

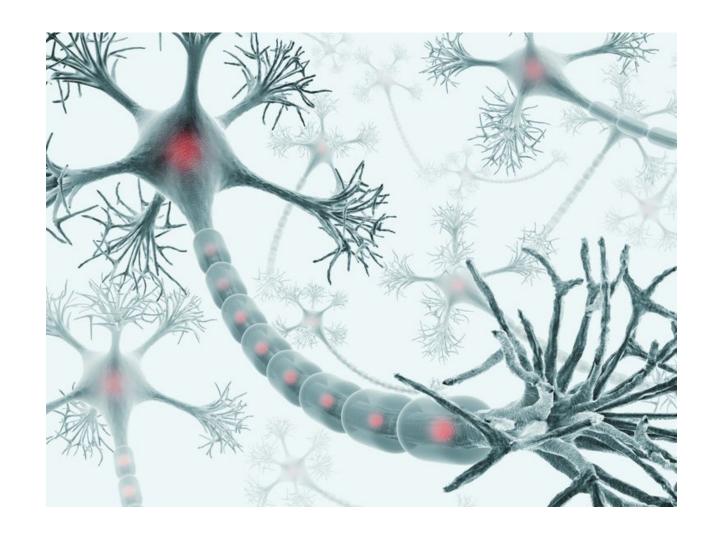
Neurocomputing

Neurons

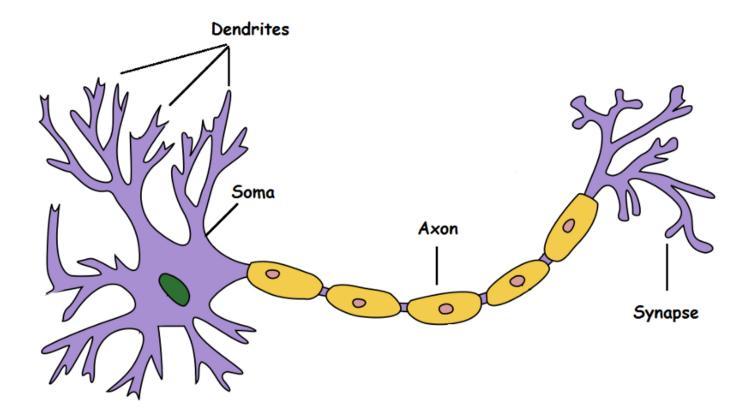
Julien Vitay

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

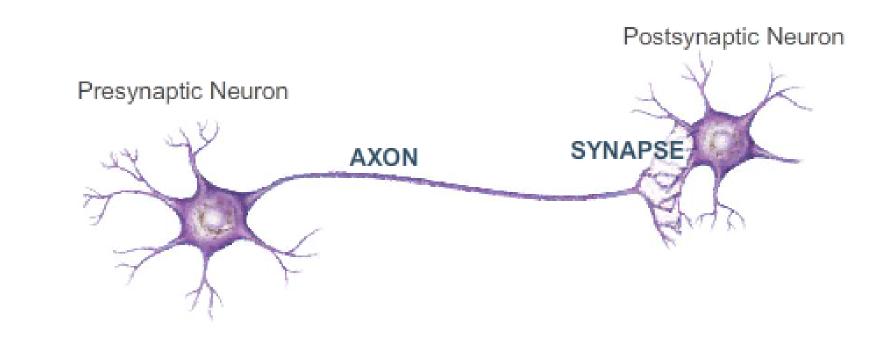


https://www.verywellmind.com/what-is-a-neuron-2794890

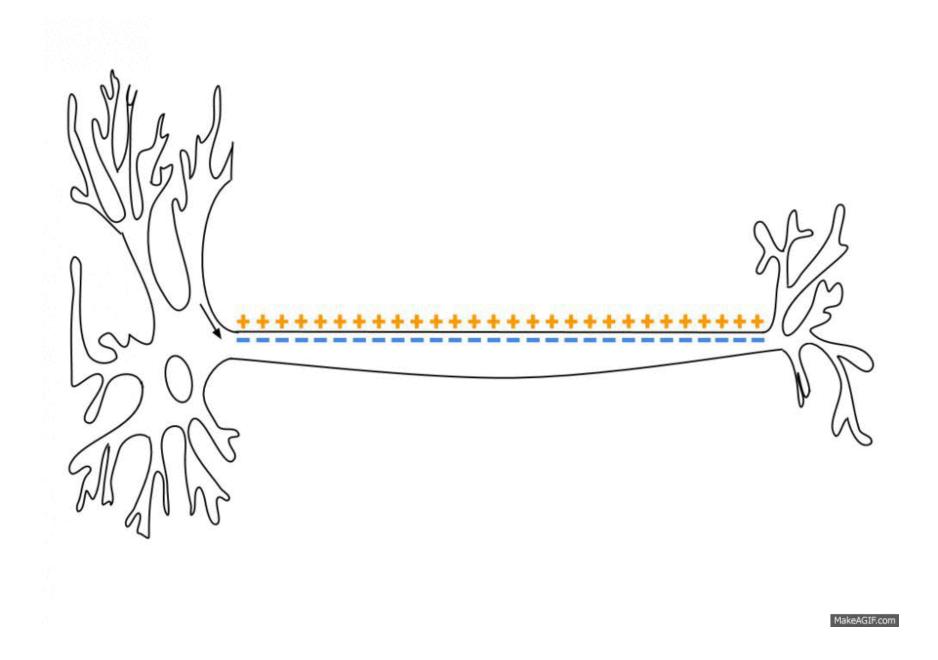


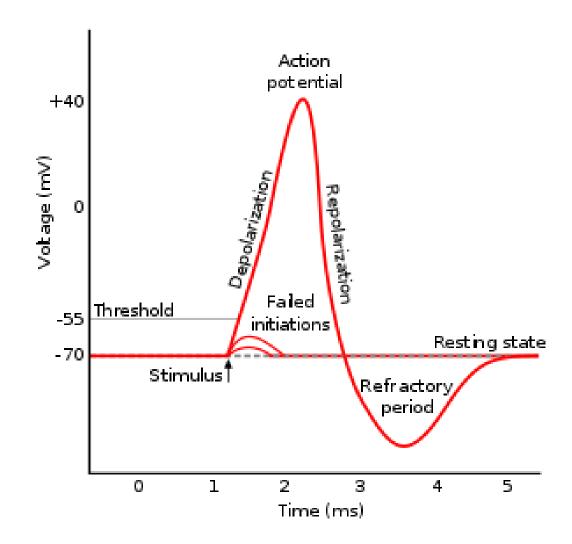
https://en.wikipedia.org/wiki/Neuron

- 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.



