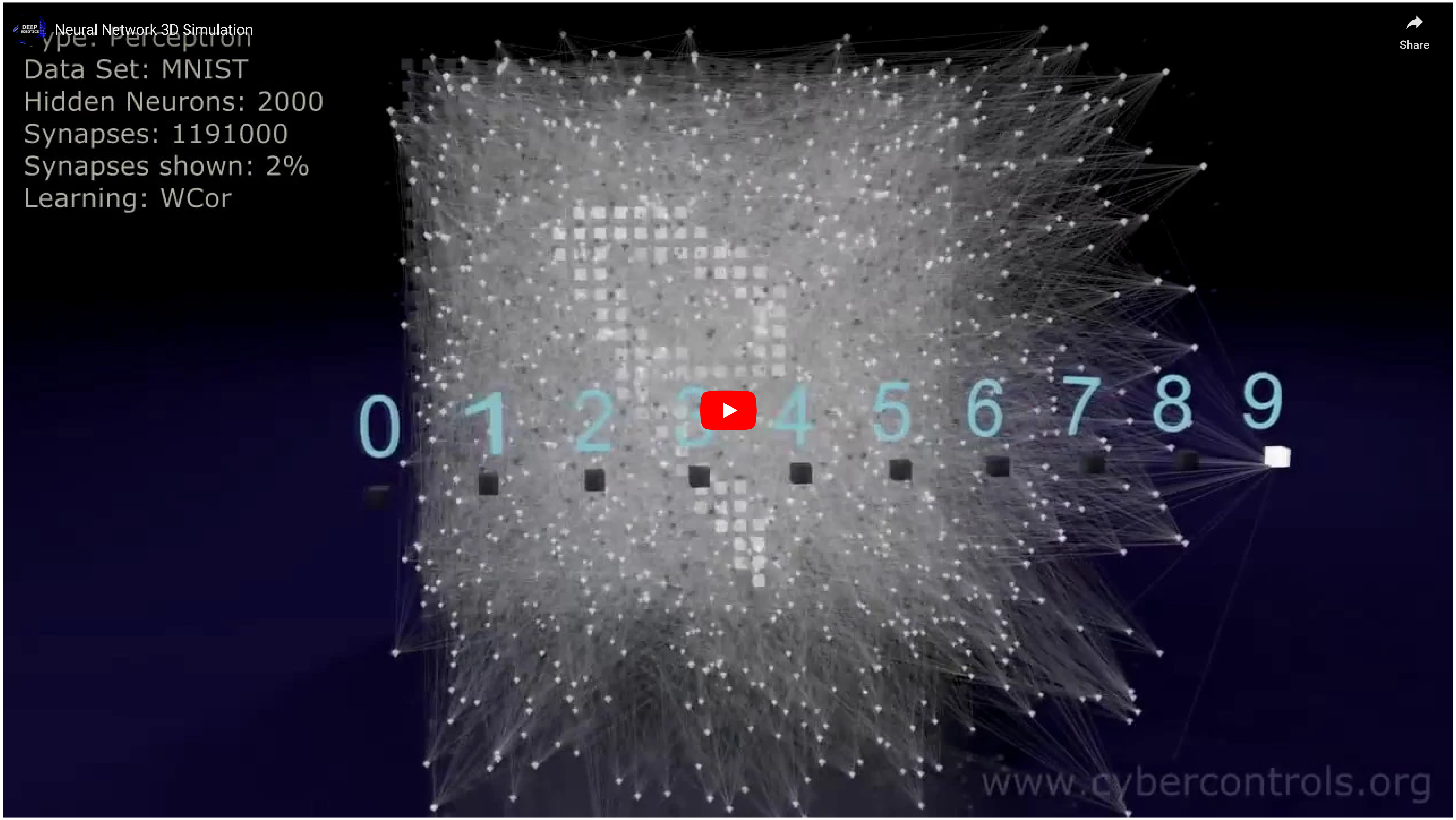




Machine learning

Computational neuroscience

Neurocomputing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Synapses: 1191000
Synapses shown: 2%
Learning: WCor
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