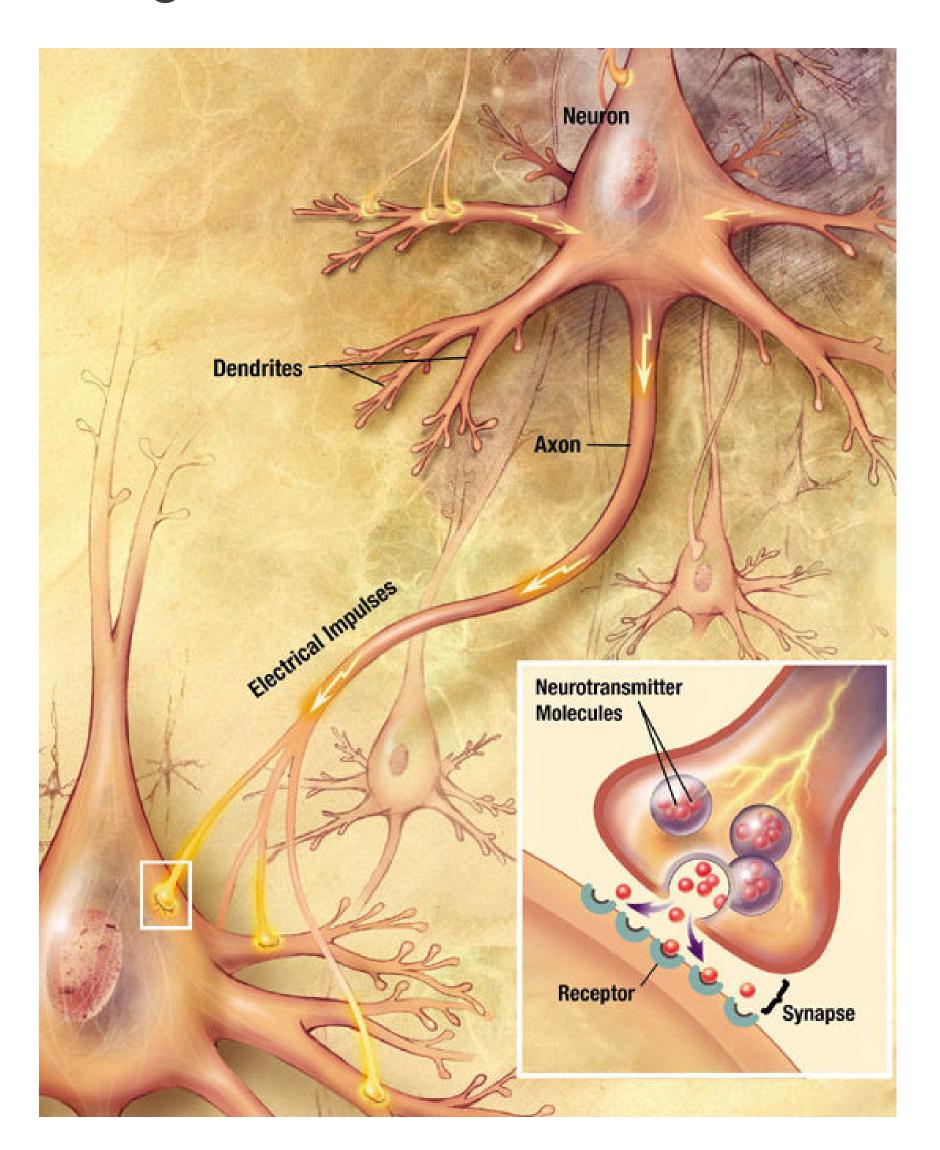
http://bcs.whfreeman.com/webpub/Ektron/Hillis%20Principles%20of%20Life2e/Ani





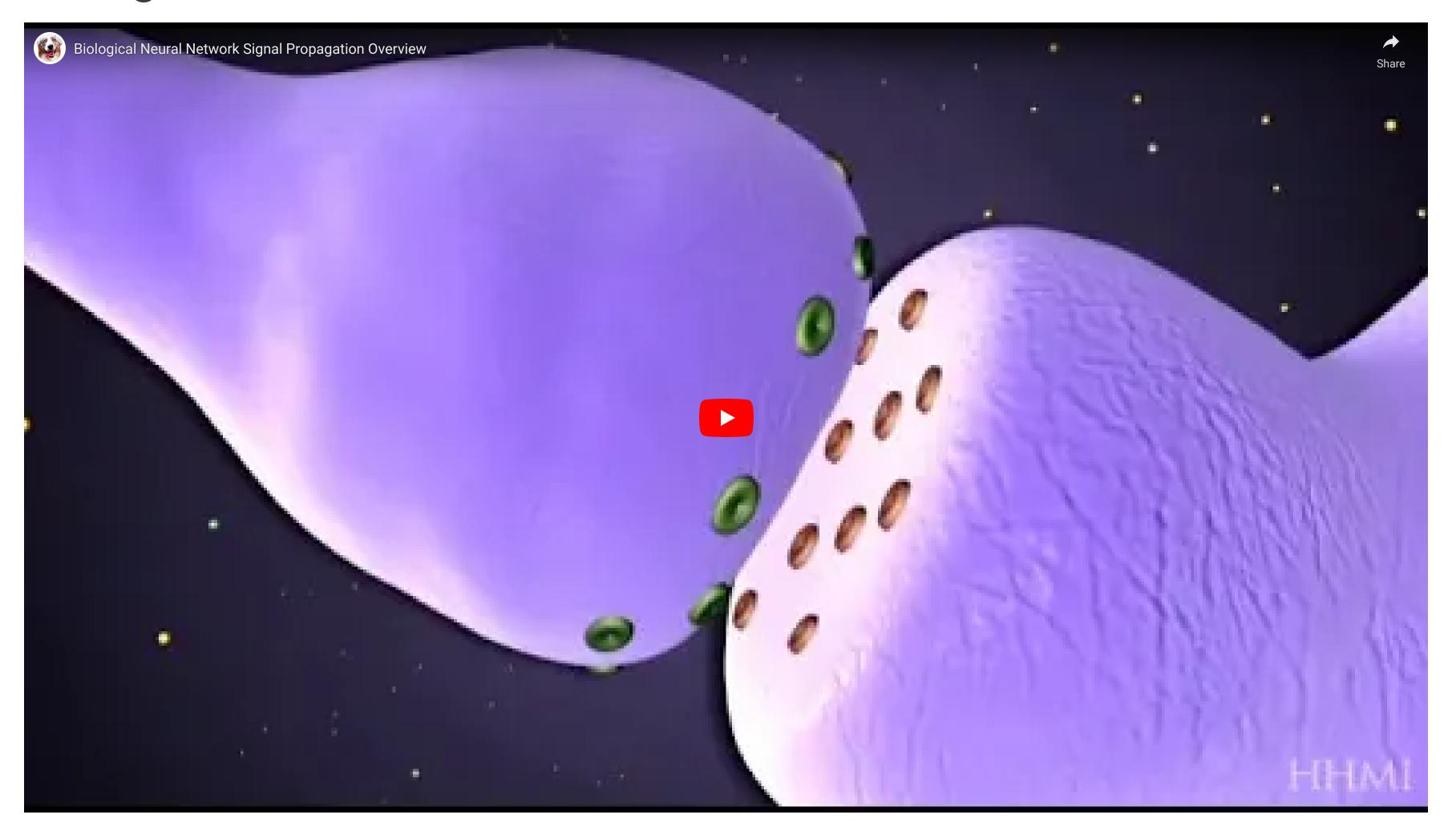
https://en.wikipedia.org/wiki/Action_potential

- 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.

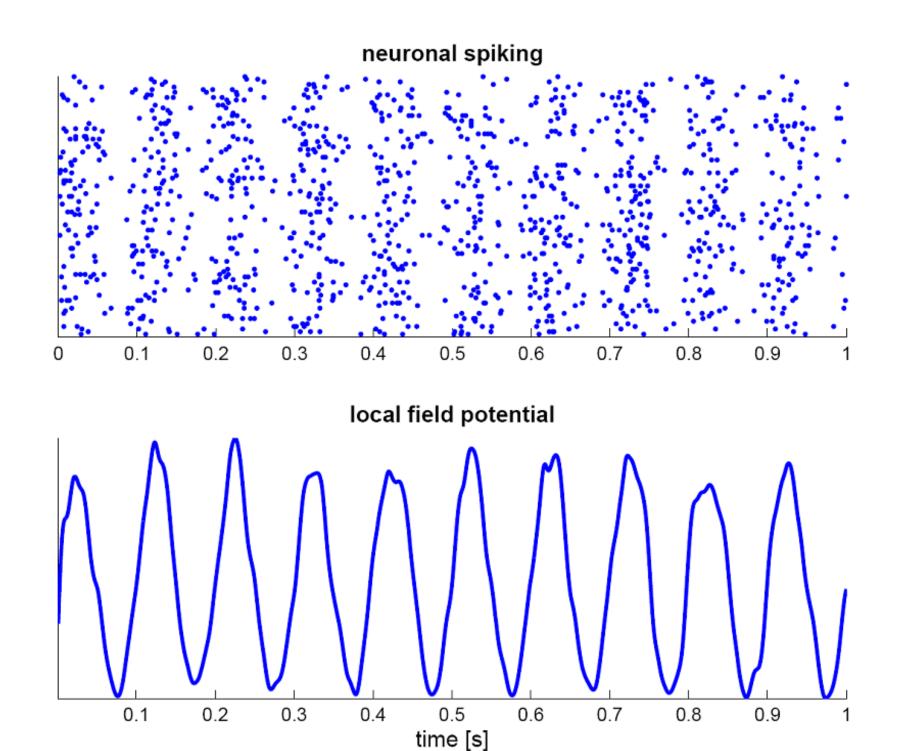


- The action potential arrives at the synapses and releases **neurotransmitters** in the synaptic cleft:
 - glutamate (AMPA, NMDA)
 - GABA
 - dopamine
 - serotonin
 - nicotin
 - etc...
- Neurotransmitters can enter the receiving neuron through receptors and change its potential: the neuron may emit a 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.

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



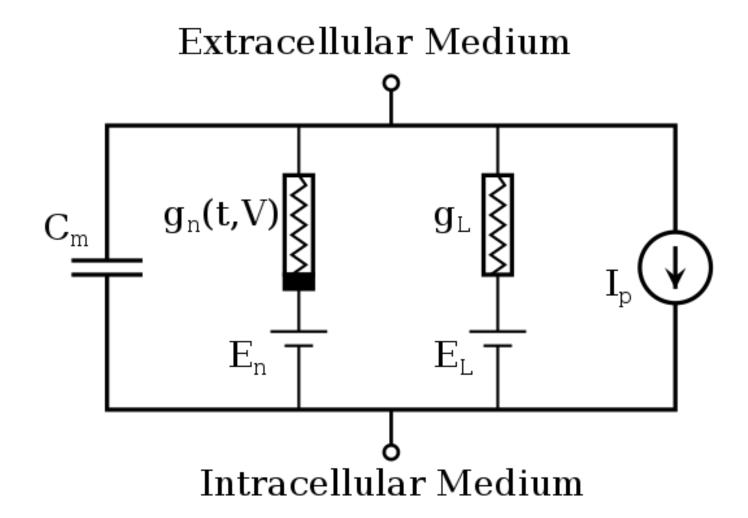
Information is transmitted through spike trains



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.

$$a_n = 0.01 (v + 60)/(1.0 - \exp(-0.1 (v + 60)))$$

$$a_m = 0.1 (v + 45)/(1.0 - \exp(-0.1 (v + 45)))$$

$$a_h = 0.07 \exp(-0.05 (v + 70))$$

$$b_n = 0.125 \exp(-0.0125 (v + 70))$$

$$b_m = 4 \exp(-(v + 70)/80)$$

$$b_h = 1/(1 + \exp(-0.1 (v + 40)))$$

$$\frac{dn}{dt} = a_n (1 - n) - b_n n$$

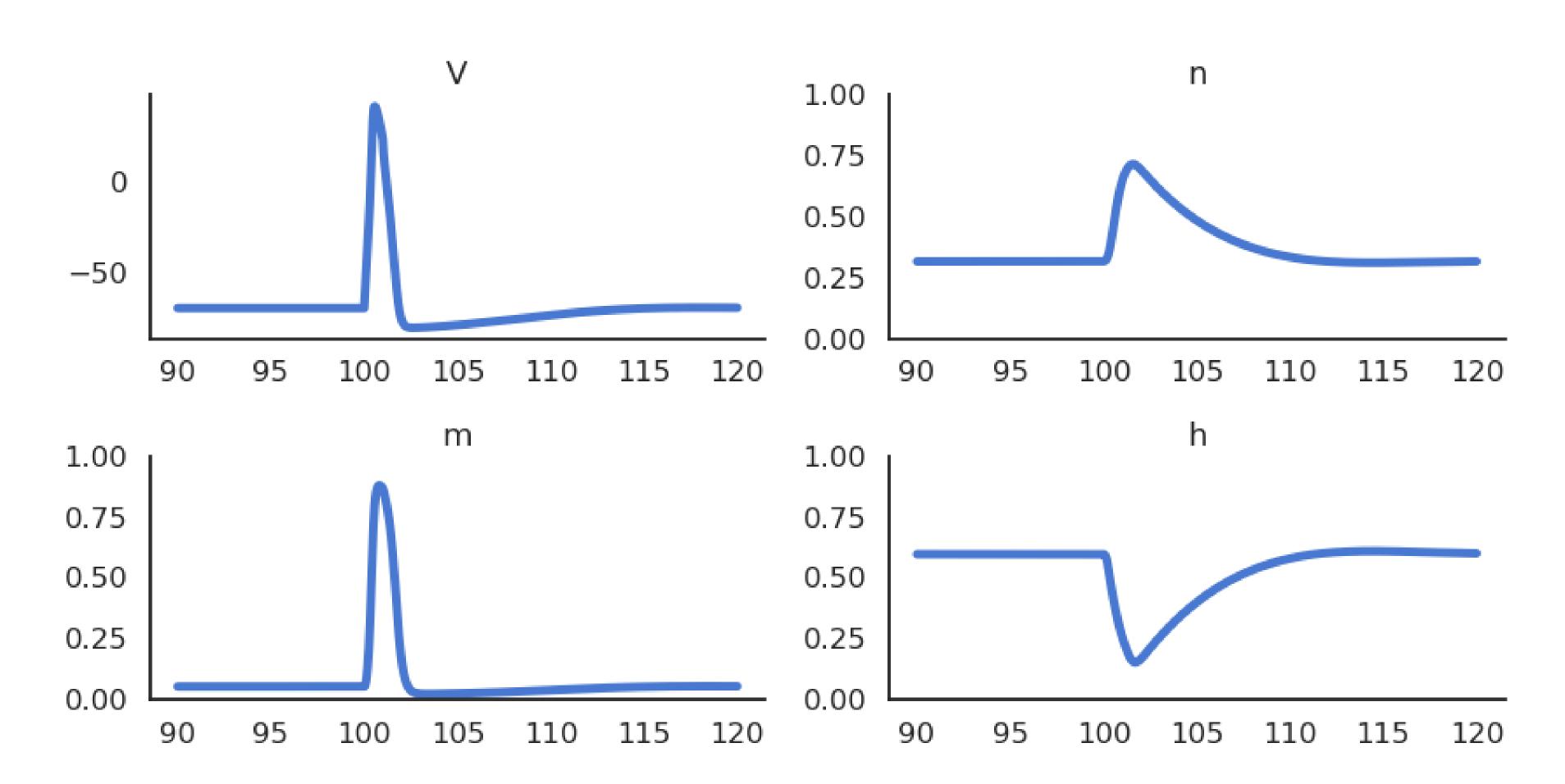
$$\frac{dm}{dt} = a_m (1 - m) - b_m m$$

$$\frac{dh}{dt} = a_h (1 - h) - b_h h$$

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

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

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

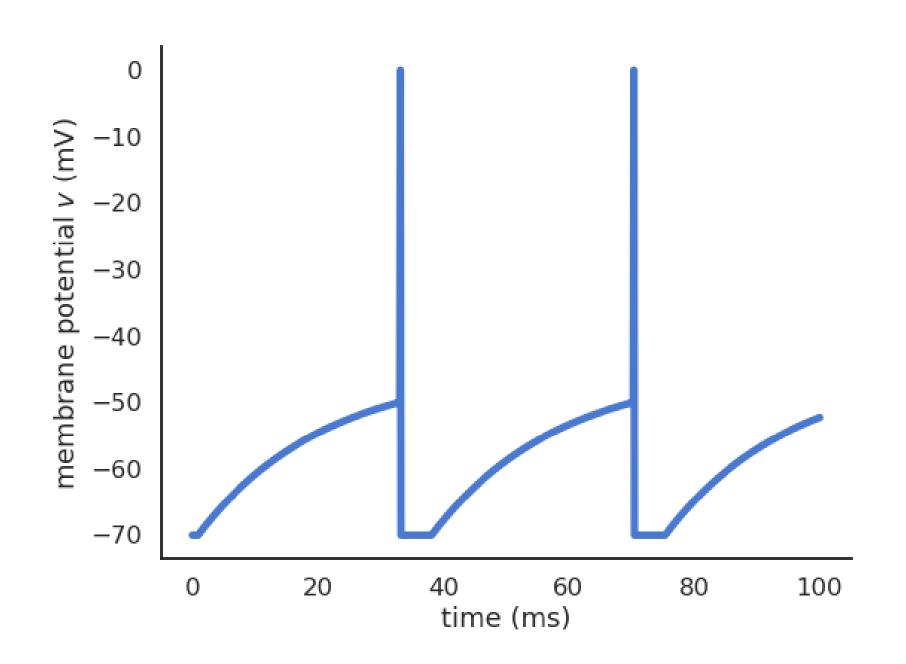


The leaky integrate-and-fire neuron (Lapicque, 1907)

- 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.

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

if $v > V_T$ emit a spike and reset.



Different spiking neuron models are possible

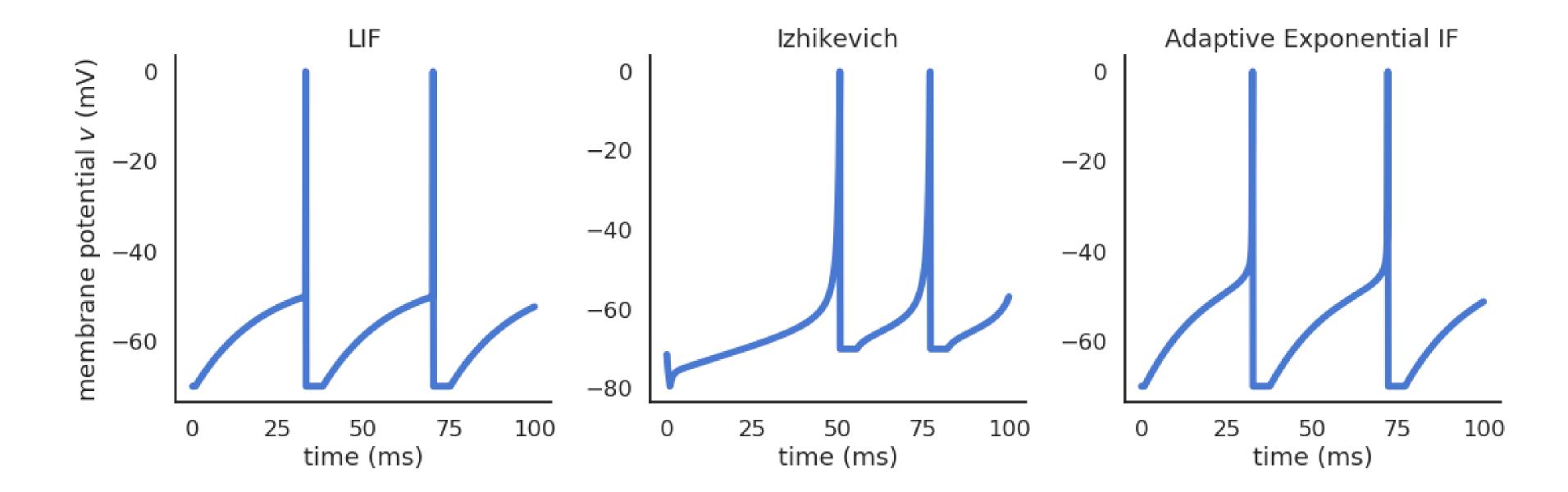
• Izhikevich quadratic IF (Izhikevich, 2001).

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

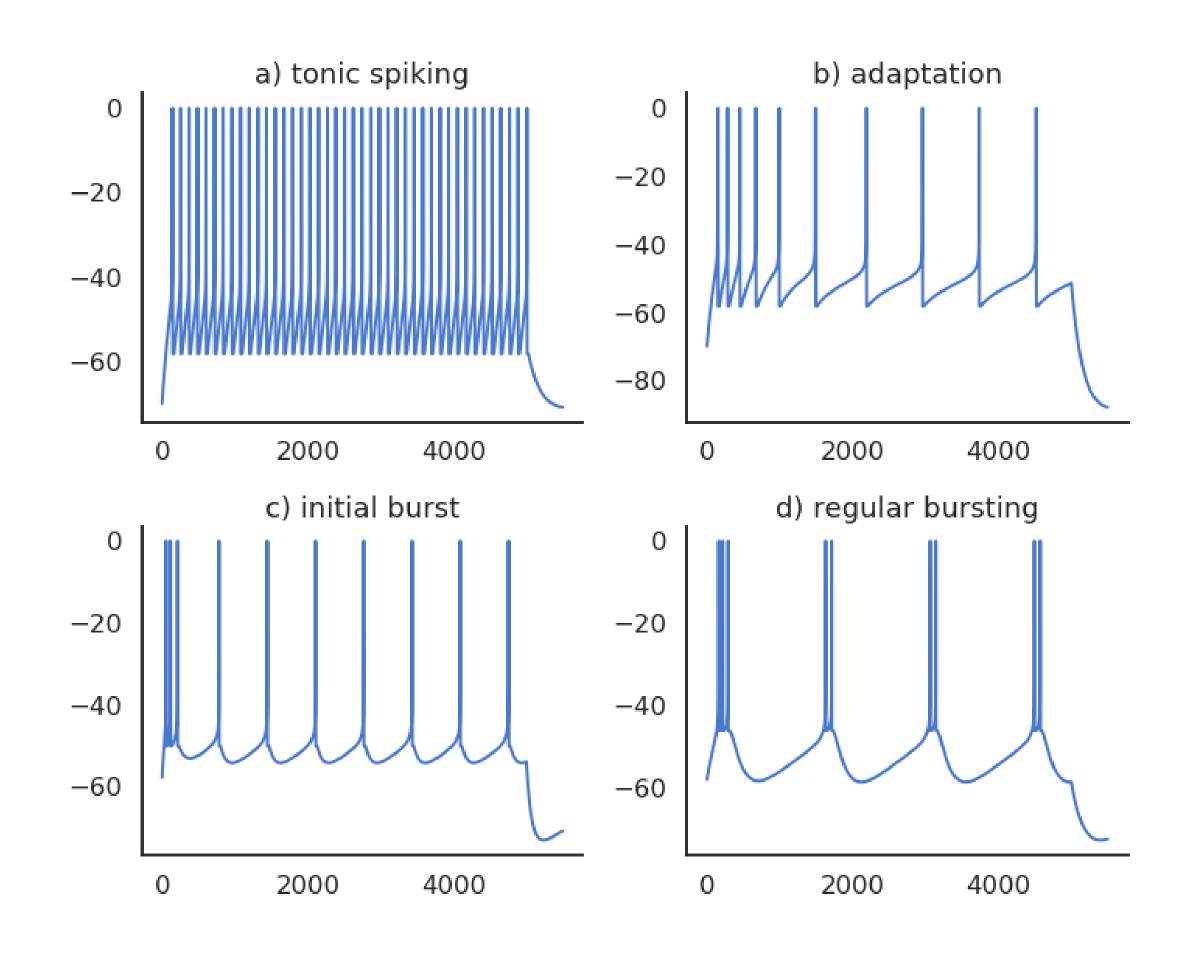
$$\frac{du}{dt} = a (b v - u)$$

 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

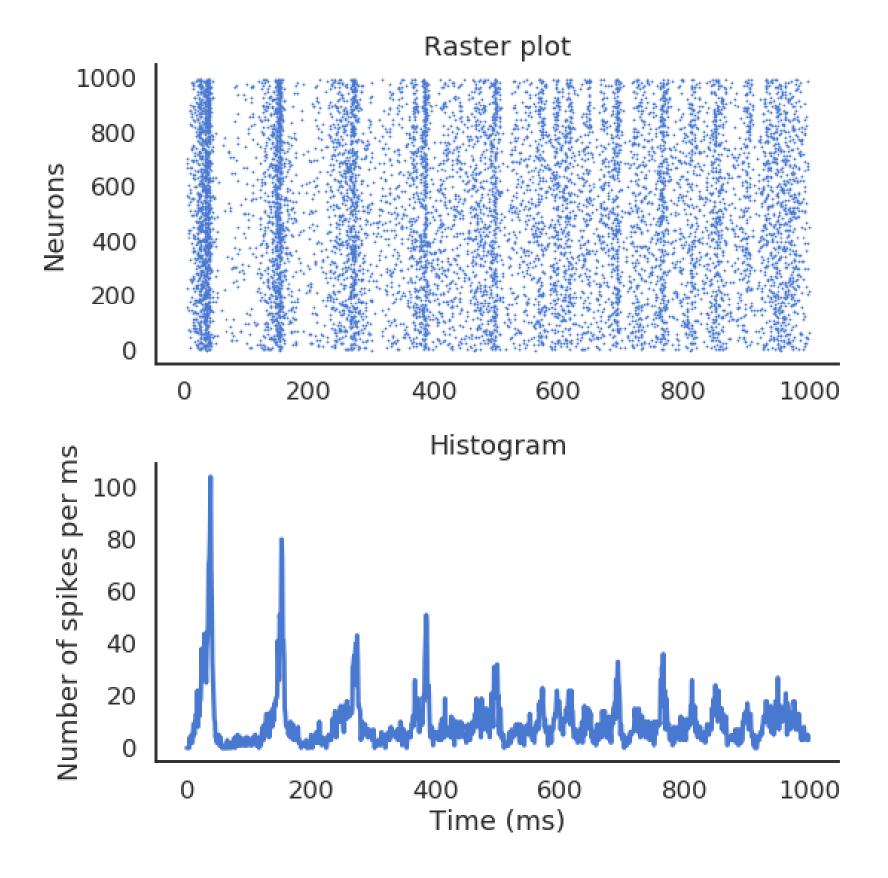


Biological neurons do not all respond the same to an input current.

- 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.

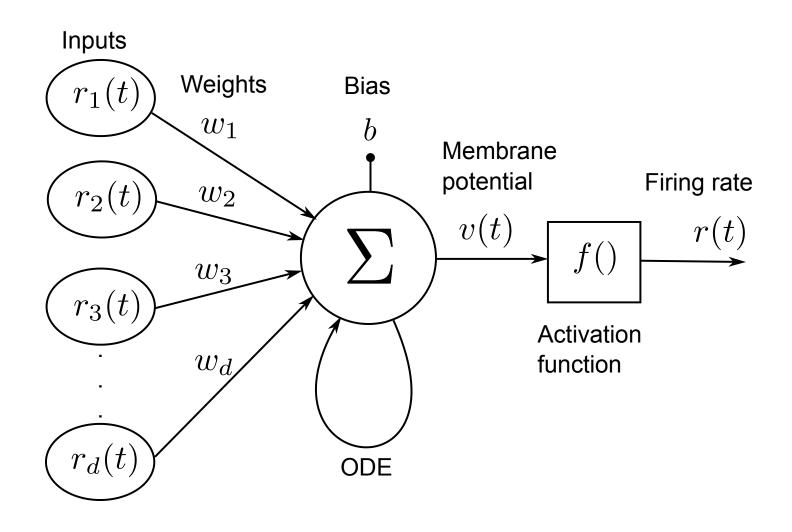
Populations of spiking neurons



- 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.

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.

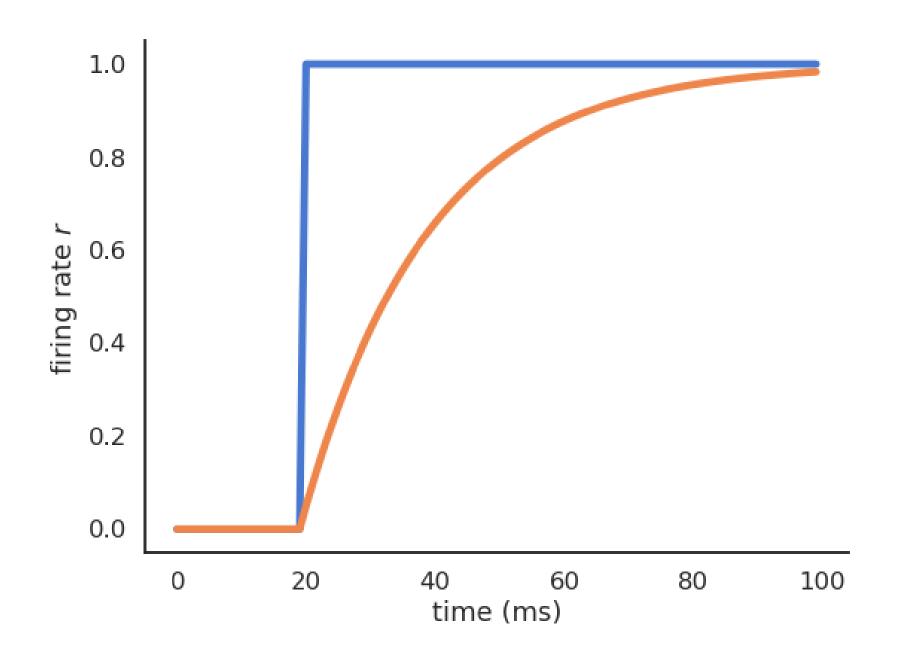


Rate-coded neuron

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

• 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:

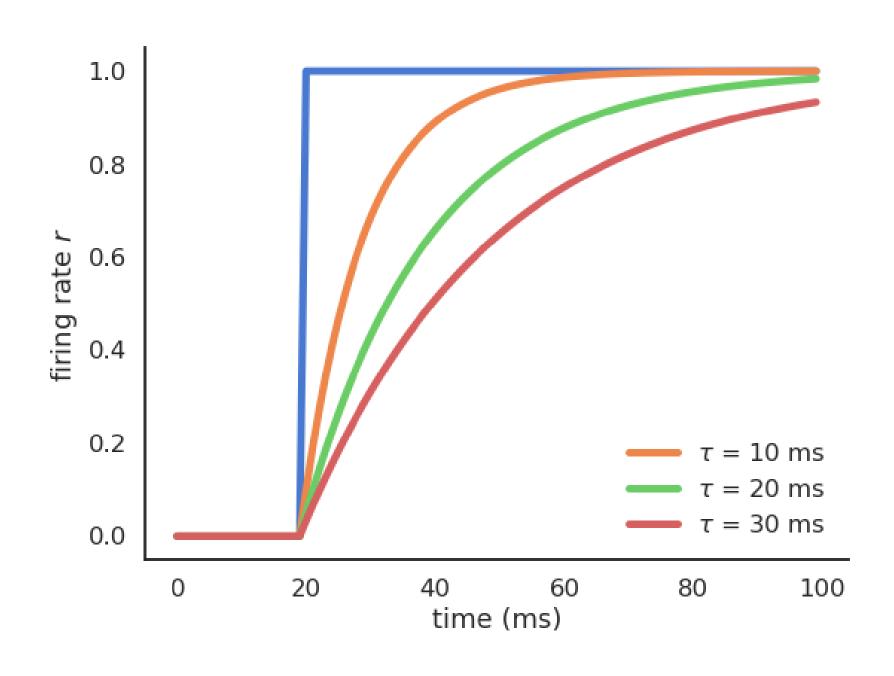
$$\tau \frac{dv(t)}{dt} + v(t) = I(t)$$
$$r(t) = (v(t))^{+}$$

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

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

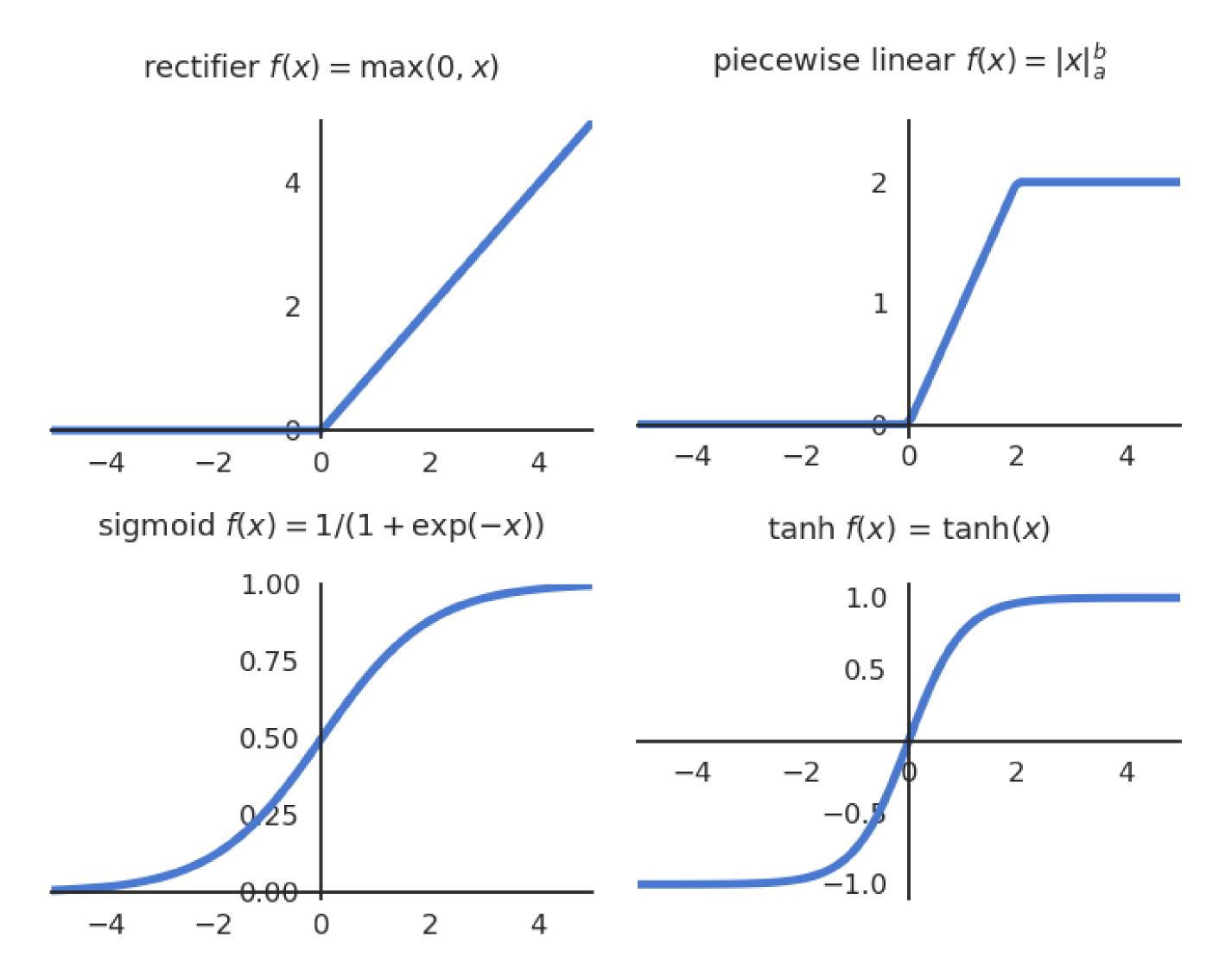
- When v(t) is quite different from I(t), the membrane potential "accelerates" to reduce the difference.
- When v(t) is similar to I(t), the membrane potential stays constant.

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

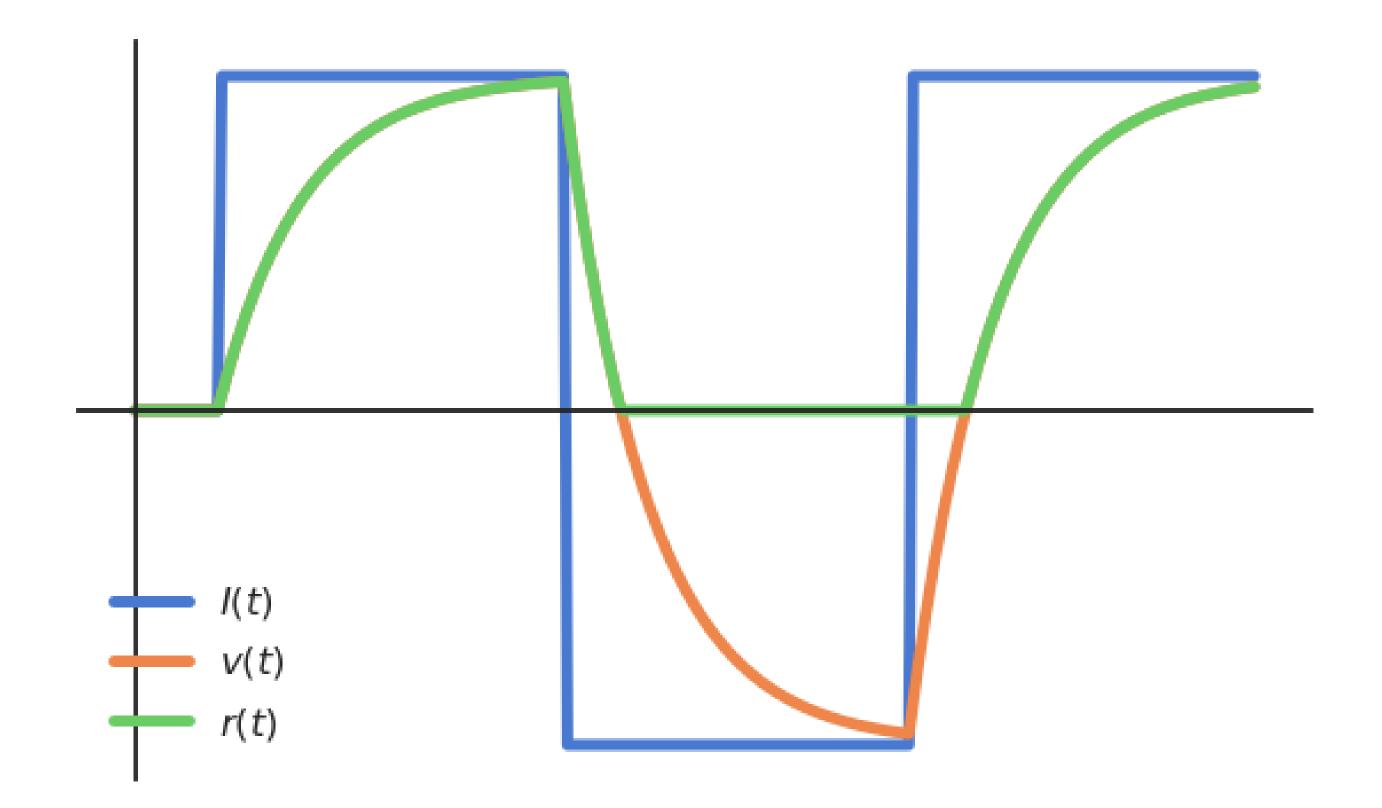


Rectifier activation function

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.

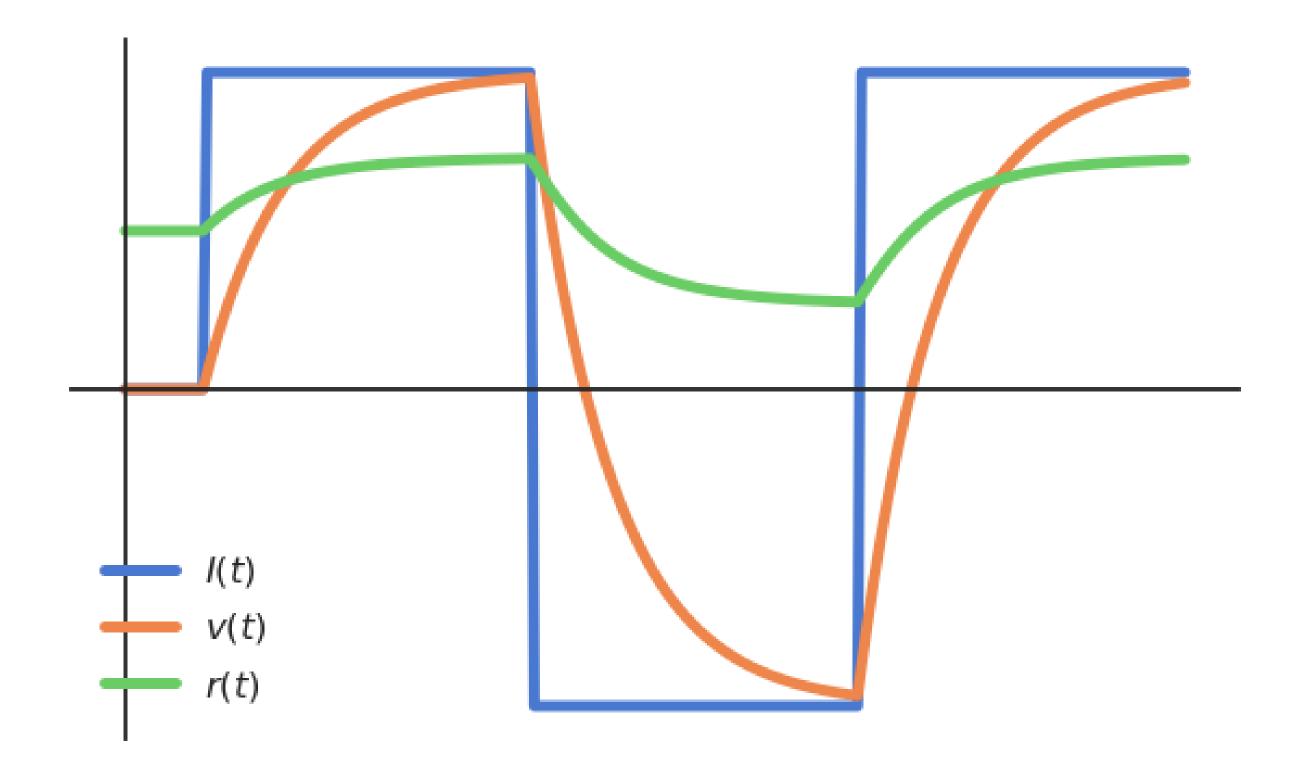


Logistic activation function

• 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.

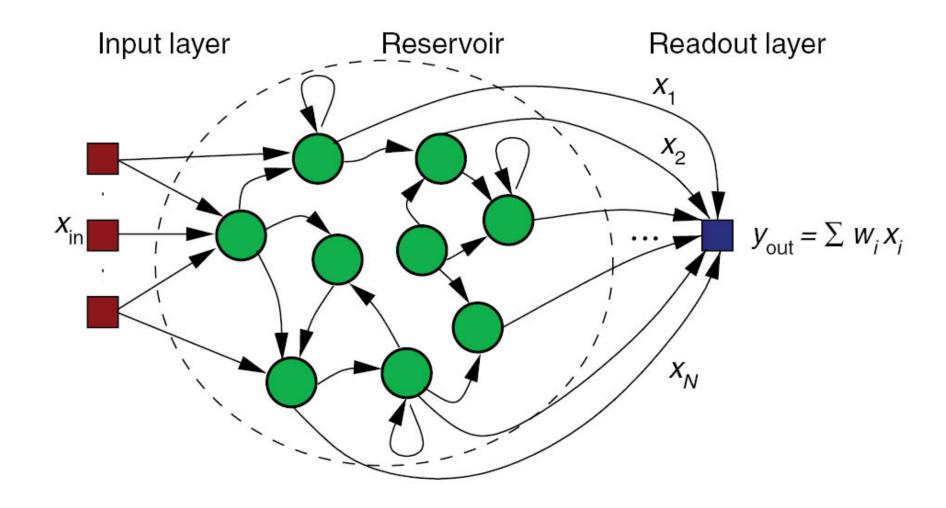


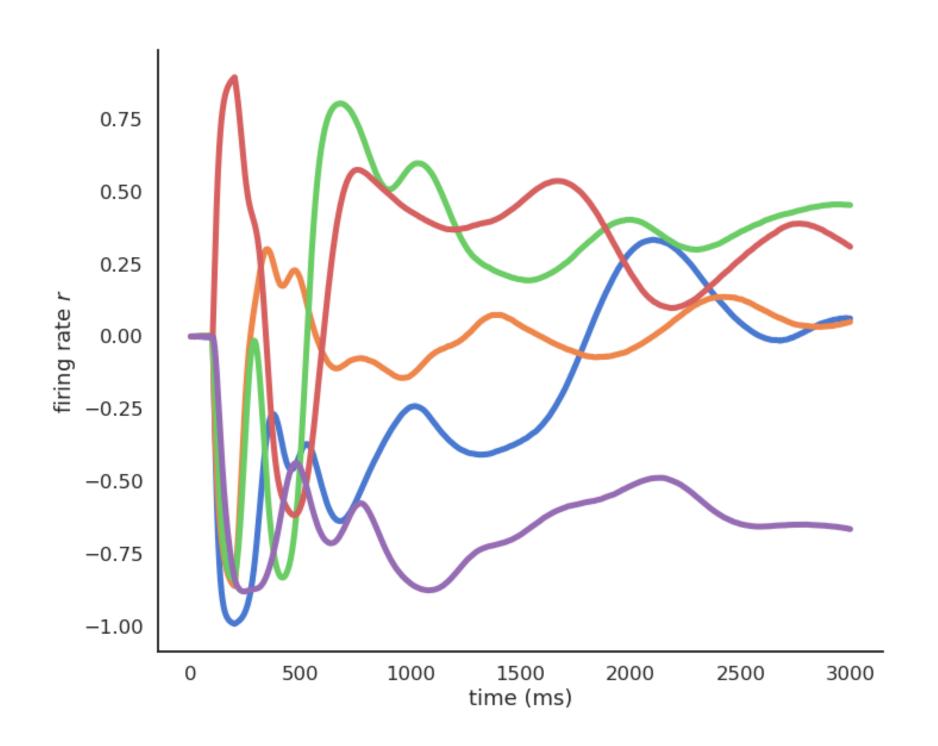
Networks of rate-coded neurons

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

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

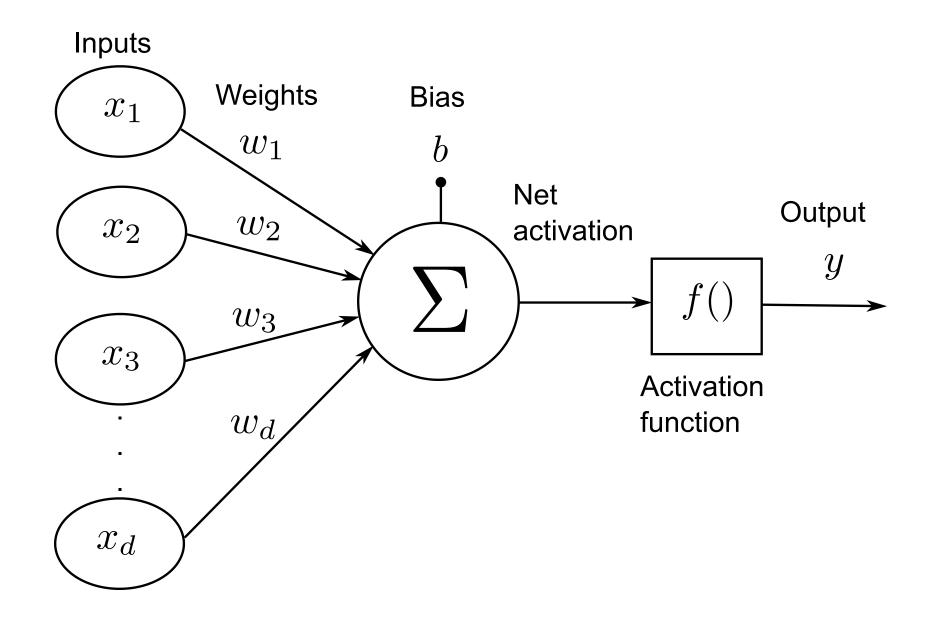
$$r(t) = \tanh(v(t))$$





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

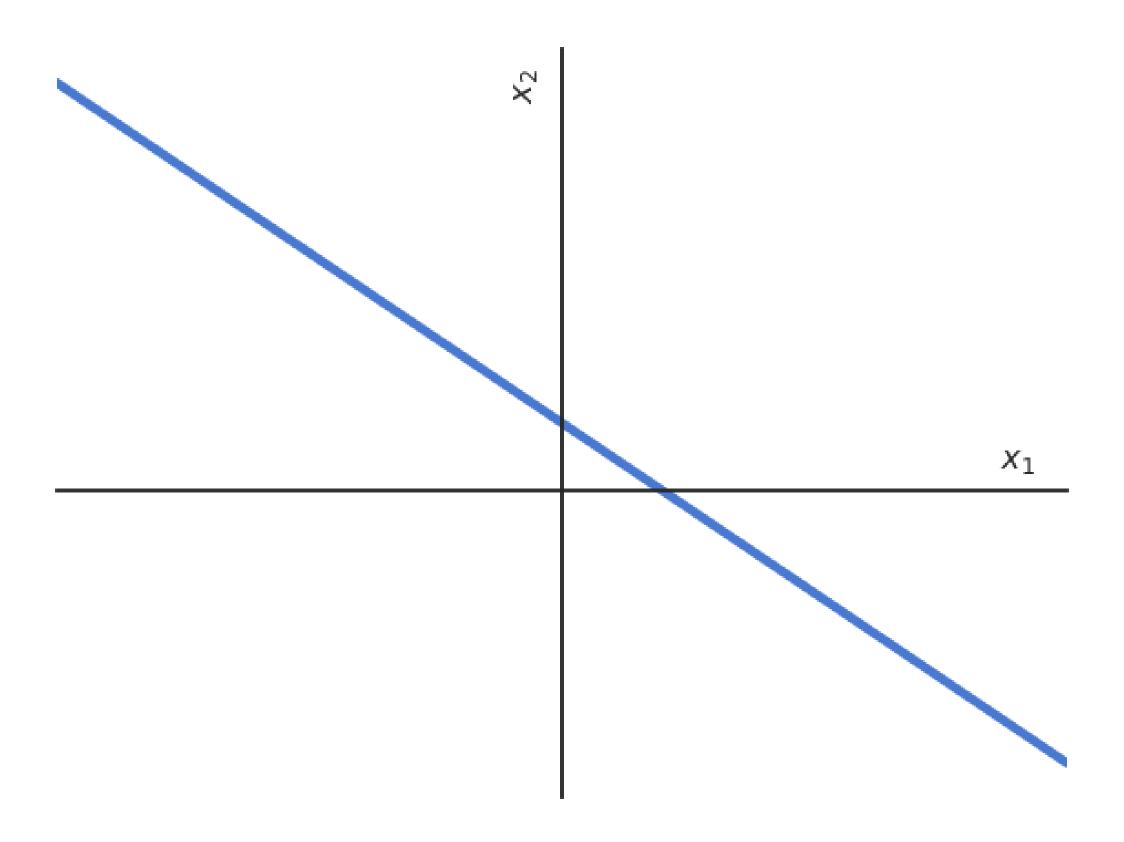
$$y = f(\sum_{i=1}^{d} w_i x_i + b)$$

- An artificial neuron sums its inputs x_1, \ldots, x_d by multiplying them with weights w_1, \ldots, 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.

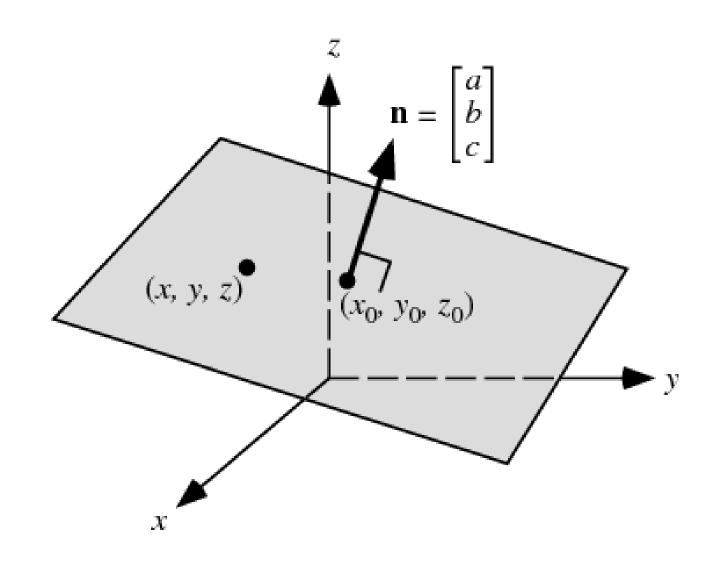
Artificial neurons and hyperplanes

- 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 $(x_1, x_2, ..., x_d)$.
- An hyperplane has one dimension less than the space.

 We can write the net activation using a weight vector w and a bias b:

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

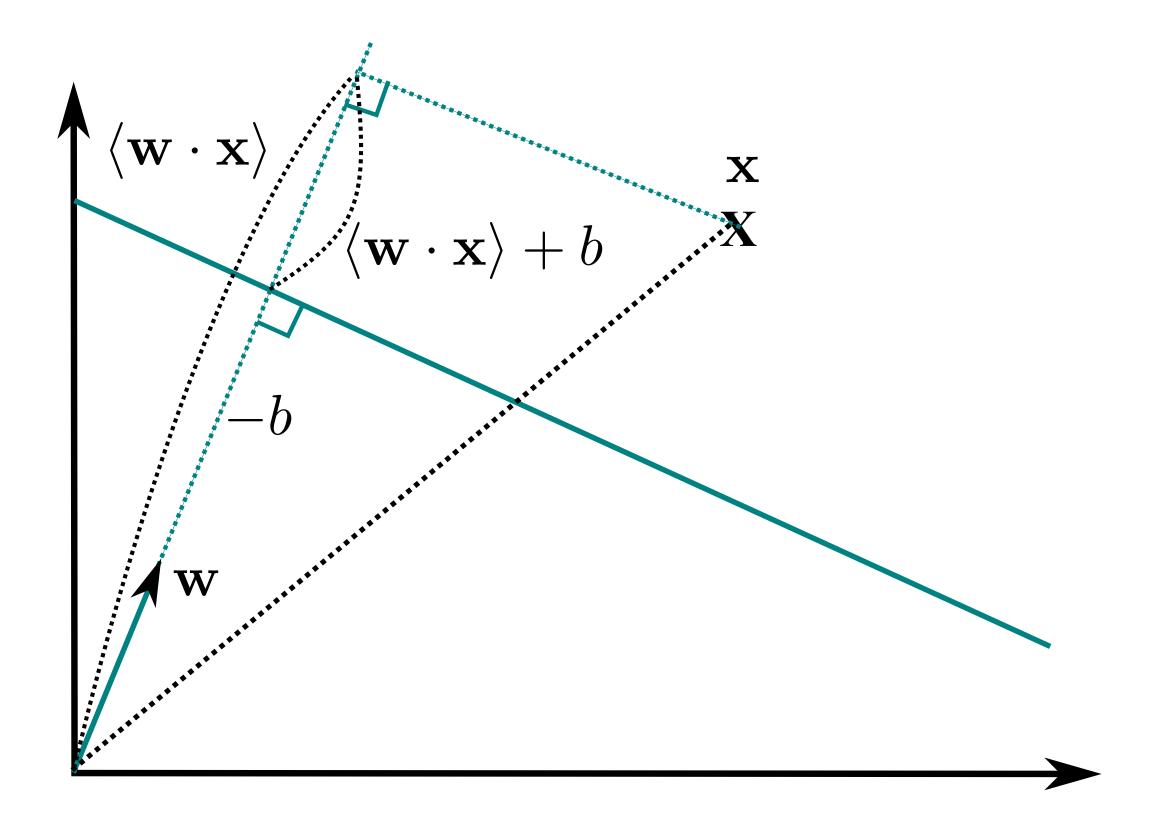
with:

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

- $\langle \cdot \rangle$ 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.

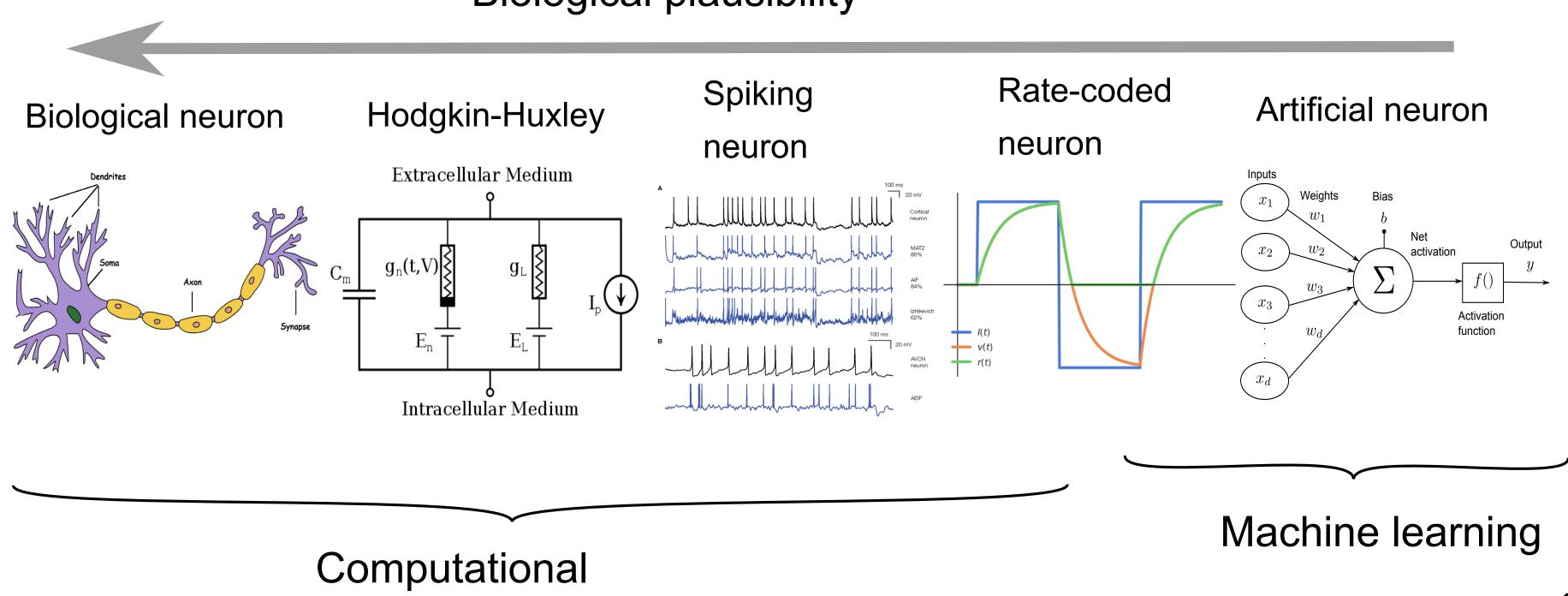
Artificial neurons and hyperplanes

- 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



neuroscience

Neurocomputing

